Marey, Etienne-Jules. - The movements of the wing of insects

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THE paper published in the last Annual Report, containing extracts from "*Lectures on the Phenomena of Flight in the Animal Kingdom*," by M. Marey, of the College of France, was translated and contributed to the Society by Mr. T. J. Bennett.

A more detailed translation has been called for, in compliance with which we must almost absorb, if not exceed, the space allotted to the Annual Report for 1872 :—

THE MOVEMENTS OF THE WING OF INSECTS.

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We have begun to study the motions of the wings, and the first question which presents itself is the frequency of these motions. On this point direct observation is of little assistance ; the acoustic method, which consists in determining the frequency of the strokes of the wing by the pitch of the buzzing of the insect is more efficient, but we have seen that even the principle of this method has been contested, and that its application presents difficulties. The graphic method remains to be considered. This method consists in making the wings themselves record the strokes which they execute. When an insect is held in captivity by force which it cannot overcome, after trial it ceases a useless resistance ; it resigns itself and abstains from all efforts to escape, its wings remain immovable, and in this way the observer who hopes to study their motions finds himself disappointed. But there are different methods of awakening the insect to its original activity ; it is sometimes sufficient to pinch the antennæ lightly ; this irritation of a very sensitive organ succeeds with the *Macroglossa*. Among the wasps the end may be attained by titillating the feet, or by holding them all together with a pair of forceps, and then releasing them suddenly, except one, by which the animal is held. The captive supposes that it is at liberty, and makes an effort at flight, which lasts about thirty seconds, or long enough to be observed. There is, however, another difficulty. The captive insect, when willing, cannot fly like an insect at liberty, because the external conditions are not the same. It experiences a greater resistance in proportion to the traction which it exerts upon the bond which holds it ; to a free insect the relation is such as a boat held by an obstruction bears to one sailing freely, or as a horse which drags a load to one relieved from harness. This resistance modifies its behaviour considerably, and obliges us to distinguish between the two different conditions of free flight and flight in captivity. It is indispensable to establish these distinctions, in order to appreciate at their true value the results to which we are conducted by the graphic as well as the other methods which we may employ.

The apparatus on which the wings record their motions is the ordinary registering apparatus, consisting of a metal cylinder, covered with smoked paper, to which a uniform rate of motion is imparted by clockwork. Let us suppose that, instead of the motions of the wings, we would simply register the oscillations of a vibrating-rod. For this purpose the extremity of the rod is furnished with a little style, which touches the blackened paper with its point, and, as the different parts of the movable cylinder pass successively before the point, the soot is detached from the places which it touches, and a trace produced. If the rod is not in vibration, it makes a long white rectilinear trace without sinuosities, a straight line which, rolled upon the cylinder, constitutes a circumference. If it is in vibratory motion, its trajectory will be a curved line, of which the sinuosities indicate all the circumstances of the motion, its phases of elevation, its depressions—in a word, all its movements—and consequently all the oscillations which the vibrating rod executes in space will be faithfully reproduced on the paper. If we would ascertain the frequency of the oscillations, it is sufficient to know the rate at which the cylinder revolves. Ordinarily a tuning-fork is employed, of which the number of vibrations is previously known, as, for example, one hundred vibrations per second. This is made to write its vibrations upon the registering cylinder below the line traced by the vibrating rod, of which the number of vibrations are desired. The comparison of the two tracings shows at once the number of the motions of the tuning-fork back and forth, that is to say how many hundredths of a second correspond to one oscillation of the rod; the number of motions of the vibrating body during a given time is thus known with great exactness.

It is not, however, as easy to obtain the tracing from the wing of an insect as from a vibrating rod, and this for several reasons. In the first place, it is very difficult to fix at the extremity of the wing a writing style; however light it may be, the rapidity of the motion to which it is submitted is sufficient in most cases to throw it off. If, however, after many trials and much precaution we are able to retain it in its place, a permanent cause of perturbation still exists from its very presence. Under the influence of this incumbrance the extent and frequency of the strokes of the wing are evidently diminished. It is easy to convince ourselves of this, by taking a *Macroglossa* and fixing it in the manner which we have previously described, that is, immovably between two strips of cork, by means of a pin. Looking down upon it, we perceive the extreme limits traversed by the wing above and below, which we have called the *dead-points.* If some substance is applied to the surface of the wing, we see by the effect of this burden, in diminishing the play of the organ, the two limits of oscillation approach one another, and the extreme upper position, which just now was almost vertical, inclines towards the horizontal. We may finally remark that it is only at the cost of considerable chafing against the surface of the moving cylinder that we can obtain a complete tracing of the movement of the wing. The wing cannot touch the cylinder, except during a very short instant of its stroke; that is, the instant when the wing reaches precisely the distance from the body of the animal to the cylindrical surface. The spherical figure which the margin of the wing describes in space, cannot have more than one point in common with the blackened cylinder. We can therefore only obtain, as the whole impression, a series of points at more or less regular intervals; and, if a more prolonged contact is desired, it can only be by curving the wing and folding it upon itself, and consequently the natural curve which the organisation of the insect obliges it to traverse will be falsified and altered. In any case the friction against the blackened surface will retard the motion, and although the retardation which it causes may be neglected when it is opposed to bodies of large size, such as a tuning-fork or a vibrating-rod, it cannot be when the vibrating object is the delicate membrane which constitutes the wing of an insect. Again, the friction, although exceedingly small, is found fully comparable with the forces which come in play in the motion of the wing, and its intervention notably alters the action of the latter. Experiment has confirmed these views. In one case an insect executing the motions of flight, and rubbing its wings somewhat roughly against the paper, furnished 240 movements per second; by diminishing more and more the contact of the wing with the cylinder, there have been obtained 282, 305, and 321. If, therefore, we would have a faithful representation, it is necessary to renounce the idea of obtaining those beautiful, regular, and continuous lines which are produced by the tuning-fork or vibrating-rod, and content ourselves with interrupted lines, half-strokes, represented by fragments, or even only isolated dots, the periodical return in these incomplete markings of definite forms permits us to infer the repetition of similar oscillations, and hence to determine their frequency. The operation is as follows: with a delicate pair of forceps we hold the insect by the lower portion of its abdomen, in such a position that one of its wings at each movement shall lightly touch the blackened paper. Each of these touches takes off a portion of the soot which covers the paper, and, as the cylinder turns, new points incessantly present themselves to the contact of the wing. A figure is thus obtained formed of a series of points or short strokes of perfect regularity if the insect has been maintained in a fixed position.

We have obtained a large number of these tracings in which the wing has only touched the surface of the registering cylinder, and has left only a point as a mark in each of its vibrations. I exhibit a number of these, and trust as soon as the return of Spring permits us to procure insects to show you the experiments by which these tracings have been produced. Those which you are now examining have enabled me to determine the frequency of the strokes of the wings of the following insects:—

	Strokes per Second.
Common fly	330
Humble-bee	240
Honey-bee	190
Wasp	110
Sphinx moth (*Macroglossa*)	72
Dragon fly (*Libellula*)	28
Cabbage butterfly	9

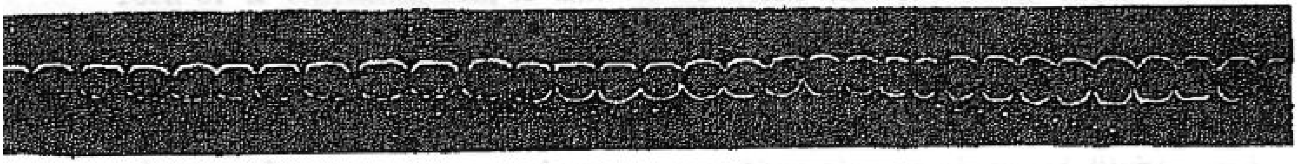
Certain authors have estimated this number of vibrations by the acoustic method, but there is a notable discrepancy between the above figures and those which they have deduced from the pitch of the sound that these insects produce in flying. In the case of the common fly,

T. Lacordaire has computed the number of the vibrations of its wings at 600 per second, that is to say, twice as many as our figures exhibit. Has there not been a misunderstanding here, as is frequently the case, in the use of the word "vibration?" Some persons wrongly consider the raising and depressing of the wing as two vibrations, and reserve the term of "simple vibrations" for one or the other of these isolated motions. On the contrary, if we follow the usage most generally adopted, the two motions together, by which the body is again in its original position, should be considered as a single vibration.

The previous observations which we have made on free flight, and on flight under restraint, somewhat curtail the range which we are tempted to accord to these numbers. The animal, according as it desires to move with a greater or less rapidity, can change, at will, not only the extent of its wing-strokes, but also, to a certain extent, their frequency. Fatigue may exercise an analagous influence to that of the will; after very rapid motions, the exhausted animal diminishes the number of its strokes, which sometimes falls to a fourth or a fifth of its normal value. It continues to relax them more and more until a period of repose and reparation permits it to resume its usual flight; nevertheless, the examination of these numbers suggests some general considerations. We have reason to think that each of the muscular contractions which determine the drawing down of the wind is the result of a single impulse (*Zuckung* of the Germans), although in man contraction is due to successive impulses, which are merged in one another when they are produced more frequently than 30 times in a second. Among insects the limit of fusion of impulses is infinitely more remote, and ends with leaving the wing immovable, in a sort of permanent tetanic contraction. It is easy to assure ourselves of this by means of living insects, or better, by means of the artificial insect which I have constructed. When the impulses become too rapid, their extent diminishes; at this moment they no longer serve for the propulsion of the animal, whose wings appear quite immovable or merely agitated by a light tremor. Nevertheless, the number of muscular waves which the fibres of insects will admit without intermingling, a number which in the fly amounts to 300 per second, forms a physiological fact very interesting to note. Among other animals the limit is not so remote; among birds fusion is produced after 75 impulses; among mammals after 30, and among reptilia after only 4. These differences correspond, in virtue of the relations which I have long since explained to you, to analagous differences in the rapidity with which the elementary impulse traverses the muscular fibre of these different animals. The muscular fibre of the insect will then be characterised, physiologically, by the property which it possesses of furnishing a considerable number of distinct impulses, as well as it is anatomically characterized by its relative size and its striation.

The graphic process which enables us to judge of the frequency of the strokes, also permits us to show the perfect synchronism of the play of the wings. For this purpose it is necessary to choose an insect of which the amplitude of the wing-vibrations is large, so that in their moment of greatest elevation they may nearly meet above the dorsal region of the animal. If the insect is placed near enough to the registering cylinder, the dorsal region turned toward the blackened surface, it is clear that at the moment when the wings approach each other they will leave their traces on the paper, thus describing a series of loops and curves, of which the perfect correspondence proves the synchronism of the motions from which they originate.

Fig. 3.



Simultaneous tracings of the wings of a wasp in short flight. The perfect synchronism of the two wings will be observed.

Furthermore, we can convince ourselves that a sort of necessary connection exists between the motions of the two wings. If we throw an insect violently upon the ground, so that it is stunned and can no longer execute voluntary motions, we observe that, by producing motions in one of the wings, the other follows, to a certain extent, the injuries inflicted on its fellow. If one of the wings of an insect is depressed, the other also bends down; if one be raised, the other elevates itself. Certain species, especially the wasp, lend themselves very readily to this experiment. According to Chabrier, the author of an extensive work on the mechanism of the flight of insects, synchronism cannot fail to exist. This author considers the depression of the wing as the only effective portion of the stroke; its elevation is a passive phenomenon due to the action of physical forces. In fact, after the depression each dorsal arc of the thorax is deflected like a bent bow, and when the muscular contraction ceases the bow springs back in virtue of its elasticity, and the wing is raised. Now, if the pressure did not act simultaneously on the two extremities of the bow, it could not be flexed as it is, and the mechanism, which we suppose, would be impossible. The reality of this synchronism is, then, a strong proof in favour of this manner of understanding the motion of the wing.

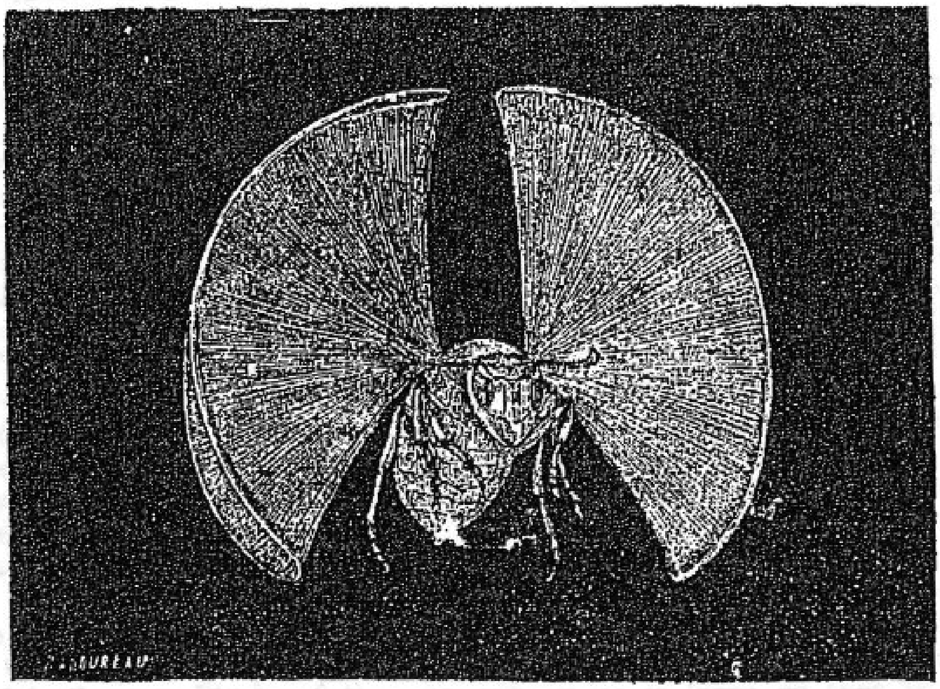
After having determined, in a general manner, the frequency of the vibrations of the wing, we seek to know the variation produced in the number of these vibrations by agents capable of influencing the activity of the animal. In the first rank of such agents must be placed heat and cold. We know that warm dry weather is essential to insects, especially coleoptera, to enable them to fly well; special observation has confirmed this fact. We are able to state that, within certain limits, the frequency of the strokes is augmented with an increase of the temperature, and that they become slower under a gradual increase of cold.

Form of the Motions of the Wings.

After having studied the frequency of the vibrations of the wings, it is necessary to study their form. For the end which we desire to obtain—that is, to arrive at a theory of the flight of insects—the most important element to comprehend is that which we now proceed to investigate, namely, the form of the trajectory which the wing describes in space, instead of the rapidity with which this trajectory is described. In order to arrive at this determination we shall have recourse to two processes, which will reciprocally correct each other—the optic method, and the ordinary graphic method.

Optic determination of the movements of the wing.—When a brilliant body moves with rapidity, it leaves upon the retina a kind of luminous train, which acquaints us with the trajectory through which the body has passed. Children sometimes amuse themselves in producing the most varied figures by brandishing in the air a stick having one end on fire. It is on this principle that the apparatus, known in physics under the name of *Wheatstone's calidrophone*, is founded. This is a rod, fastened upright on a heavy foot, to which complex vibrations may be given, and to the ends of which a brilliant metallic bead has been affixed. If the rod is put into vibration the brilliant bead describes in space luminous figures, which vary with the different combinations of the vibratory motions. If a brilliant spangle can be attached to the extremity of the wing of an insect, this spangle, traversing without cessation the same points in space, leaves a continuous luminous figure exempt from the imperfection which is caused by friction in the case of the graphic cylinder. The extremity of an insect's wing can thus be rendered brilliant without mutilating it in any way; it is sufficient to place upon it a drop of varnish, to which a small piece of gold-leaf is applied. The varnish dries so rapidly that the insect cannot throw off this little reflector of light, and nothing more is necessary than to hold the animal in a fixed position to observe the play of light upon the small brilliant surface. Under these conditions the bee and the wasp furnish a well-marked "figure of eight."

Fig. 4.



Aspect of a wasp, the extremity of whose primary wings has been gilded. The animal is supposed to be placed in a ray of light.

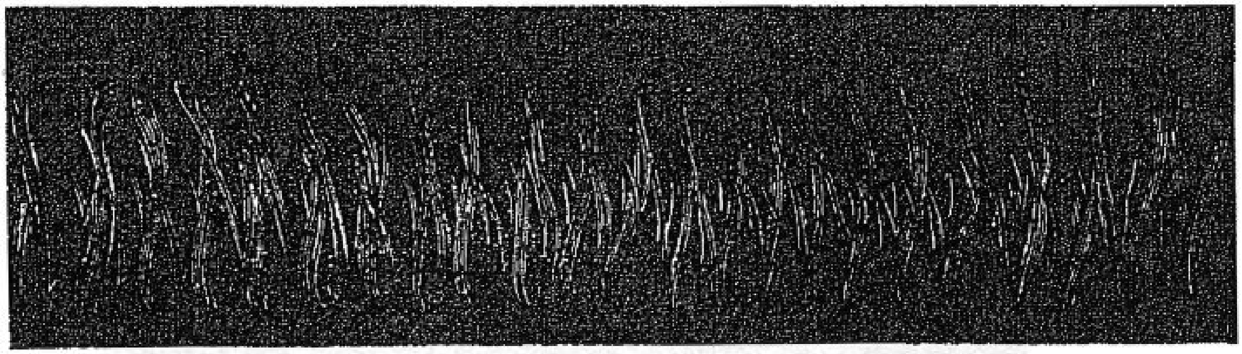
The figures of eight are more or less widened or compressed, according to circumstances. Sometimes the point of the wing seems to move almost in one plane. In the dragon-fly *(Libellula)* a figure of eight is also observed, but much more elongated; the loops are narrow and laterally compressed. With the *Macroglossa galium* it sometimes seems as if the preceding form had disappeared, and is replaced by a sort of ellipse. However, in examining it closely, it is soon perceived that this ellipse is surmounted by a little loop, very slightly developed relatively to the curve which supports it. It seems that one of the loops is enlarged at the expense of the other, but this last has not entirely disappeared, and the vestige what remains testifies to the persistence of the figure of eight which is encountered in most other cases, and which may serve as the general type.

Changes of the plane of the wing.—The luminous figure which the gilded wing of an insect gives in its motions also shows that, during the alternate motions of flight, the plane of the wing changes its position in relation to the axis of the body of the insect. During the period of elevation the upper face of the wing is directed backward, while it turns a little forward during its descent. In fact, if we gild a large extent of the upper face of the wing of a wasp, taking care that the gilding shall be limited to this face, it is seen that the insect, placed in a ray of light, gives the figure of eight with a very unequal intensity on the two sides of the image, as is seen in the preceding figure. It is evident that the cause of this phenomenon is found in a change of the plane of the wing, a change in consequence of which the angle of incidence of the solar rays, while favourable during the ascent of the wing, is unfavourable during the descent. If the animal is turned so that the luminous figure is observed inversely, the figure of eight presents, in an inverse position, the striking inequality of its two halves, catching the light in a portion which was just before without it, and losing it where it had previously shone. We further find, in the employment of the graphic method, new proofs of the changes of plane in the wings of insects during flight. This change of plane is of great importance, for in this rests, as we shall see, the immediate cause of the propulsion of the body of the animal by the application of the motive force.

Method of contact.—Does the extremity of the wing really describe this double loop which we perceive, or is this form the result of an optical illusion—a play of flight? Though such an objection is hardly probable, it is necessary to refute it. To assure myself more entirely of the reality of the displacement of the wing than the optic method rendered perceptible, I have introduced, while the wing was in motion, the extremity of a little bodkin into the interior of the loops of the figure of eight, and I have established that in the interior of these curves free spaces really exist of a funnel shape, in which the bodkin penetrated without encountering the wing, while if I attempted to touch the intersection where the lines cross, the wing immediately struck against the bodkin, and flight was interrupted. Still greater precision can be brought to bear on the appreciation of these motions, and, knowing that the wing describes a double loop, it may also be known in what manner it transverses the branches. It is sufficient to bring near to the wing in motion a leaf of paper blackened on both sides; the wing, in pursuing its course, strikes against one of the sides of the paper, and the trace which it leaves testifies to the manner in which the motion is accomplished.

Graphic method.—This method is not applicable to our problem without important modifications. We have just seen that it is difficult to obtain tracings of any extent, because the wing cannot remain long in contact with the blackened cylinder, which it leaves and approaches successively. Under these special conditions it is necessary to have recourse to an artifice, and since it is impossible to obtain a satisfactory trace at a single stroke, we should try to divide the difficulty and separate the operation into several periods. The preceding experiments simplify the interpretation of the tracings very much, and we can reconstruct the figures which the optic method has indicated from the slender elements which they afford. I have considered in the complete course of the wing of an insect, such as is represented in Fig. 4, three distinct zones, of which I have obtained the tracings separately; an inferior zone, corresponding to the lower portion of the figure of eight; a median zone; and a superior zone corresponding to the middle and upper parts of this figure. Bringing together the tracings obtained in these three zones, I have been able to reconstruct the entire curve. In registering the tracings of the median zone, figures much resembling each other are obtained, presenting the two crossed lines shown in Fig. 5.

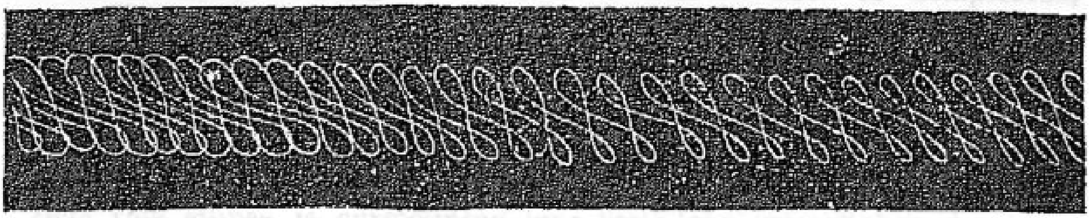
Fig. 5.



Trace of the median course of the wing of the *Macroglossa galium* (Bedstraw sphynx moth).

The multiple tracings of the figure are formed by the fringed extremity of the wing, which presents many small points. The upper portion is in the form of a loop, as well as the part which corresponds to the lower course of the wing, and these three parts successively obtained give, when united together, the complete representation of a figure of eight, such as is obtained in acoustics in registering by Kœnig's method the vibrations of a Wheatstone's octave rod; that is, a rod which vibrates twice transversely for each longitudinal vibration. The slower motion of the cylinder produces the condensation of the end of the tracing.

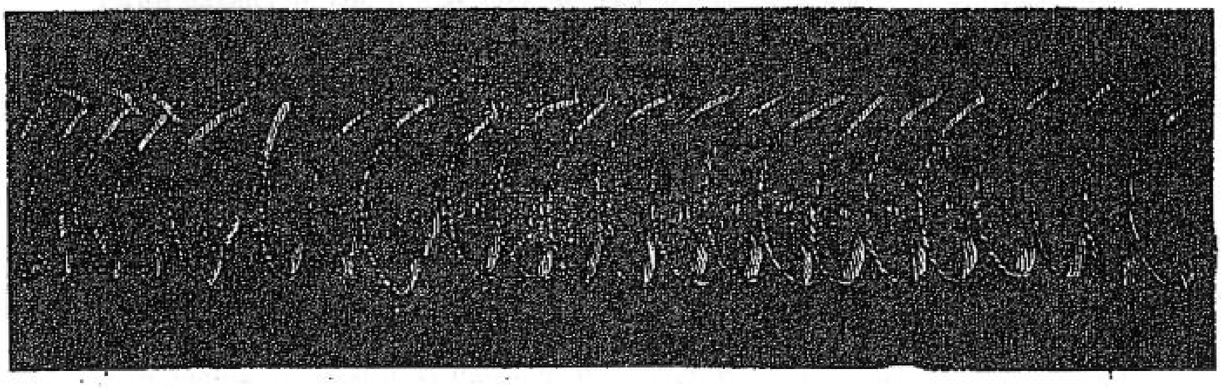
Fig. 6.



Trace of a Wheatstone's octave rod.

The experiments can also be varied by obtaining, not the tracing of the point of the wing, but that of the anterior border of this membrane striking laterally against the cylinder. It is clear that in describing the upper loop, this edge will approach the cylinder, then deviating, in a similar manner it will describe the lower loop, so that in its complete course it will rub twice against the blackened surface, and leave two white traces separated by an interval. This is observed in Fig. 7.

Fig. 7.



This figure shows from the tracing of the wing of a wasp the upper loop and the whole extent of one of the branches of the figure of eight. The median portion of this branch is only dotted on account of the feeble friction of the wing. We may, therefore, be permitted to conclude that if the trace of an insect's wing could be obtained entire at one operation, the same figure would be presented which we have seen described in space by the gilded spot on the wing of the wasp, namely, a figure of eight, which our ingenious acoustician, Kœnig, was the first to obtain with a spiral Wheatstone's rod, making two horizontal to one vertical oscillation.

It now appears to me sufficiently established that in the more extended motions of flight the wings of insects describe a figure of eight in space. Furthermore, that the luminous figure which a speck of gold on a wing presents in its motions, has shown us that the periods of ascent and descent of the wing are accompanied by a change of plane in that organ. It is this fact which will shortly enable us to explain the mechanism of flight in insects.

C

Mechanism of the Flight of Insects—How they Propel Themselves.

The preceding lessons have been devoted to the study of the frequency and the form of the strokes of the wings of insects. You have seen that the frequency varied in different species, and in passing from the butterfly, for example, to the house fly, or the gnat, the variations may be considerable. The flight of the butterfly is slow, the strokes of its wings succeed each other at considerable intervals, propelling it by bounds and jerks, and producing an irregular and capricious flight. The gnat darts with rapidity straight at its object, emitting along its path a clear, sharp, strident sound. Between these two extremes we find all intermediate stages. Furthermore, the same insect, under different conditions, varies the rapidity of its motions within extensive limits; when free from all restraint its movements are rapid and precipitous, but when captured they are immediately relaxed, and although the frequency of the movements of the wing varies, the form of the motion does not change. It is in all cases the same, always a double loop, a figure of eight. Whether this figure be more or less apparent, whether its branches be more or less equal, matters little; it exists, and an attentive examination does not fail to reveal it.

Before drawing from this fact the conclusions which it warrants; before extracting from it the solution of the problem with which we are occupied—that is to say, the mechanism of flight—let us rapidly review the history of the question, and see how far previous authors have advanced in its solution. Without going further back, we find in the work of Borelli a chapter devoted to this subject, in which he considers the force which the bird or insect must employ to sustain or move itself in space. He estimates that this force is enormous; that it is, in the case of the bird, more than ten thousand times greater than the weight of its body. We still find this exaggeration in recent works. The academician, Navier, falls into an analogous error, and after him M. Babinet accords, in his turn, a power to the inhabitants of the air far superior to that with which they are gifted by nature. However, by the side of these errors we find a great number of correct ideas, since confirmed by observation. Borelli knew that the principal motion of the wings was an elevation and depression, executed in a vertical plane, and he asked himself how it was possible that this motion, which, it seemed to him, could only serve to elevate the animal or to depress it, should nevertheless contribute to onward motion. For this, it was necessary that the vertical force should be changed into a horizontal force. Examples of this transformation are frequent. If a wind blowing horizontally strikes against a flat board inclined forward at an angle of, say, forty-five degrees with the horizon, the action of the wind will tend to throw it backward and upward; or, if the board is moving forward with a momentum, it will tend to elevate it. We have here an illustration of a well-known principle of mechanics—the resolution of a single force by an inclined plane into two forces—which gives in part an explanation of the flight of insects and of water birds. But insects have four wings instead of two. Is the office of these four organs the same; and if not, in what do they differ? Borelli does not treat of this question. It is discussed, however, in a particular case, by an anonymous author, who has left us an interesting manuscript on the habits of bees. This work, intended to complete and to correct the work of Réaumur, came from the Condamine Library, and belongs to M. Harnet. The author has observed bees at the moment when they hum at the mouth of the hive, trying to enter it and deposit their treasure. In examining the play of light on their trembling wings, he thinks that he saw the upper pair alone alternately raised and depressed, while the lower pair were animated only with a feeble horizontal motion. Here the question seems to have been abandoned, although the interest with which it is now regarded is far from inconsiderable. Beside the interest which it offers from the purely scientific point of view, in the mechanism of a function as widely employed as aërial locomotion, still another interest is attached to this study. The insect and the bird realize one of the oldest and most unsuccessful aspirations of the ambition of man. All space belongs to them; they go and come in the aërial ocean, while he is chained by his weight to the earth. Man has sought by various methods to escape from this confinement. The knowledge of the processes by which Nature attains the end to which he aspires, would perhaps have spared him many fruitless attempts and loss of much time and great waste of invention. In 1823 a work appeared in which this question of aërial locomotion is treated *ex professo*, and no longer in an incidental manner. The author, the Chevalier de Chabrier, studied the conditions of mobility of the wing, and arrived at the solution of an important question: how muscular action is transmitted to this movable organ. Is it directly, or by some intervention? The muscle, responds Chabrier, is not directly attached to the wing; it acts upon the arch of the back. When it contracts, the curvature of this arch is augmented; when it relaxes, the back returns to its original curve, like an unbent bow. In the motion of the wing, therefore, there is only one active period, the moment of depression; the period of elevation is passive. Elasticity, therefore, plays an important part in this function. Here, as in all mechanical organs, it absorbs and then gives out power; it regulates speed and produces continuity of motion.

But Chabrier was soon carried away by an exaggeration similar to that of Borelli and of Navier, though in a contrary direction. According to him, an insect needed an insignificant force for its propulsion in space. No effort was necessary to sustain it in the atmosphere; the animal floated there like an inflated balloon. In order to fly it filled its multitude of respiratory canals with air, and this, becoming heated, raised the animal as it elevates a hot-air balloon. It is not necessary to say that this conception of an *aërostatic insect* is an error. Without doubt an insect, before attempting a flight, lays in a quantity of air by a sudden respiration, but this provision of air contributes only an insignificant part toward the end which Chabrier assigned it.

The greater portion serves to prepare the organs of flight for the operation of their function. Jurine, of Geneva, in particular has shown that the nervures of the wing membranes are small tubes which only acquire the rigidity and extension necessary to flight by inflation with air. We must refer to another contemporary, Strauss Durckeim, to find the elements of the theory to which my observations have conducted me. In his book on the Theology of Nature, a vast chaos of ingenious ideas, in which some profound, among many puerile, thoughts are to be found, there are many facts essential to the solution of our problem. Strauss Durckeim has conceived the ideal type of the insect-wing, the diagrammatic wing; that is to say, has reduced the organ to its essential parts. It consists of a rigid nervation or frame-work in front, a flexible web behind; this is all the apparatus. An apparatus thus constituted possesses the essential requisites for flight; otherwise constituted it will not serve this purpose, as is the case with the false-wing of the *Phryganidæ*, which has its principal nervation behind. It is enough that such a structure should be made to rise and fall successively: the forward border being rigid and the other flexible, it naturally disposes itself in an inclined position, receiving the reaction of the air obliquely, and thus transforms a part of the vertical impulse into a horizontal force. The two parts of the wing above mentioned are both indispensable in the same degree their respective offices complement each other in producing a single result. Ingenious experiments, due to M. Girard, throw light upon these facts. Destroy the anterior nervation, without removing the thin membrane, and the insect cannot fly; destroy the flexibility of the membrane by covering it with gum, and flight also becomes impossible. Here we cannot urge the objection that the superincumbent matter interferes by its weight like a burden which weighs down the animal; for, following out the experiment, we see that as soon as the coating becomes dry, small fissures are produced, flexibility reappears, and with it the possibility of flight returns. These observations assist us in comprehending the part which the anterior portion of the wings of the *Phryganidæ* play; which constitute the analogue of the stiff nervure, while the hinder wings represent the flexible membrane. The two wings of an insect thus complement each other.

I shall not further prolong this retrospect. I have limited it to the essential ideas entertained by our predecessors, and to those which will serve us in the future. The preceding experiments, joined to those which you have seen performed under your own eyes, seem to me to establish the following facts, namely: the motions executed by an insect during flight are limited to an elevation and a depression of the wings. It is true that other motions take place in the wings of insects. They are seen to move backward, and in repose to extend parallel to the axis of the body. We also see insects moving their wings backward and forward in preparation for flight. But these motions are not directly connected with aërial locomotion. The dragon-fly *(Libellula)*, which propels itself so rapidly, exhibits none of these lateral movements; its wings move exclusively in a vertical plane as if they turned on a hinge. But we have seen, in the optic method, that the course of the wing in space can be followed by gilding its extremity, and placing it in a ray of sunlight. Now this arrangement furnishes us with a figure of eight, and we further know that during each complete vibration the wing changes its inclination twice. These movements are not controlled directly by the muscles. They are the mechanical effects of the resistance of the air acting alternately on the upper and lower surfaces of the wing in its alternate movements. When the wing leaves the upper limit of its position it inclines neither to one side nor to the other, its plane being parallel to the length of the animal. But when the impulse of the air is exercised, or as soon as the wing begins to be depressed, the rigid portion, the anterior nervation resists flexure while the flexible membrane which follows it gives way; drawn down by the nervation which lowers it, elevated by the air which uplifts it, this membrane takes an intermediate position; it inclines about 45 degrees, more or less, according to circumstances. The wing continues its downward motion thus inclined toward the horizon. Thus the reaction of the air, which combines its effect and acts perpendicularly upon the surface which it strikes, can be decomposed into two forces, a vertical and a horizontal force; one serving to elevate and the second to propel the animal. After this first period the wing membrane will have arrived at the end of its course; the direction of its motion is changed, its action is reversed. A moment of repose, infinitely short, separates these two phases during which the wing resumes its normal position parallel to the axis of the body. The nervure draws it up again, the air resists as before, and from this conflict results a position between the horizontal and the vertical—an inclination of 45 degrees. This second period contributes as did the first, to locomotion. How remarkable is the simplicity of apparatus by which the desired end is attained!

The horizontal force which is generated by the inclination of the plane of the wing is transmitted to the body of the animal and helps to push it forward. But as the body of the insect does not instantaneously take up the motion which is imparted to it, a part of this force is expended in curving the nervure of the wing which, at the same time that it is lowered, is pushed forward. Here is an artifical wing of large size constructed in accordance with the type which we have described; an anterior nervation represented by a stiff rod, with a membrane behind formed of paper pasted upon its edge. Try to strike down an object immediately before you, and you will not succeed. If you strike at an object before you with a downward blow the wing will be resisted by the air, and it will deviate greatly from the point at which you are aiming. From this deviating motion of the wing from the change of plane which it effects, the looped figure which it describes evidently results. It is the combination of these motions which generates the figure of eight previously described. We can now safely say that the two experimental facts are now interpreted by our theory.

A very slight difference has been observed between the two sides of the wing in certain insects; the lower surface is less polished than the upper; it is furnished with rugosities, hairs, or points, which according to Chabrier, give more hold on the air and reduce the loss of force by sliding. This disposition may contribute to insure the predominance of the useful effect of the lowering over the elevating motion. Furthermore, this predominance of the depressing action of the wing does not exist in all insects. These find that force as well in the period of elevation of the wing as in the period of its depression, turning almost horizontally the plane in which their wings move. The numerous varieties which the mechanism of flight presents among the species of insects which we have observed will be studied later; they do not conflict with the fundamental principles which I have just announced.

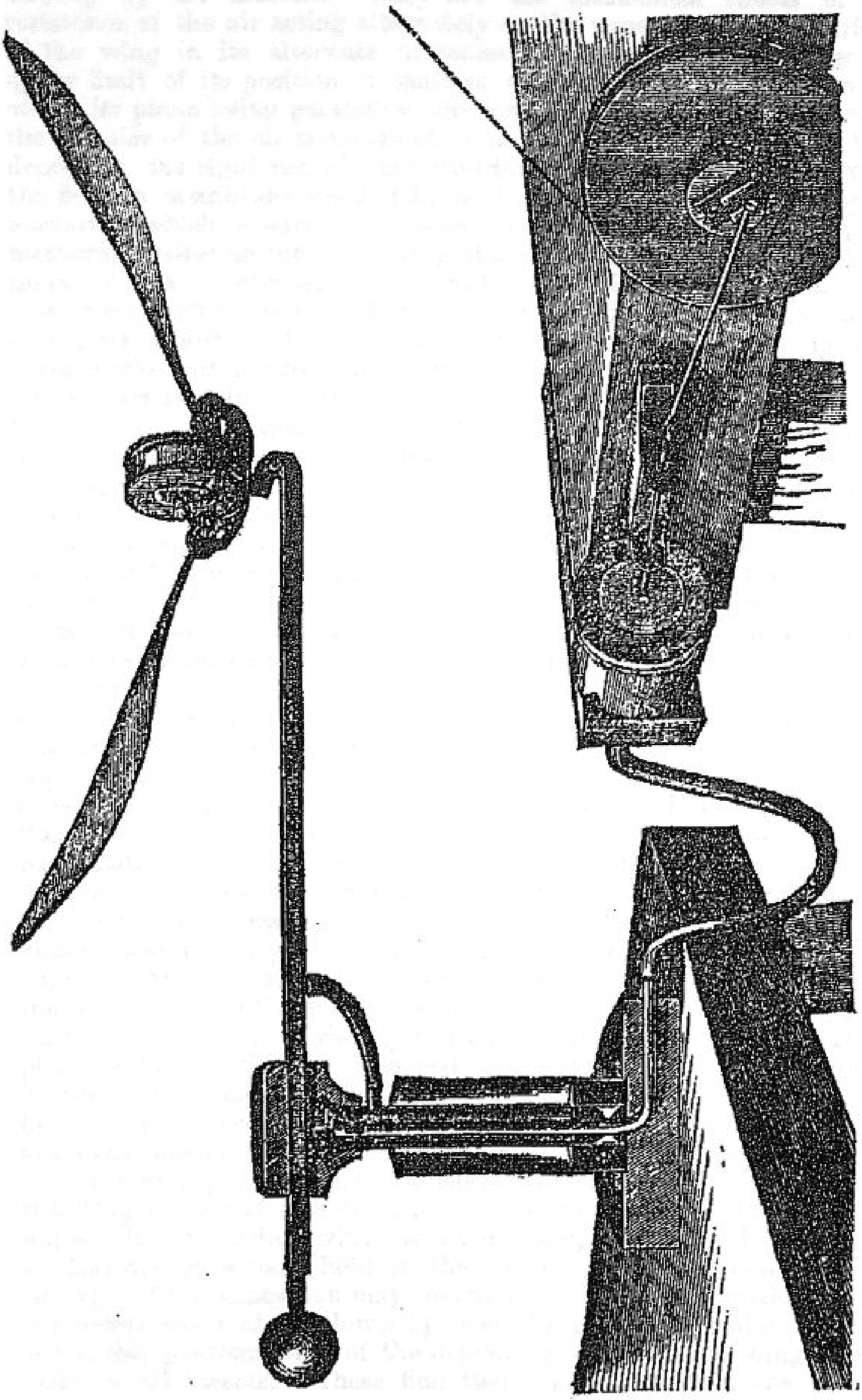
The mechanical conditions which we have just passed in review I have realized in a theoretical apparatus, from which I have obtained the same results as afforded by living insects. This artificial insect is represented by Fig. 8.

An air-pump, moved by a rotary apparatus, alternately compresses and relaxes the air in a tube which traverses the central pivot of the apparatus, where a sort of mercurial gasometer hermetically seals it while permitting the free rotation of the arms. The horizontal branch is hollow, and conducts the air into the apparatus, which is closed by a hollow metallic drum, of which the two circular faces are closed by two sheets of rubber. By the play of the air-pump these two sheets are inflated or contracted both together. They communicate the rapid motions of elevation or depression to the wings by two angular levers. The wings presenting, like those of an insect, conditions of unequal flexibility, decompose the resistance of the air, and impart to the apparatus a rapid rotary motion around the central pivot.

Imagine two artificial wings, as nearly alike as possible, both inserted on one of these little drums, which I have frequently described. They receive through this drum absolutely synchronous motions of elevation and depression. This apparatus is fixed at the extremity of an arm balanced by a counterpoise, and turning upon a pivot. This arm is hollow, furnishing a canal by which the effect of inflation can be transmitted to the movable drum of the wings. We may consider the drum as representing the body of the insect, and nothing prevents us from really giving it the shape of this animal. The rigid nervures, furnished with flexible membranes disposed to the right and left, will be the two wings, and the animal, instead of being free, will be fixed at the extremity of a movable rod; there is, therefore, only a single motion possible, which is that of turning around the pivot, carrying the attached rod with it. In effect, if I put the air-pump in motion, the artificial insect moves, flaps its wings, and really flies. At each stroke there is a change of plane of the alar membrane; at each stroke the point of the wing describes a figure of eight; and in a general way this theoretical animal, this artificial insect, reproduces all the particulars which the observation of real insects has revealed to us.

This apparatus affords many other advantages besides those of verifying theoretic ideas. It enables us to make new experiments, to which living beings will not lend themselves. We can change one of the conditions, for example, the form of the wings, their extent, or the rapidity of the stroke, or any other of the circumstances, while all the others remain constant; we may thus discover the influence which each of them singly may have on the mechanism of flight. It is by such experiments that we can assure ourselves of the following fact. In the course traversed by the wing there is only one region useful in the propulsion of the insect; that is the median region. In the two extreme portions the wing has not experienced that change of plane which renders

Fig. 8.



Representing the artificial insect or scheme of the flight of insects.

its action effective. Thus we see if we diminish the extent of the motions of the wing, the tractile power produced by the apparatus diminishes considerably, and finally ceases altogether. If the membrane of the wing is too broad, another phenomenon results. The hinder edge of the wing remains almost immovable in space, especially during motions of small amplitude; the nervure only is animated with rapid motion. The air, therefore, is struck by planes inclined inversely to those which act upon it in normal flight, so that the apparatus retrogrades and turns around its pivot in a direction contrary to its usual motion.

Experimental flight also shows the adaptation of certain forms of wings to obtain the most rapid translation of motive force. These are precisely the forms which we find in nature. The nervure of insects does not carry the wing membrane back to its point of insertion. Those parts near the articulation have little vitality; they contribute very little toward a useful result, embarassing the neighbouring parts, without compensation of any kind. The membrane should not exist except when vitality itself exists in a corresponding degree. Finally, the extent which the alar membrane should have, to best utilize the disposable force, can be determined experimentally. M. de Lucy has compared, in the case of a certain number of animals, the surfaces of the wings to the total weight of the body. He finds an extent of 30 square millimetres in a gnat weighing 3 milligrammes; 1,663 square millimetres in a butterfly weighing 20 centigrammes; 750 square centimetres in a pigeon weighing 290 grammes; 4,506 square centimetres in a stork weighing 2,265 grammes; 8,543 square centimetres in an Australian crane, weighing 9,500 grammes. But to facilitate the comparison it is necessary to reduce these figures to a common measure; and in spite of the barbarous phrases to which they lead us, we obtain:

	Square metres.
The kilogramme of the gnat represents	10·0
The kilogramme of the butterfly represents	8·0
The kilogramme of the pigeon represents	2·586
The kilogramme of the stork represents	1·988
The kilogramme of the Australian crane represents...	0·899

The extent of the wings, therefore, is not proportionate to the size of the animal. A wing being given, a maximum rapidity of stroke corresponds to it. To augment the rapidity of the stroke, in hope of indefinitely accelerating the rate of flight, would be illusory; it is possible to accelerate it up to a certain point, but beyond this maximum limit additions become useless. Increasing progressively the action of the air-pump, the strokes of the wings are more rapid, and at first the rapidity of flight will be augmented. Continue the increase, and the rate of flight diminishes. The amplitude of the motion also experiences a considerable reduction, so that at the limit the wings appear motionless, or animated only by a slight quivering. Passing this extreme limit, the apparatus retrogrades. A given wing then corresponds to a fixed rate of progressive strokes; for, by the effect of inertia, the frequency of the strokes is increased only at the expense of their extent, and, when the extent diminished, the propelling force diminishes with it. I leave to yourselves the task of explaining these facts, which are the simple consequences of the principles I have previously explained. I also leave to you the comparison of the mode of progression of insects with the other modes which are seen in other animals or in various mechanical contrivances. You will discover almost everywhere the mechanism of the revolution of forces on the principle of the inclined plane. You will find it in the motion of the tail of a fish, the principal organ of its locomotion; in the sculling motion of a waterman's oar, and even in the screw of a steam propeller.

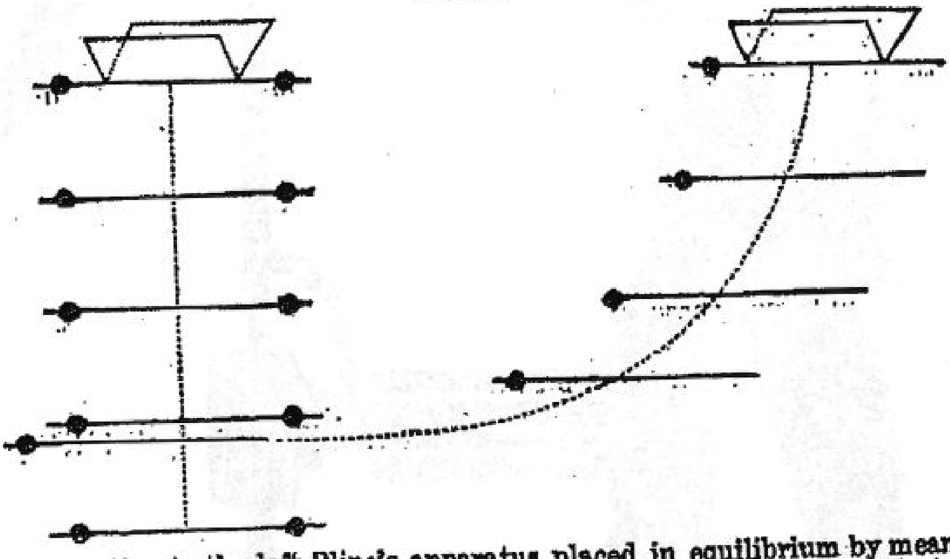
Flight of Birds.

By the simple inspection of a bird's wing it is easily seen that its mechanism for flight is not the same as that of an insect. Let the manner in which the feathers of birds are laid, one over another, be observed, and it will be evident that the air resists the motion of the wing only from below, so that in an inverse direction it finds an easy passage between the long beards of the feathers, which, in this motion, are no longer pressed together. This well-known arrangement, the effect of which Prechlt* has clearly pointed out, has led to the belief that to sustain the bird against gravitation the wing needs only to oscillate in a vertical plane, in consequence of the predominance of the resistance of the air acting from below over that acting conversely.

* * * * * *

All thin curved bodies tend to slide upon the air in the direction of the radius of their special curve. If we bend the anterior or posterior edge of our little apparatus at a certain point in its oblique course, we shall see it rise, notwithstanding the force of gravity, though its motion soon ceases. What has happened in this case?

Fig. 13.

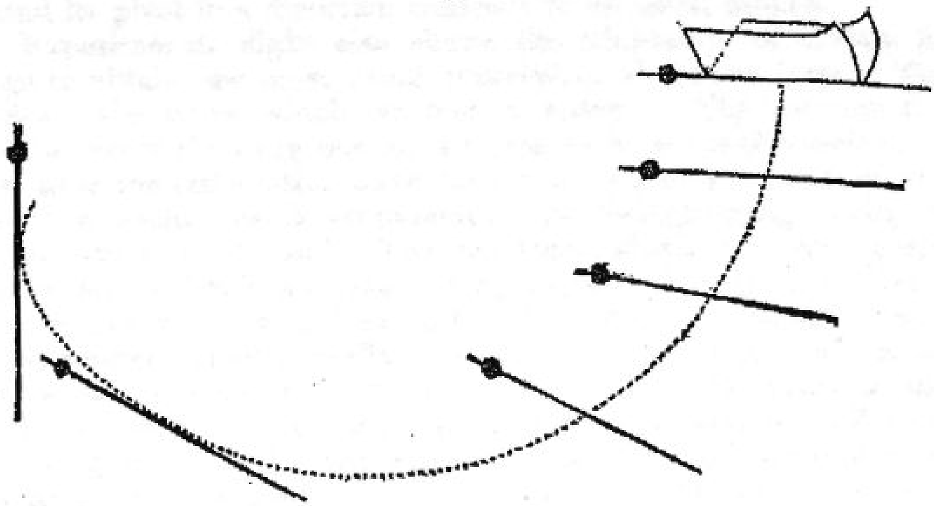


Representing to the left Pline's apparatus placed in equilibrium by means of two equal balls at the extremities of the rod which lies at the bottom of the angle of the bent paper. This, as is indicated by the lower representations of the rod, falls vertically. To the right the same apparatus, with only a single ball, is represented. It descends in a parabolic curve, represented by the dotted line.

* Untersuchungen über den Flug der Vögel. 8vo. Vienna, 1846.

When there has been but little rapidity in the fall of the object, the curve of its surface remains motionless, because the air offers resistance only in proportion to the rapidity with which they move. Therefore, when this rapidity has been sufficiently great a steering effect is produced, which elevates the anterior extremity of the object and imparts an ascending motion to it. But very soon the weight, which was the motive

Fig. 14.

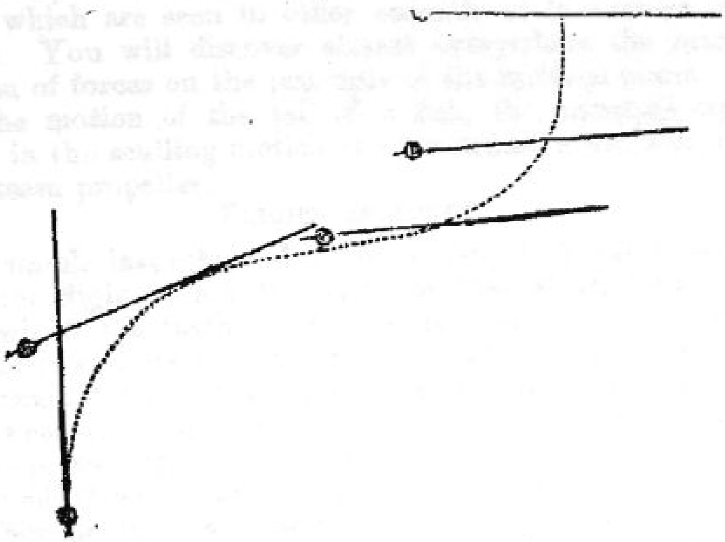


The posterior corners of the two planes of the apparatus have been bent upward and inward, so that after a descending curve the apparatus rises, as the dotted line indicates.

power of the apparatus, becomes a retarding force, and in proportion as the object ascends its motion becomes slower, and finally ceases. After this, retrogradation begins, to be followed by another rise, and so on, until by successive oscillations the apparatus finally reaches the earth. I may add that if a slight concavity is given to the object below, the reverse takes place, and we see at a certain moment the trajectory sharply deflected downward, and the object strikes the earth with great violence. In the second case, at the moment when the steering effect is produced, the weight is in a favourable position for a precipitate descent, and opposed to the ascending reaction.

I emphasize these effects because they are frequently produced in the flight of birds. The old treatises on falconry describe the interesting evolutions of the birds employed in hunting. Without going back further, we find in Huber (octavo, published at Geneva in 1784) a description of the curvilinear movements of the falcon, to which they gave the name of *passades*, and which consisted in an oblique descent of the bird, followed by a rise in its course. "The bird," says Huber, "when about to strike the earth, carried away by its own rapidity, would be dashed to pieces if it did not call into action a certain faculty, which it possesses, stronger than its descending motion, to rise even high enough to make a second swoop. This motion is sufficient, not only to arrest its descent, but even to carry it without effort as high as the elevation from which it came."

Fig. 15.



The posterior corners of the paper have been bent downward. After passing through a parabolic curve the object takes a very rapid descending course.

There is certainly exaggeration in the statement that the bird remounts as high as the elevation from which it descended without further effort. The resistance of the air must overcome part of the force acquired during the descent, and which is transformed into ascending force. We see, however, that the phenomena above described is confirmed by observation, and that it has been considered in some sort as a passive act in which the bird expends no muscular power. The act of hovering in some cases presents a great analogy with the phenomena just described. When some birds, pigeons for instance, have used their wings during a certain distance, the wings are seen to be perfectly quiet during a few seconds gliding through the air, either horizontally or rising or falling. The descending motion has the longest duration; in fact, it is only an extremely prolonged descent in which motion is maintained by the force of gravity, which diminishes it in the horizontal or ascending plane. In these latter forms the wing, more or less obliquely directed, takes hold on the air like the toy kite, with this difference, that motion is imparted to this by pulling the string when the air is calm, while the bird utilizes momentum previously acquired by an oblique descent or previous strokes of the wings.

I have already said that observers have admitted that certain birds, which they call sailors, can sustain and direct themselves in the air by means of the wind alone. This theory appears paradoxical. It is incomprehensible that a bird, motionless in the wind, should not yield to the resistance of the air through which it glides. If the *passades* or swoops which the falcon executes can sometimes carry it against the wind, this can only be a transient effect, compensated for by being carried away by the wind more rapidly in another moment. However, this theory has been sustained with great talent by some observers, especially the

Count d'Esterno, the author of a remarkable memoir on the flight of birds. "Every one," he says, "can see some birds practising this method of flight; to deny it is to deny self-evident facts." I myself have noticed this mode of flying, but it has seemed to me that it is executed in general under the following special conditions: Along the cliffs of the coast of Normandy I have seen the gulls and sea-mews performing their evolutions without moving their wings. I have seen the daws and rooks flying in the same manner around old cathedrals. But the same birds, when they left these special stations, have always appeared to me to use the rowing method of flight; that is to say, making regular strokes of their wings, sometimes interrupted in the daws by swoops of short duration. I then sought to determine the direction of the wind, and this is what seemed to me to occur: When a bird finds itself in the neighbourhood of a cliff, where the air is calm or agitated by eddies in a contrary direction to the prevailing wind, it can pass successively from the calm to the agitated air, and conversely. A sea-mew surrendering itself to the force of the wind, receives an impulse which carries it with a certain rapidity, and if, by simply turning, the bird enters a region of calm air, it can utilize the impulse which the wind has given it in returning to the height which it had left. Plunging again into the zone of agitated air, it recommences the evolution which I have just described, without moving its wings, except to give them different inclinations. The daws and rooks appear to me to find the same conditions around the cathedral towers. The authors who have reported the most curious cases of sailing flight have observed them in mountainous regions. It is a condor in the Cordilleras, or an eagle in the Pyrenees. The sailing flight has often been described of certain birds of prey, who, in the middle of a plain, rise and turn without moving their wings I myself have often seen harriers fly in this manner, but I have always determined, also, that in this case the spiral which they describe is altered by the wind, and that the birds are definitely carried to leeward with a more or less rapid motion.

Even when reduced to these limits the influence of the wind on the flight of birds is very difficult to explain. It is complicated by very different conditions in which the motion acquired by the bird, opposed from various directions by the force of the wind, gives rise to the most varied combinations of motion. It is also known that in the upper regions of the air various currents exist, sometimes even in a contrary direction to those which obtain near the surface of the earth, so that the bird, passing from one to another, finds forces which carry it in opposite directions.*

Finally, the question of sailing flight seems to me one of the most difficult to solve. It would be temeritous to absolutely condemn the opinion of observers upon such vague theories and ideas as we possess upon the subject.

One of the most interesting points in the conformation of birds

* The late Mr. Espy suggested that the phenomenon of sailing in the flight of birds is due to upward currents of air which take place in warm weather, or beneath clouds, and especially up the side of a mountain against which the wind is blowing.—J. H.

consists in the determination of the relations of the extent of the alar surfaces to the weight of the animal. Is there a constant relation between the weight and these surfaces? This question has been the cause of numerous controversies. It has been already shown that if birds of very different kinds, yet of the same weight, be compared, the wings of some species are found to have four or five times the extent of others. The birds which have large wings are usually those which have been called "sailors," while those which have the wing short and narrow are generally classed as "rowers." But if we compare two "rowing" birds with two "sailing" birds; if, for still closer comparison, we take them from the same family, in order that the only differences shall be those of form, a somewhat constant relation will be found between the weight of the bird and the surface of its wings. But the determination of this relation should be based upon certain considerations, which have long escaped the attention of naturalists. Mr. de Lucy sought to measure the surface of the wings and the weight of the body in all flying animals. Now, to establish a common unit among animals of such different kinds and forms, he reduced all the measures to an ideal type, of which the weight should always be one kilogramme. Thus, after having proved that the gnat, which weighs three milligrammes, possessed wings with a surface thirty millimetres square, he concluded, in the types represented by the gnat, the kilogramme of animal was supported by an alar surface of ten square millimetres. By making a comparative table of the measures taken from a great number of animals of different kinds and various forms, he arrived at the following figures:—

Species.	Weight.	Wing surface.	Surface per kilogramme.
Gnat	3 milligrammes...	30 sq. millimetres ...	10 sq. millimetres
Butterfly	20 centigrammes	1,663 sq. millimetres..	8½ sq. millimetres
Pigeon	290 grammes	750 sq. centigrammes	2,586 sq. centimetres
Stork	2,265 grammes ...	4,506 sq. centimetres	1,998 sq. centimetres
Australian crane	9,500 grammes ...	8,543 sq. centimetres	899 sq. centimetres

From these measurements, in spite of variations in detail, the evident result is obtained, that animals of large size and great weight sustain themselves with a much smaller proportional alar surface than smaller animals. A similar result already shows that the office of the wing in flight is not merely passive, for a sail or parachute should always have a surface proportioned to the weight which acts upon it; considered, on the contrary, from its true point of view, that is to say, as an instrument for striking the air, the wing of the bird should, as we shall see, present a relatively smaller surface in birds of large size and great weight. The astonishment exhibited at the result of the determinations made by Mr. de Lucy disappeared when it was remembered that there was a geometrical reason why the alar surface could not increase in proportion to the weight of the bird. In fact, if we take two objects of the same shape, two cubes, for example, of which one shall be twice as large in diameter as the other, each one of the faces of the larger cube will be four times as large as the corresponding face of the smaller, while the weight of the greater cube will be eight times that of the lesser one. For all similar geometrical solids, the linear dimensions having a stated relation to each other, the surfaces are as the square and the weight as the cube of their similar linear dimensions. Two birds of similar form, but having, one of them, the spread of the wings from tip to tip twice as great as in the other, will have respective wing surfaces in the proportion of 1 : 4, and weight as 1 : 8. M. P. Demondésir, who applied these principles before me, thought that he had found in them a reason for the smaller size of birds being capable of flight, while those of a larger kind, such as ostriches and cassowaries, do not fly; he observes that if these birds had as large wings as the heron in proportion to their weight, they could not fold them completely, and would drag them as long and embarrassing appendages. These observations would be correct according to the theory of "sailing" flight, but, in "rowing" flight, the amplitude of the stroke of the wing, increasing in proportion to the size of the bird, multiplies the resistance which the wing meets from the air, and the reaction bears a similar proportion to the weight of the birds themselves. Dr. Hureau de Villeneuve, upon the same principle, has sought to determine the alar extent which would enable a bat of the same weight as a man to fly. He found that each of its wings would be less than three metres in length.

A remarkable work by Hastings* has appeared this year on the relative extent of the wings and the weight of the pectoral muscles in the different species of flying vertebrate animals. The author first shows that among birds the existence can be established of a certain relation between the surface of the wings and the weight of the body. But we should be careful to compare only comparable elements; that is to say, the length of the wings, the square root of the alar surfaces, and the cube roots of the weight among different birds. Let l be the length of the wing, a its area, and w the weight of the body, we can compare among themselves l, $\sqrt{a}$, $\sqrt[3]{w}$.

Examining different types of birds, Hastings made weights and measurements, from which the following table is extracted:—

Species.	Weight. w.	Surface. a.	Relation between them. $\sqrt{a}\ \sqrt[3]{w} \div \sqrt[3]{w}$.
Laurus argentatus	565·0	541	2·82
Anas nyroca	508·0	321	2·26
Fulica atra	495·0	262	2·05
Nettion crecca	275·5	144	1·84
Laus ridibundus	197·0	331	3·13
Machetes pugnax	190·0	164	2·23
Rallus aquaticus	170·5	101	1·81
Turdus pilaris	103·4	101	2·14
Turdus merula	88·8	106	2·31
Sturnus vulgaris	86·4	85	2·00
Bombycilla garrula	60·0	44	1·69
Alauda arvensis	32·2	75	2·69
Parus major	14·5	31	2·29
Fringilla spinus	10·1	25	2·33
Parus cæruleus	9·1	24	2·34

* Archives Neërlandaises, t. iv. 1869.

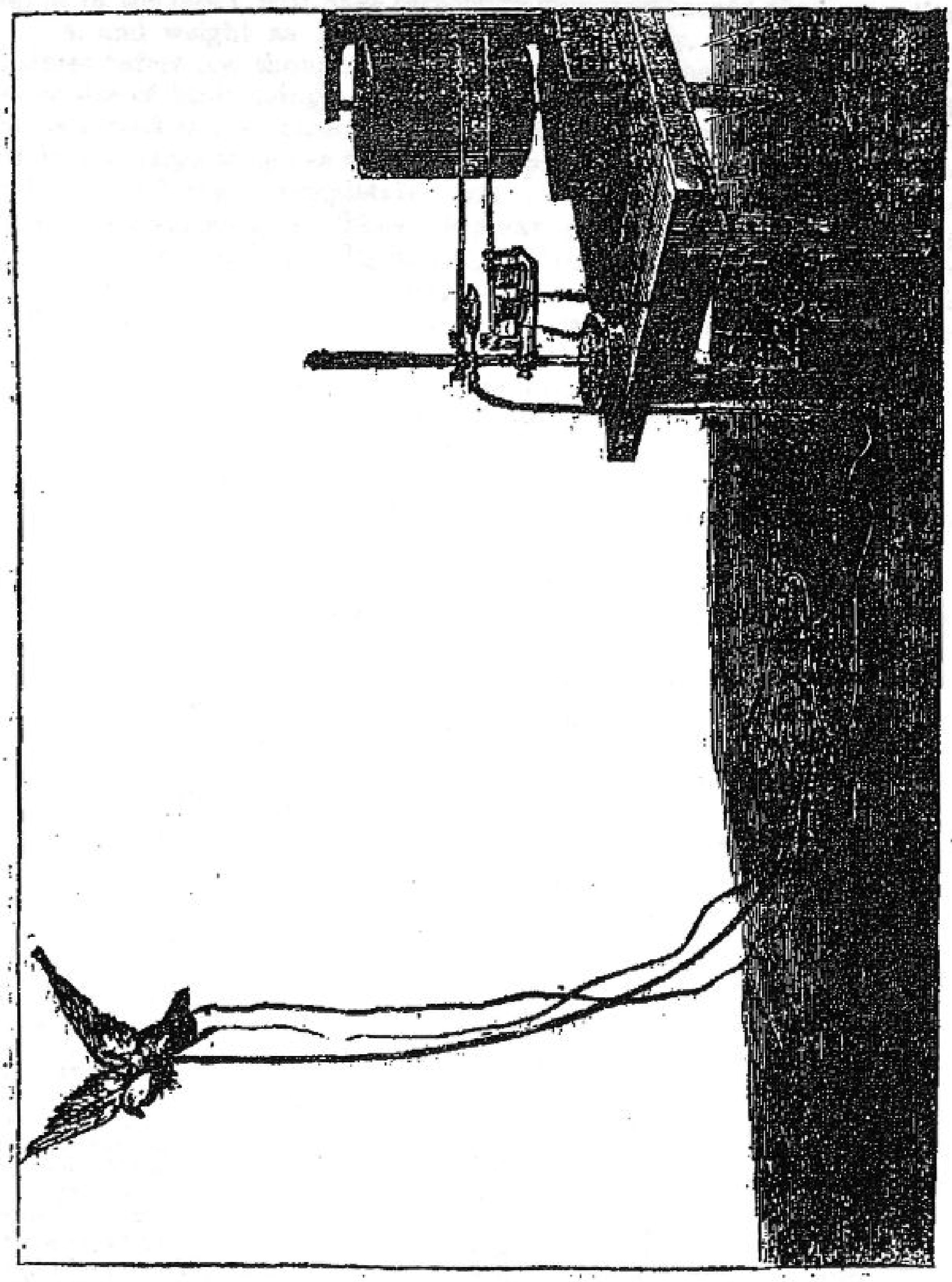
The weight of the pectoral muscles is, on the contrary, in simple proportion to the total weight of the bird, and in spite of the differences which correspond to the different degrees of aptitude to flight with which each species is endowed, we perceive that the proportion of the weight of the pectoral to the total weight is about one-sixth in the greater number of birds.

Each animal capable of sustaining itself in the air must develope a force proportional to its own weight, and should possess an amount of muscle proportioned to this weight; for, as we have seen, if the chemical action which takes place in the wings of birds be always of the same nature, this chemical action and the power which it generates will be proportionate to the size of the muscular masses. Now, how is it that the wings of birds in which the surface varies as the square of the linear dimensions suffice to move bodies of which the variation is in proportion to the cubes of these dimensions? Here it is necessary to bring in the theory of power; that is to say, of resistance multiplied by the square of the distance through which it acts in a given time, admitting a uniform rate for the downward stroke of the extremity of the wing in two birds to be compared, and which have the proportion of 1 : 2 in their linear dimensions. The surface of the wings of the larger bird will be, as we have already said, four times as great as that of the smaller one; now, as the resistance of the air against surfaces moving at the same rate is proportionate to their extent, if we call the resistance experienced by the wing of the small bird r, that for the large bird will be $4r$. But these birds, in the downward stroke of their wings do not execute motions of equal amplitude. In the large bird each point of the wing will travel twice as far as the similar part of the smaller bird. If we call the space traversed g, the resistance r, which the wing of the small bird encounters, we shall have rg for the work done by the wing, and $4r$ $2g$ or $8rg$ for the work done by the bird. We see, then, that this work increases in the same proportion as the weight of the animals we are comparing.

Another conclusion results from the preceding considerations. If we admit that the wing possesses the same velocity in both birds, the duration of the stroke will increase with the space traversed by the wing; that is, it will be proportioned to the linear dimensions of the bird. Observation confirms this view by showing that large birds make fewer strokes than small ones do. We have not yet been able to determine exactly the number of strokes of the wings of birds to ascertain if their frequency presents an exact inverse ratio to the size of the animal, but it is easy to see that it is in this manner that the frequency of the wing-strokes of birds varies.

The graphic method, which is easily employed in determining the frequency of the wing-strokes of insects, cannot be similarly employed with birds. It is necessary to adopt some method of transmitting signals from the flying bird to the registering apparatus. For this purpose I have first used the *electric telegraph*, which furnishes the means of solving the following questions:—1. What is the frequency of the strokes of the wings of a bird? 2. What are the relative durations of the periods of elevation and depression of the wings? The experiment consists in placing at the extremity of the wing an apparatus which breaks or closes an electric circuit at each of the alternate motions, while at the further part of the circuit is placed an electro-magnetic apparatus, which makes a trace upon a turning cylinder. Fig. 16 shows this method of studying

Fig. 16.



Apparatus for registering the motion of the wing of a pigeon by double signals. In one case a small India-rubber tube transmits the record of the muscular action; in the other the periods of elevation and depression of the wing, with their relative durations, are noted by an electric signal.

the flight of a pigeon, together with another method of transmitting signals. In this figure the two wires are separated from each other.

The writing style traces a crenulated line, of which the changes of direction correspond to a change in the direction of the motion of the wing.

In order that the flight may be as free as possible, a fine, flexible cord, containing two wires, establishes the communication between the bird and the writing telegraph. The two ends of the two wires are attached to a very small light apparatus which, from the resistance of the air, executes a kind of valvular motion. When the wing is elevated the valve opens, the circuit is broken, and the line traced by the telegraph rises. When the wing descends the valve closes, the circuit is also closed, and the line is depressed.

Applied to different kinds of birds, this apparatus registers the frequency of the strokes of the wing in each. The number of species which I have as yet been able to study is very small; I have, however, obtained the following results:—

Number of Vibrations of the Wing per second.

Sparrow	13
Wild duck	9
Pigeon	8
Hen-hawk, *Buteo vulgaris*, a hawk called in England and France the "buzzard" or "*busard*"	5¾
Screech-owl	5
Harrier, *Circus rufus*, marsh harrier of England, *buse* of France..	3

The frequency of the strokes varies according as the bird is starting, is in full motion, or at the end of its flight. Some birds, as we know, have periods when the wing is motionless, and when they move by means of the momentum acquired.

It is interesting to observe the relative duration of the periods of ascent and descent of the wings. Contrary to the opinion expressed by some observers, the descending period is generally longer than that of elevation. The inequality of the two periods is especially evident in birds which have large wings and make few strokes. Thus, while the periods are almost equal in the duck, which has very narrow wings, they are unequal in the pigeon, and much more so in the harrier.

The following figures exhibit the results obtained from several species of birds:—

Species.	Total distance traversed during one complete oscillation of the wing.	Proportional distance.	
		Ascent.	Descent.
Duck	6·66 centimetres per second	3·0	3·66
Pigeon.........	7·5 centimetres per second	3·0	4·5
Harrier	21·5 centimetres per second............	8·5	13·0

D

It is more difficult than might be supposed to determine the precise instant of the change of direction in the line traced by the telegraph. The attraction of the magnet and the relaxation have an appreciable duration, if the blackened cylinder turns with sufficient velocity to measure the rapid motions which we seek to analyze. The inflections of the line traced by the telegraph then become curves, of which it is somewhat difficult to determine the precise origin. There is therefore a limit to the precision of the measurements which can be made by the electric method. I think that we cannot approximate by this method nearer than $\frac{1}{50}$ of a second to the duration of a motion.

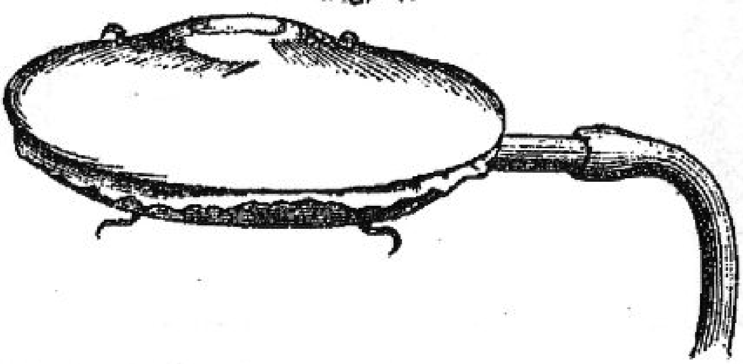
Another kind of signal allows the estimation of the frequency of the stroke at the same time that it furnishes indications of the successive action of the principal motive muscles of the wing.

Myographic method.—In 1867 I indicated a myographic method which might be applied without mutilating the animal upon which the experiment was performed. It consists in employing the swelling of a muscle to afford evidence of its changes in length—that is to say, by its contraction or relaxation. Muscles, not being sensibly compressible, cannot change their length without at the same time changing their transverse diameter. A rapid or short, feeble or energetic contraction of a muscle, hence, is accompanied by an increase in diameter, affording the same features of rate or intensity. At each descent of the bird's wing the great pectoral muscle thus exhibits an increase of size, which can be indicated by the registering apparatus.

I have made use of flexible air tubes of India-rubber in transmitting these effects, a method which has enabled me at times to register at some distance the beating of the heart, the pulse, and the motions of respiration.

The bird flies in an enclosure fifteen metres square and eight metres high. The registering apparatus being placed in the centre of this enclosure, twelve metres of rubber tubing are enough to establish a constant communication between it and the bird. A sort of corset is applied to a pigeon (*see* Fig. 16). Under this corset, between it and the pectoral muscle, is placed a little contrivance intended to exhibit the swelling of the muscle. It consists of a small shallow metal basin containing a spiral spring, and closed over by a thin sheet of rubber. This basin, thus closed, communicates with the transmitting tube.

Fig. 17.



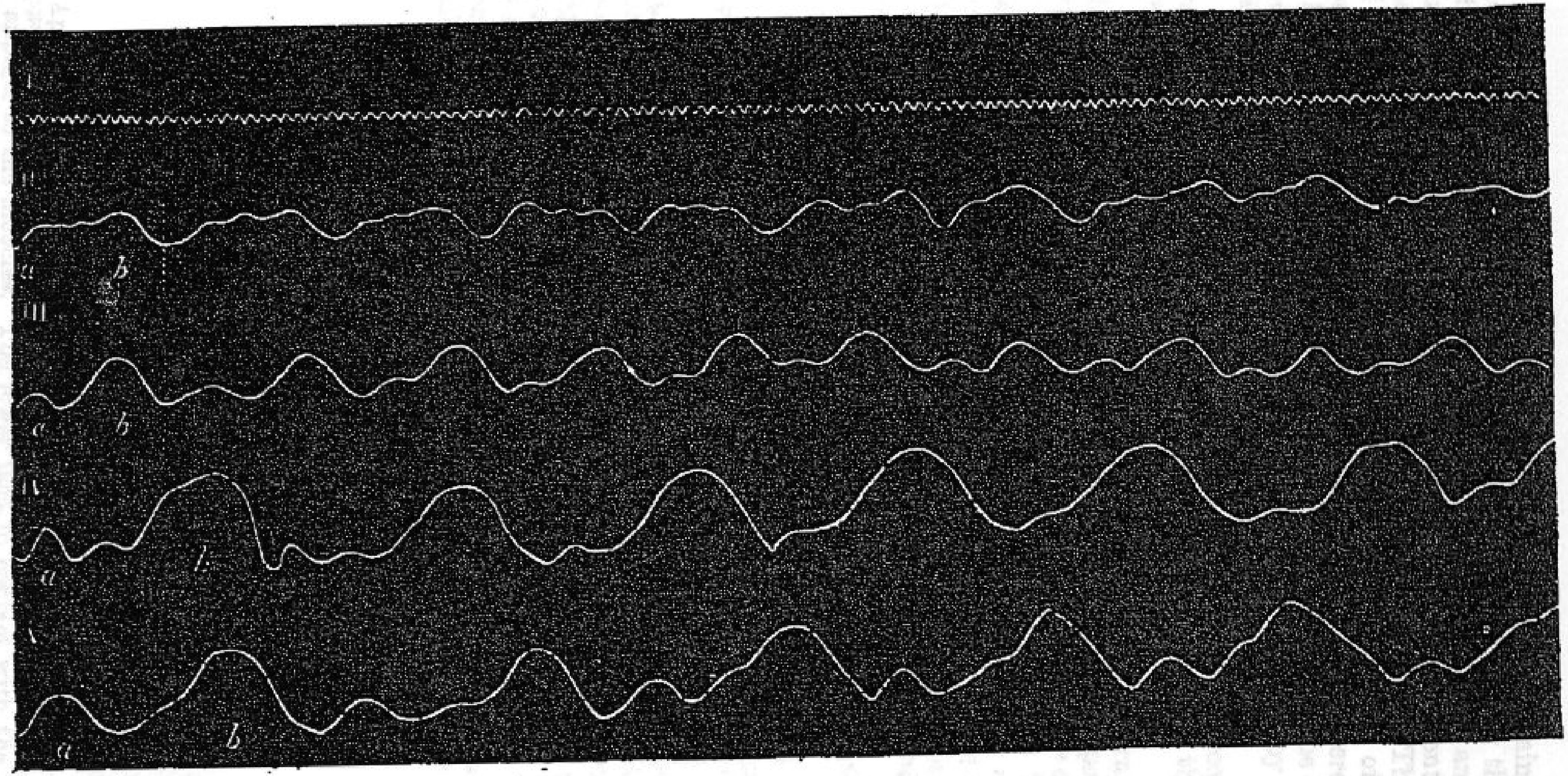
Apparatus for exhibiting the contraction of the thoracic muscles of birds. The upper convex face is formed of a sheet of rubber, held up by a spiral spring, and is applied to the muscles. The lower face, in contact with the corset, carries four little hooks which are caught in the cloth and hold the apparatus in its place.

Any pressure applied to the face of the apparatus depresses the rubber. The air is forced out of the basin and escapes by the tube. If the pressure ceases, the air re-enters the basin in consequence of the elasticity of the spring which raises the rubber. An alternate inspiration and aspiration is by this means established in the tube, and the motion of the air transmits to the registering apparatus a signal of the more or less intense pressure which has been exerted upon the rubber cover of the basin. The registering apparatus I have used in all my experiments is also composed of a basin, covered by a rubber membrane communicating with the transmitting tube. The motion imparted to the first basin is transmitted by the air to the rubber cover of the second. The motions of the membrane of the receiving apparatus, amplified by a lever, are written on the smoked cylinder. Fig. 16 represents the general arrangement of the experiment in which the electric telegraph and transmission by air are exhibited together. We see the pigeon under experiment furnished with its corset and apparatus for showing the movements of its pectoral muscles. The transmitting air-tube ends at the registering apparatus, which writes on a revolving cylinder. At the extremity of the pigeon's wing is an arrangement which opens or closes an electric circuit as the wing rises or falls. The two wires of the circuit are represented separately, and two cells of Bunsen's battery are seen in their connection with the helix, which, furnished with a lever, registers the telegraphic signals of the motions of the wings. One precaution is indispensable—the rubber tube which connects the bird and the apparatus must be prevented from stretching. When the bird flies it raises more or less of the tube, and if this is elastic it will become elongated by its own weight, producing a rarefaction of the air contained in the two receptacles, and the registering lever will trace muscular curves on a descending line. To prevent this inconvenience, the tube may be tied here and there to the telegraphic cord by means of ligatures, taking care that the tube is a little longer than the cord, and that it is not subjected to traction. These precautions being taken, nothing prevents the successful transmission of signals. No trouble need be taken in regard to the elasticity of the tube in a transverse direction; its walls are so thick that their elasticity is not brought into play by the feeble changes of pressure to which the air they contain is subjected.

The bird is let loose at one end of the enclosure, the dove-cote in which it is ordinarily kept being placed at the opposite end. The bird naturally flies toward the latter. During its flight the tracings represented by Fig. 18 are obtained.

The trace is seen to differ according to the kind of bird experimented upon. However, in all the traces we perceive the periodical return of two motions, *a* and *b*, which are produced in each vibration of the wing. What is the signification of these two muscular actions? It is readily seen that the undulation *a* corresponds to the action of the muscle which elevates the wing, and *b* to that of the muscle which depresses it. This can readily be proved by comparing the trace of the muscular action in the electric trace of the elevation and depression of the wing. These two tracings, placed one under the other, show that the period of elevation of the wing agrees with the extent of the undulation *a*, and the period of depression with the undulation *b*.

Fig. 18.



Myographic tracings of the pectorals obtained from various kinds of birds during flight. I. Tracing of the tuning-fork to be used in measuring the absolute duration of each muscular motion; this tuning-fork vibrates 200 times a second. II. Tracing of the muscles of a pigeon obtained, as in Fig. 16. III. Tracing of a wild duck. IV. Tracing of hen-hawk V. Tracing of a harrier.

But to establish this agreement we must take the unequal rapidity of the transmission of the electric and aërial signals into account. We may consider the electric transmission as instantaneous, while the aërial transmission is at the same rate as the rapidity of sound through the air, that is, 334 metres per second. If the points of the two styles are placed vertically one above another, the tracings will not be exactly superposed, but the electric signal will precede the other by a distance corresponding to a certain fraction of a second, according to the length of the tube which has been employed. We can even compute, from the length of the air-tube, the amount of retardation, but it is more certainly ascertained by a special determination for the particular tube which may be in use. In a previous experiment, motions were simultaneously transmitted by the tube and by electricity, and the discrepancy determined. In the apparatus which I am using, the constant discrepancy is ·04 of a second. I should therefore set back the electric signals by a corresponding distance, in order that they may agree with the signals transmitted by the air-tube. Fig. 19 shows the superposed tracing from a harrier after correction.

It is easy to understand how the undulations *a* and *b* are produced in all the tracings of the muscles of birds. In fact there exist two distinct planes of muscles in the upper part of the region investigated near the end of the sternum. The most superficial is formed by the great pectoral which lowers the wing, the deeper by the median pectoral or elevator of the wing, the tendon of which passes behind the bifurcation of the sternum to attach itself to the head of the humerus. The two superposed muscles act by their swelling upon the apparatus applied to them. The median pectoral swells when it contracts, signalizing the undulation *a* by its action; the great pectoral signalizes the lowering of the wing in the undulation *b* in a similar manner.

We can verify the correctness of this explanation by a very simple experiment. Anatomy shows us that the median pectoral is narrow, and only covers the inner portion of the great pectoral along the keel of the sternum. So if we displace the little apparatus which reveals the motion of these muscles, and carry it further outward, it will occupy a region where the median pectoral does not cover the great pectoral, and the tracing only presents a simple undulation which corresponds to *b* in the figures.

It is, therefore, sufficiently demonstated that the undulations *a* and *b*, in the muscular tracings of the birds upon which I have experimented, correspond exactly to the principal elevating and depressing muscles of the wing; but we cannot attach much importance to the form of these tracings for deducing the precise nature of the motion effected by the muscle. In fact, these motions appear to override one another. So the relaxation of the median pectoral is probably incomplete when the great pectoral commences to act. We should expect no more from these tracings than they naturally furnish, that is to say, the number of vibrations of the wing, the greater or less regularity of its movements, the equality, inequality, and energy of each of them. Restricting the enquiry within these limits, the experiments show that the strokes of the wings of birds differ in frequency and amplitude in the different moments

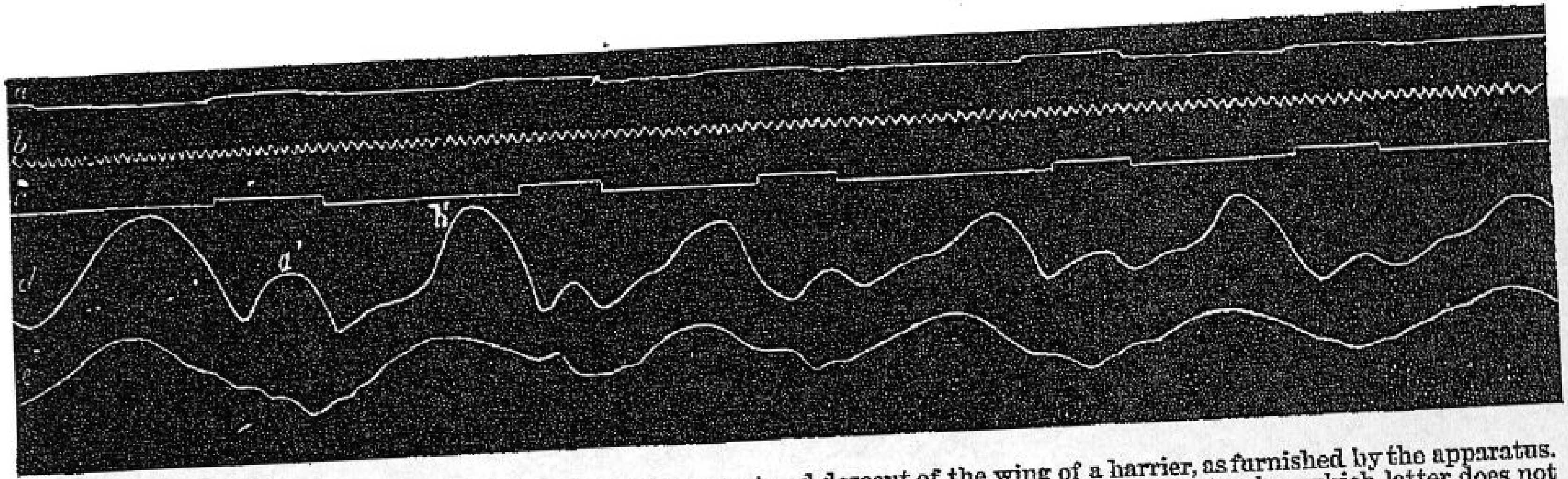


Fig. 19.—Line *a* represents the electric tracing of the ascent and descent of the wing of a harrier, as furnished by the apparatus. Line *b* is a tracing of a tuning-fork vibrating 200 times a second. Line *c*, correction of the electric tracing, which latter does not represent the changes with sufficient abruptness in the figure (*a*) obtained directly from the wing. Line *d*, tracing of the action of the pectoral muscles in the harrier by the air apparatus; *a'*, period of elevation of the wing; *b'*, period of depression. Line *e* will be hereafter referred to; it represents the vertical oscillations of the bird during flight.

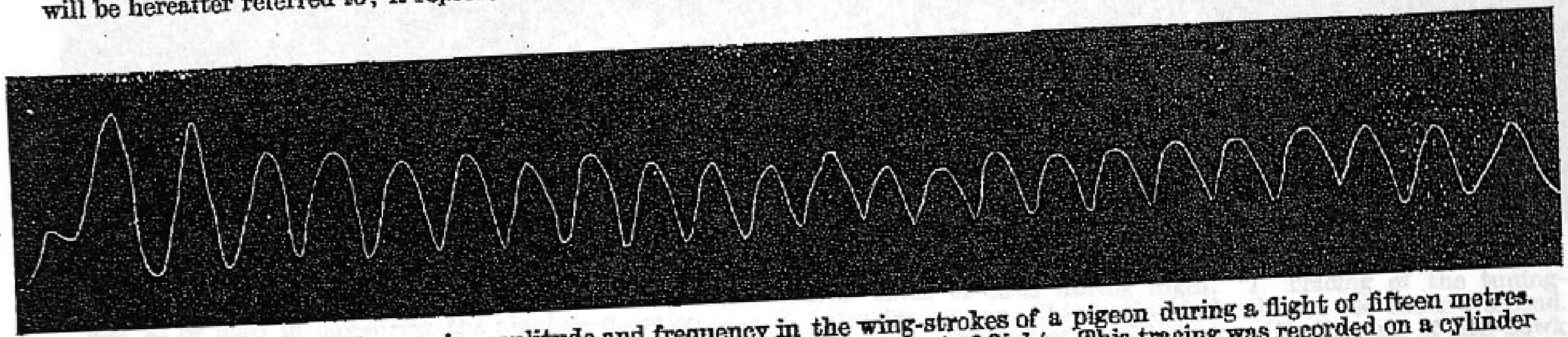


Fig. 20.—Showing the difference in amplitude and frequency in the wing-strokes of a pigeon during a flight of fifteen metres. To the left the extended traces indicate the movements at the commencement of flight. This tracing was recorded on a cylinder which moved very slowly, allowing the record of a large number of strokes to be compressed into a small space.

of flight. At starting the strokes are fewer but more energetic; they attain, after the first two or three, a regular rhythm, which they lose at the moment when the animal is about to alight.

We shall find in other experiments more complete indications of the variation of the movements of the wing during the different periods of flight.

Such are the certain indications which can be derived from the method of signalizing established between the flying bird and the registering apparatus. But if it is wise to guard our conclusions by more rigorous experiments, it may at least be permitted us to attempt to discover whether the tracings of these muscles cannot furnish us with further information in regard to the motions from which they are derived. I have elsewhere demonstrated that the form of the motion produced by a muscle when it is excited varies according to the resistance which this motion encounters. Thus, in applying the myograph to the muscle of a frog, I have seen that if contraction be impeded by an obstacle the duration of the muscular shock becomes greater on account of that obstacle. Theory, also, would foretell us, that if the muscle presents certain modifications in the different phases of its contraction, the result of unequal resistance overcome at different periods, the swelling of the muscle should also present the same phases. If the tracing is the exact impression of the motions produced by the muscle, it can inform us of the nature of the resistance which the wing of the bird encounters in the different phases of one of its vibrations.

Let us take the most simple example. As the median pectoral and great pectoral are very unequal in size, we may suppose that if the resistance is equal in the two periods of elevation and depression, the duration of the former would much exceed that of the latter; and, as exactly the contrary is the case, we may conclude that the rising wing does not strike the air but cuts it apparently with its edge, so that the resistance to the elevation is very feeble, and is very strong to the depression of the wing. Now, if we examine the tracing of the depression of the wing we shall find there, within certain limits, the expression of the different amount of resistance which the wing encounters in the different phases of its depression. It is necessary by previous experiments to determine the effect of certain special kinds of resistance, which we may call elastic resistance, in order to better understand the signification of different forms of muscular motion.

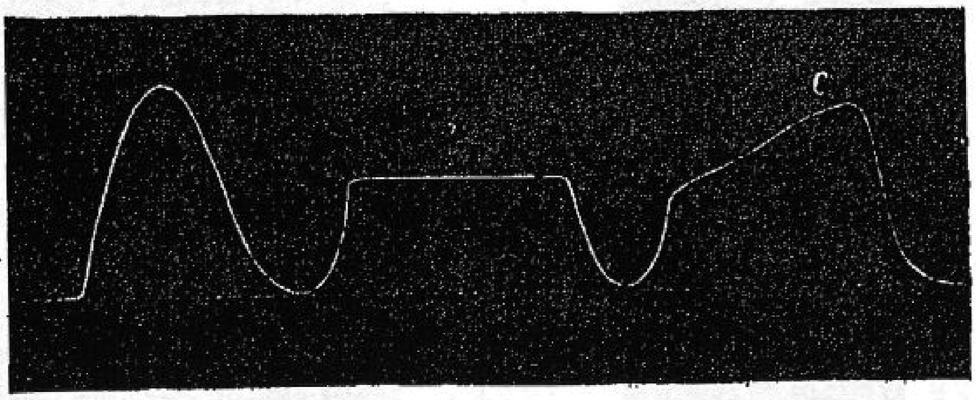
Let us take the muscle of a frog, apply it to the myograph, and excite contraction in it by means of electricity. The form of this contraction varies in the following manner under the influence of different kinds of resistance opposed to the action of the muscle: If a weight be suspended to the muscle it gives the tracing *a*, Fig. 21. If it encounter an absolute obstacle to all further diminution of length, after a few instants of contraction it gives the trace *b*. Finally, if it encounters an elastic obstacle, as a rubber thread, which presents a surmountable resistance, the muscle gives the curve *c*. It seems as if these different forms were sufficient to characterize the nature of the resistance that the contraction of the muscle has had to overcome.

In the first case it is the inertia of a body; now this body submitted to the muscular force during a limited period, should have an accelerated motion at first and then a diminishing motion. This is precisely what the form of the curve *a* indicates. In the second case it is not necessary to explain how the horizontal line which forms the summit of the curve *b*, expresses the cessation of all contraction in the presence of an absolute obstacle. Lastly, in the curve *c*, the presence of an obstacle is betrayed by a deflection of the curve; that is, by a change in the rapidity of the motion which produces it; but the contraction does not cease because the obstacle is not insurmountable, but it becomes slower on account of the greater resistance presented.

I have been able to convince myself that in the above-mentioned experiments the swelling of the muscle presents the same phases as its change of length. In fact, I have transmitted to the myograph the motion produced by the swelling of the muscle, and have obtained tracings identical with the preceding. Finally, wishing to know if the apparatus which I have used would faithfully transmit the different phases of the swelling of muscle, I made the following experiment: I applied the little drum which had served to obtain the tracings from the birds (Fig. 18) to my own biceps muscle, fixing it exactly in place by means of a bandage, and put it in communication with the registering apparatus. I then made sudden voluntary motions, as similar as I could make them to each other, but applied to overcome various forms of resistance. In one case I lifted a weight; in another my hand was absolutely arrested in upward motion by being placed beneath a heavy table; in still another, I tied my hand to a fixed object with a rubber band which, by a short flexure of my fore-arm, required the utmost efforts of the muscle to stretch it.

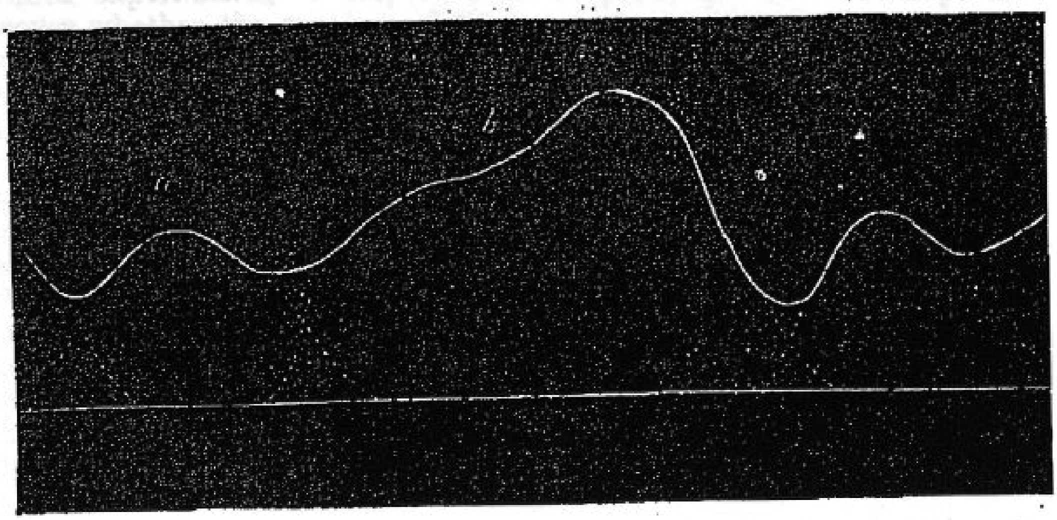
Now the tracings which express the swelling of the biceps in these three experiments reproduce the three types represented in Fig. 21, and

Fig. 21.



show very clearly that voluntary exertions had been subjected to different forms of resistance. I tried to force upon the muscles identical motions in each case, which was always a short vigorous flexure, but the nature of the resistance modified these muscular actions which were intended to be similar to each other, and imparted to them the various phases and durations which are exhibited in the figure. This being settled, let us return to the muscular tracing of the great pectoral of the bird. I have said that the exact commencement of this motion is undetermined, the elevator of the wing not having fallen into repose before the depressor commences to act, and if we would represent the probable curve of the action of these two muscles from that which the myograph obtains for us, it will be necessary for us to complete the tracing by means of dotted lines as in Fig. 22.

Fig. 22.



Trace of the action of a harrier during flight: *a*, action of the elevating muscle; *b*, of the depressing muscle. The dotted lines which descend to the axis of the curve complete the probable form of the motions of the two muscles of the wing.

Thus reconstructed, the form of the curves of the elevator and depressor reveals the nature of the resistance which each of these muscles has encountered. The curve *a* of the median pectoral is that of a muscle acting on a weight; it seems to indicate that the inertia of the wing is the only obstacle which the elevator muscle has to overcome. The curve *b* shows us a deflection, during part of which the contraction of the muscle takes a slower motion; it is here that the resistance of the air is interposed. These things happen, then, exactly as in the experiments which I have made upon my own muscles and those of the frog. But you may ask why the deflection of the curve is not produced sooner; and if the depressor muscle can rapidly contract for a certain period before encountering sufficient resistance from the air to impede its motion. This is just what happens; we have the proof of it in the anatomical disposition of the attachments of the great pectoral muscle. We shall see hereafter how the motion of the humerus around its articulation is produced; at present I will only say that in the first part of its action the great pectoral in contracting produces a pivot-like motion of the wing upon the head of the humerus, and that in this first motion the muscle does not experience the resistance of the air which retards its contraction an instant later.

The reader will perhaps consider that an inordinate number of deductions are made from the forms of the curves of the muscles; but those who will familiarize themselves with the use of the registering apparatus, and in particular with the myograph, will soon be convinced that chance does not enter into the formation of the curves, but that the details should find their explanation in the dynamic conditions of the production of muscular power.

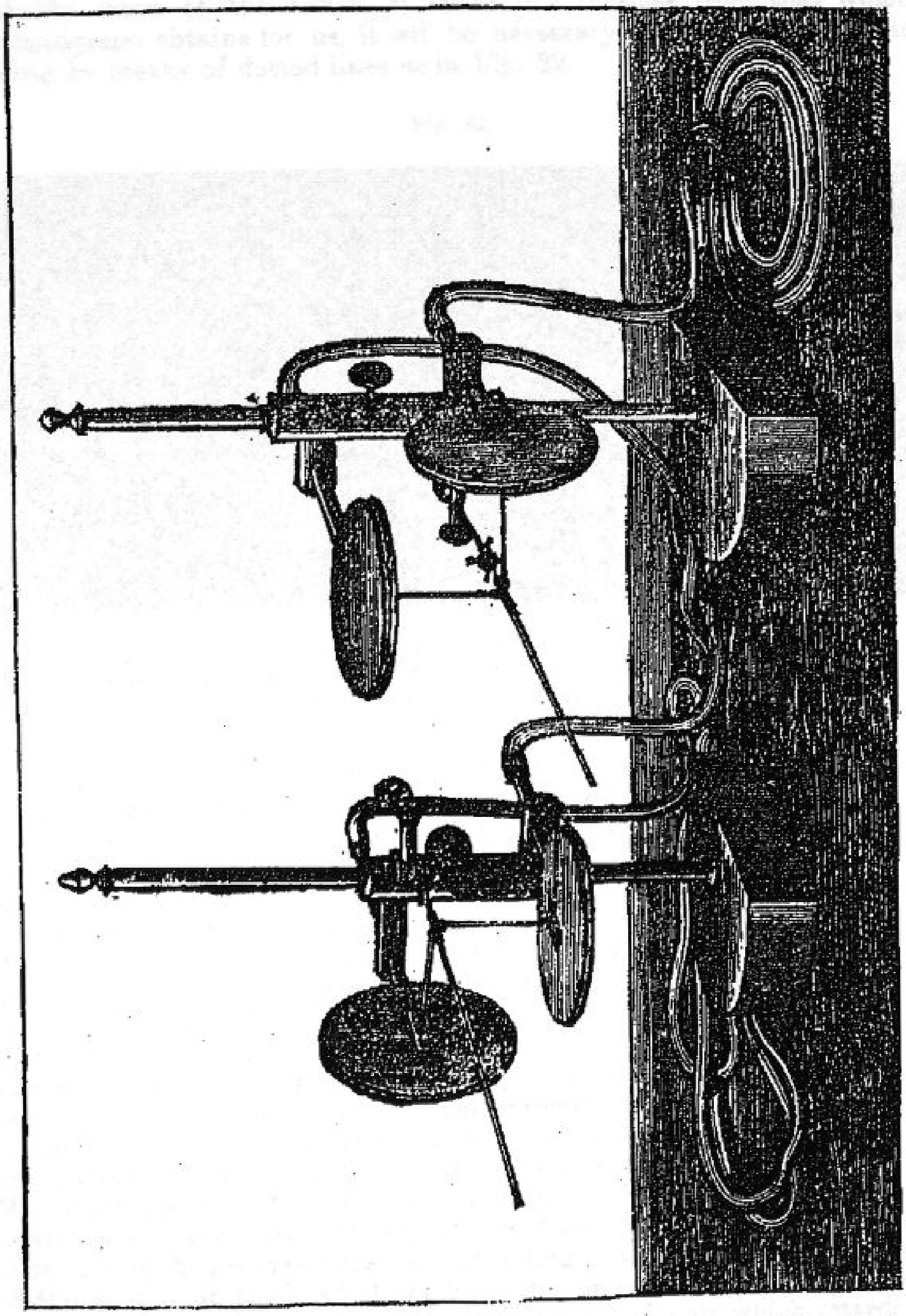
Motions executed by the wing of a bird during flight.—We have seen, in regard to the mechanism of the flight of insects, that the fundamental experiment has been that which has shown the trajectory of the point of the wing in each of its evolutions. The knowledge of the mechanism of flight flows, so to speak, naturally from this first idea. The same determination is equally indispensable for the flight of birds, but the optic method is here inapplicable; the motion of a bird's wing, while too rapid to be followed by the eye, is not sufficiently rapid to form a persistent impression of its entire trajectory upon the retina. The graphic method, which I have hitherto employed, only furnishes impressions of motions which happen to follow a straight line, and it is only by combining this rectilinear movement with the revolving cylinder with a smoked surface that the expression of the rapidity with which the motion is effected at each instant is obtained.

The problem is to find the means of registering on an immovable plane all the motions which the point of a bird's wing makes in space, as if a style had been placed at the end of the wing, and this style traced or rubbed on a piece of paper by its side. It is still further necessary to have a figure of the same nature as the luminous figure of the gilded wing of an insect, that the piece of paper on which the trace is to be made shall remain motionless in regard to the centre of motion of the wing of the flying bird, or in effect that it shall follow the bird in all its phases of impulsion through space.

Now, physics teach us that all motion susceptible of registration in one plane can be generated by the rectangular combination of two rectilinear motions. The tracings obtained by Kœnig by arming a vibrating Wheatstone's rod with a style, the luminous figures of musical chords which M. Lissajous has produced by the reflection of a ray of light from two vibrating mirrors perpendicular to one another, are well known examples of the formation of a plane figure by means of two rectilinear movments. Thus, admitting that the motions of elevation and depression of the wing can be transmitted at one time, as well as the back and forward motions of this organ, by supposing that a writing style can simultaneously receive the impulse of these two motions, perpendicular to each other, this point will write on the cylinder the exact figure of the motions of the bird's wing. I tried at first to construct an apparatus which would thus transmit such a motion to a distance and register it, without concerning myself with the way in which I might apply this rather weighty mechanism to the bird.

Fig. 23 represents this provisional apparatus, the description of which is indispensable for the comprehension of the second mechanism, which I shall describe hereafter. Upon two solid feet, carrying vertical supports, are seen two horizontal arms parallel to each other. These are two aluminium levers which, by the transmitting apparatus to be described, should both execute the same motions. Each of these levers is mounted on a ball-and-socket joint, or double articulation, which

Fig. 23.



Apparatus intended to transmit to a lever at a distance all the motions executed by another lever around one of its extremities.

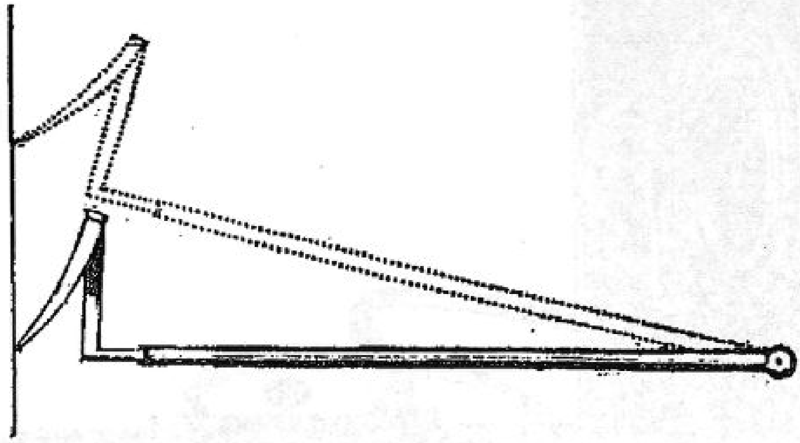
permits all kinds of motion; thus each lever can be carried above, below, to the right, or to the left. It can by its point describe the base of a cone of which the joint will be the apex. In fact, it will execute any kind of motion which the experimentor may choose to impart to it. It is also necessary to establish the transmission of motion from one lever to the other at a distance of ten or fifteen metres. This is done by means of a process with which the reader is already familiar—the use of drums and air tubes.

The lever, which is seen at the left in the figure, is fastened by a metallic arm articulated at one of its extremities to the membrane of a drum placed below it. In the vertical motions of the lever the membrane of the drum rises or falls by turns, producing a throbbing motion of the air in another drum through a long tube, which establishes a communication between them. In the apparatus to the right in the figure, the second drum is placed above the corresponding lever articulated with it, and faithfully transmits all the motions which have been imparted to the first drum to the left. These movements will be in the same direction in both levers on account of the inversion of the position of the drums. If we depress the first lever it presses down the membrane of the drum below it, inducing a pressure which lifts the membrane of the second drum and consequently lowers the second lever; conversely the elevation of the first lever produces an influx of air, which raises the membrane of the second lever.

Proceeding in the same manner to transmit motions in a horizontal plane, I have placed at the right of one of the levers and at the left of the other a drum with the membrane in a vertical plane, which imparts lateral motions to these levers; these motions are transmitted by a special air-tube, as before. In the apparatus thus constructed, if we move the end of one of the levers with the finger, the other lever will be seen to execute the same movements with perfect fidelity. The only difference consists in a slight diminution of amplitude. This happens because the air contained in the tubes and drums is slightly compressed, and in consequence does not transmit the whole of the motion which it receives. It is easy to remedy this defect, if it be one, by placing the ball-and-socket joint a little nearer the point whence the motion is transmitted to the second lever. But it is better not to attempt too great amplification, because the friction is thus augmented and the force which should overcome it is diminished.

After having determined that the transmission of such motion can be effected in a satisfactory manner by means of this apparatus, I have sought for the means of tracing these movements upon a plain surface. The difficulty which before presented itself when I endeavoured to apply the graphic method to the study of the wing-strokes of insects, again appeared, but this time there was no means of eluding it, and I contented myself with partial tracings. The point of the second lever described a spherical figure in space which could not be tangent, except as a point, to the smoked surface, which should receive the trace. In consequence, I should have to register the projection of this figure on the plane. Helmholtz has also encountered the same difficulty in the construction of his myograph, and had solved it by causing the point of the writing style to rub continually on the smoked surface by means of a weight. But as I could not attach a weight to the extremity of my lever, I resorted to the following expedient, shown at the end of the lever in Fig. 24. It is large at the base in order to resist all lateral deviations

Fig. 24.



Elastic point tracing upon smoked glass.

from friction; this base is fixed on a vertical piece of aluminium which is attached to the extremity of the lever. In this way the point of the contrivance, which performs the office of a style, is situated exactly opposite the end of the lever whose motions it registers. If the lever be elevated and takes the position indicated by the dotted lines in Fig. 24, in traversing this space it has described the arc of a circle, and its extremity will be no longer on the same plane as before, but the elasticity of the contrivance will have carried the point of the style forward, and it will therefore continue to be in contact with the plane upon which it is tracing. Thus the lever elongates or shortens according as the case requires, and its point continually rubs upon the plane. I should add that the surface upon which the tracings are received is of finely polished glass, and that the contrivance which I have used is so delicate that the pressure which it exercises produces scarcely any friction.

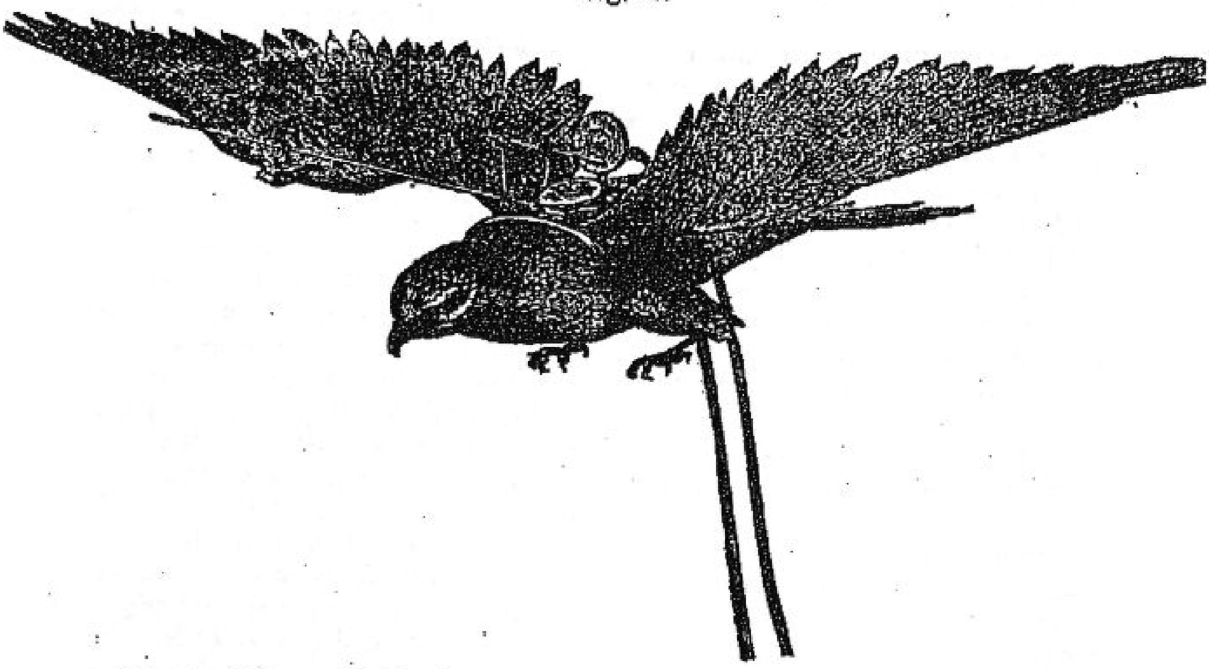
The apparatus being thus constructed, it must be submitted to verification, to ascertain whether the motions are faithfully transmitted and registered. To do this both levers of Fig. 23 are furnished with similar styles placed against the same smoked glass; and moving one of the levers with the hand, for instance, so as to write my name, the other lever should reproduce the same signature. It frequently happens that the transmission is not equally good in both directions, which is perceptible by the deformity of the transmitted figure, which is increased more or less in height or breadth. This deficiency can always be corrected, since it is due to the membrane of one of the drums being stretched more than that of the other, and hence yielding less easily to pressure. It is very easy to equalize the tension by tightening the membrane of the other drum until the figure traced by the first lever is identical with that traced by the second.

The modifications by means of which I have rendered this transmission applicable to the study of the motions of the wing of a flying bird, are as follows:—

The apparatus necessarily being heavy, it required a large bird to carry it. Strong adult harriers served for the experiments. I fixed a light strip of wood upon the bird's back, upon which the apparatus was placed, by means of a kind of corset, which left the wings and feet free. That the lever might faithfully execute the same motions as the bird's wing, the joint of the lever should be placed in contact with the humeral articulation of the harrier. As the presence of the drums by the side of the lever does not permit this immediate contact, I had recourse to a parallelogram, which transmitted to the lever of the apparatus the movements of a long arm of which the centre of motion was very close to the articulation of the bird's wing. Finally, to obtain an identity of motion between the arm and the harrier's wing, I fixed on the bastard wing, that is to say, on the metacarpal portion of that organ, a well cut screw-vice, furnished with a ring, through which passed the steel arm of which I have just spoken.

Fig. 25 represents the harrier flying with the apparatus in question; below hang the transmitting tubes of the registering apparatus.

Fig. 25.



Harrier flying with the Apparatus, which transmits the motions described by the extremity of its wing.

After a great many fruitless attempts and changes of construction of the apparatus, which, being very fragile, broke at almost every flight of the bird, I succeeded in obtaining satisfactory results. During flight the registering lever described a kind of ellipse, but I was obliged to give up registering this figure upon a stationary glass. The motions of the wing differing at different moments of flight, the style did not pass over the same points, and I obtained a very confused tracing. I then resolved to use a glass moving horizontally at a uniform rate in order to obtain an extended figure, which I could afterward submit to a geometric correction, and thus obtained as it would be if traced on a stationary surface a figure for each instant of flight.

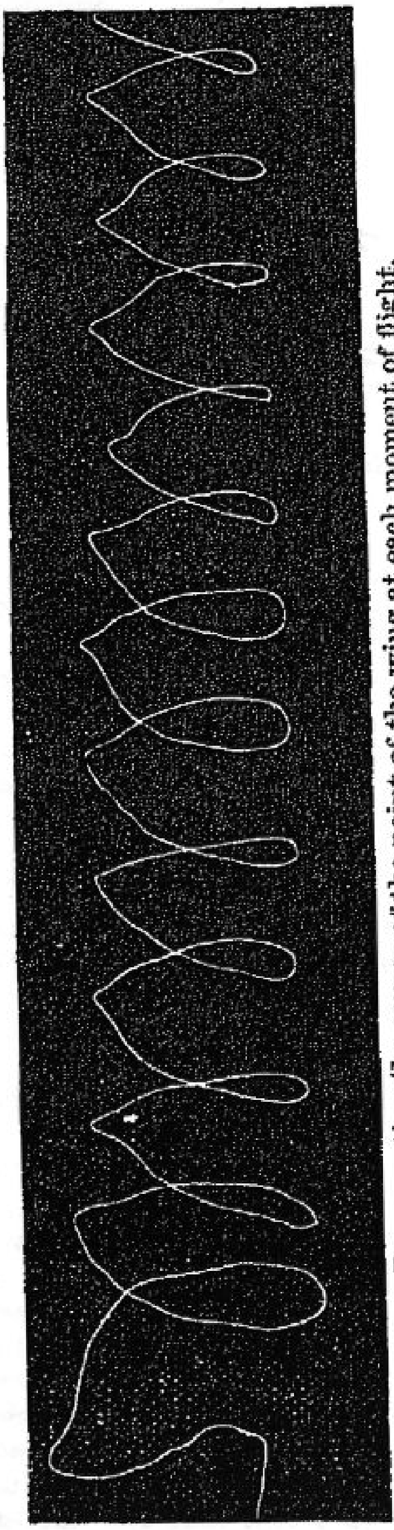


Fig. 26.

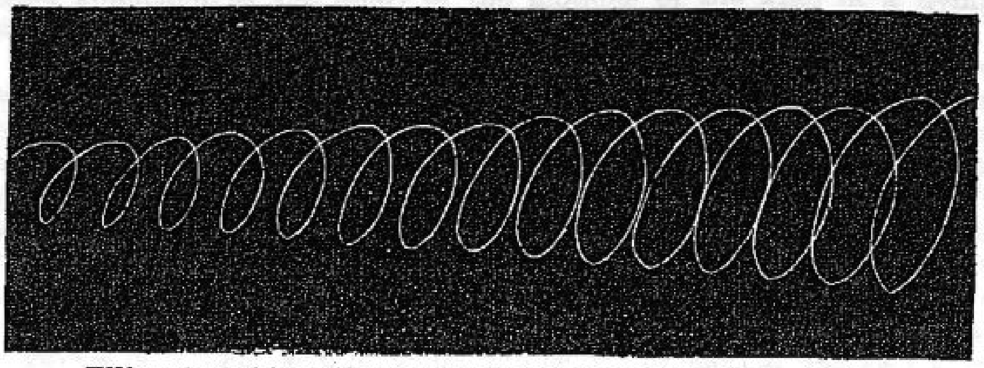
Representing the course of the point of the wing at each moment of flight.

Fig. 26 represents one of the numerous tracings which I have thus obtained. The perfect uniformity of these tracings gives me entire confidence in their correctness. To analyze the meaning of this curve it is necessary to know how the bird flies, how the apparatus is arranged, and in what direction the smoked glass moves while receiving the tracing. The observer being placed opposite the glass on the smoked side, sees it move from the right to the left; between the glass and himself is a tracing apparatus with the lever rubbing upon the smoked surface directly in front of him. The bird flying from right to left, in a plane parallel with that of the glass, carries the lever of the apparatus on his right wing, so that the respective levers of the two machines are always parallel to each other. This being known, the tracing should be read from left to right. We have seen that the tracing consists of a kind of ellipse, which the motion of the glass extends into a spiral. The movements, more extended at the beginning of flight, gradually lose a little of their amplitude, and retain a uniform character for some time.

This figure somewhat resembles that which we obtain from a Wheatstone's rod, according to the unison which traces the ellipse which its point describes upon a surface moving from right to left. Fig. 27, showing the tracing of this rod, admits the comparison of the two.

The wing of a harrier thus describes a sort of ellipse, but it is necessary to determine more exactly its shape, and to correct the error caused by the motion of the glass plate.

Fig. 27.

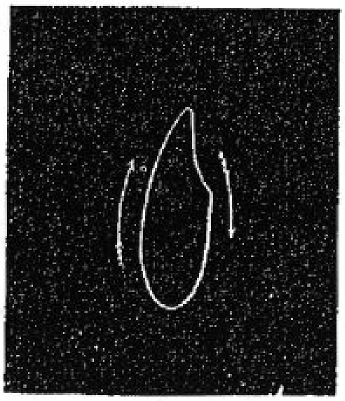


Ellipse traced by a Wheatstone's rod upon a turning cylinder.

Such a correction is impossible unless we know the elevation attained by the wing at the end of successive and equal intervals of time. This once obtained, if we trace parallel horizontal lines representing the position of the wing at each of these successive moments, these lines will cut the descending curve at points which correspond to the successive equal intervals of its course. It is clear that if these successive points of the curve have been produced at equal intervals of time, each of them, under the influence of the motion of the glass plate, will have a constant deviation toward the right, bearing a stated relation to the preceding point. The correction thus consists in carrying the second point back toward the left twice this amount, the third point three times this amount, and so on. The ascending portion of the curve should also be submitted to this correction, and similarly each part of the tracing. But it is precisely the height which the wing attains in the different ascending and descending motions of its course which we do not know; but this want can be supplied by the apparatus in the following manner:—

Since the principle of this mechanism is founded upon the transmission of two motions, perpendicular to each other, vertical and horizontal, it suffices to suppress the transmission of the horizontal motion to obtain the curve of elevation immediately; that is to say, the expression of the height of the wing at each instant of its course. For this I obstruct the tube of lateral transmission, let the bird fly, and obtain the curve of the heights of the wing at each moment.

Fig. 28.



Course in space of the extremity of the wing, reduced from the motion of the bird.

The correction being made, and Fig. 26 being selected to show the course of the point of the wing during one of its evolutions, and projected upon a stationary plane, we obtain Fig. 28.

The arrows indicate the direction in which the wing moves.

Is this the form characteristic of all birds; or is it only that of the harrier in the conditions of flight in which it has been placed?

The last supposition appears to be the most probable; we can see, even while comparing the form of the tracing at different instants of its flight while under experiment, that the ellipse is greater and more open in the first strokes of the wing than in the last. It is, however, necessary to except the second stroke of the wing, which has given me a narrower ellipse than in any other in all the experiments which I have made. I do not know to what this special form is to be attributed, but have thought it worth while to mention it on account of its constancy.

Of the rotation of the humerus and the changes of the plane in the wing during flight.—The wing of a bird, like that of an insect, must meet with a sufficient resistance from the air in its motion upward and downward to incline its flexible portion, namely, that which forms the webs and coverts. This cause does produce a change of the plane of the wing, but there is another even more powerful, for it places the wing at the outset of the depressing motion in a favourable position for the double propulsion which is produced. I refer to the pivot motion which the humerus executes around its axis at each contraction of the great pectoral. It is enough to examine the bony crest on which the large tendon of the great pectoral is inserted, and to consider that this crest is situated on the anterior edge of the humerus, to comprehend that the action of the great pectoral, whose fibres are carried backward and downward, should produce a rotary motion of the humerus around its longitudinal axis. The conformation of the humeral articulation is perfectly adapted to this motion. Finally, the existence of this rotation is rendered still more necessary by the resistance which the air presents to the back of the wing and opposes to the descent of its feathered portion. We can demonstrate the existence of this motion and measure its extent by means of the registering apparatus. But I have thought it best to defer these researches, especially as they necessitate the construction of special apparatus, which would require numerous experiments, and would produce, after all, results of very slight importance. In fact, we are enabled to deduce from the attachment of the muscles the nature of the motion which they produce, and this deduction is especially easy.

I have always sought to verify the existence of this rotary motion of the humerus, and to measure its extent, by the application of electricity to the muscles of the bird. In the experiment for measuring the static power developed by the contraction of the great pectoral muscle, previously described, I noticed that at each excitement of this muscle the humerus executed a rotary motion upon its axis. I fixed in the humerus a rod, perpendicular to its axis, and was enabled, by the angle formed by the two positions of this rod, to demonstrate that the rotation in the harrier corresponded to an angle of thirty-five or forty degrees. It seemed that the limits of this angle were fixed by the attachments of the median and great pectoral muscles. If traction be exerted upon the two antagonistic muscles of a newly-dissected bird, it will be seen that the median pectoral raises this member so that its upper face is turned somewhat backward. The action of the great pectoral changes this position of the wing completely, and carries its upper face strongly upward and even a little forward. These expressions, upward and downward, are relative to a plane cutting the bird into a dorsal and a ventral half; but this plane, doubtless, is not entirely parallel with the horizon during flight. But it is certain that the resistance of the air should give a much more pronounced deflection to the feathers during the more rapid descent of the wing.

The most difficult to measure of the influences which change the plane of the bird's wing is that which relates to the pressure of the air on the feathers. Perhaps it may not be impossible to devise an apparatus capable of measuring it, but it so varies with the variations of the velocity with which the wing is lowered, that any measurement which might be obtained would be only the expression of a particular case. It is very probable, on the contrary, that the change of plane due to the action of the pectoral muscles is a much more constant phenomenon. We can infer the action of the two motions of the bird's wing from what has been said of the mechanism of the flight of insects. It is evident that the descent of the wing will have the double effect of raising the bird and of imparting to it a horizontal motion. As to the ascent of the wing its office cannot be the same, because the imbrication of the feathers does not offer a resistant surface to the air.

Everything tends to show that the ascending wing cuts the air with its anterior edge, but, as we shall see, another phenomenon occurs which uplifts the body of the bird during the elevation of the wing; this is the transformation of the impulse which the bird has acquired during the lowering of the wing. This impulse is changed in rising, by a mechanism analogous to that which raises the toy kite.

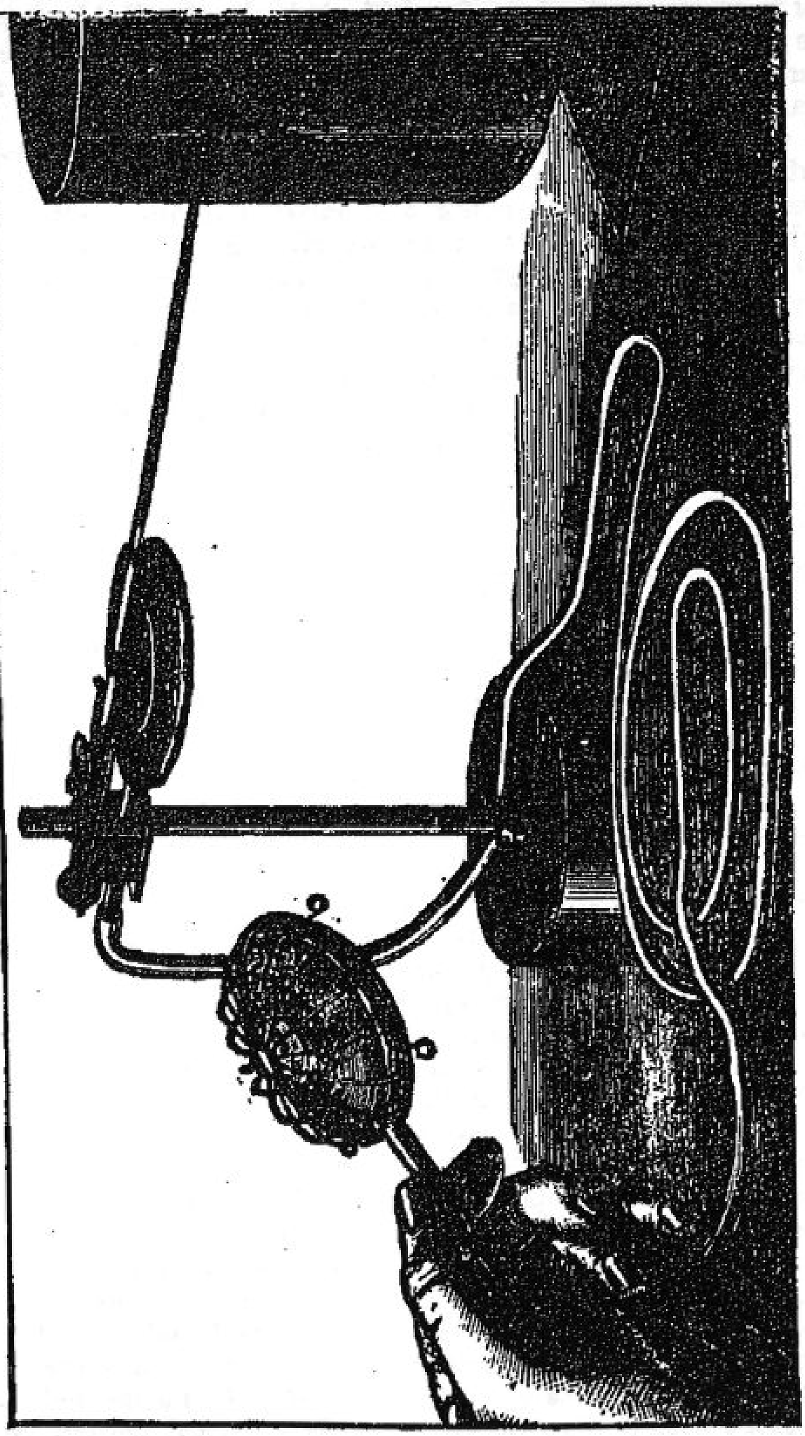
In a remarkable study of the flight of birds, M. Liais has been led, through observation and deduction, to adopt this theory, to which the experiments about to be described, I trust, will add new proofs in its favour.

Before leaving the subject it is necessary to mention the existence of certain other motions in the flight of small birds. I refer to the folding and unfolding of the wings. But the existence of these motions does not seem to be constant, and the eye cannot perceive the least trace of them during the flight of the large birds upon which I have experimented. I shall, therefore, omit the study of these motions, and of their possible effects, and restrict my conclusions on the mechanism of flight to a certain number of determinate species of birds.

The study of the motions of the wings of birds during flight necessarily includes the effect produced by each of these movements. We are tempted to deduce these effects from the nature of the motions which generate them, but it is safer to obtain the solution of this complicated problem from experiment. Two distinct effects are produced during flight: first, the bird is upheld against the force of gravity; second, it is propelled horizontally. Is the bird in the air sustained at a constant elevation, or is it rather subject to oscillations in the vertical plane? Does it not exhibit, by the intermittent effect of the strokes of its wings, a series of ascents and descents, the frequency and extent of which cannot be observed by the eye? Is not the bird also subjected to a variable velocity in its horizontal course? Does it not receive a jerking motion from the action of its wings? These questions can be solved by experiment in the following manner: Since we possess the means by which distant motions produced by pressure exerted upon a drum filled with air are made to record themselves, we must seek to connect the movements which we would study with a pressure of this kind. The oscillations which the bird executes in the vertical plane should be made to produce alternately strong or feeble pressure on the membrane of the drum, according as the bird rises or falls. The same should be done in seeking the variations of its horizontal velocity. Suppose that a flying bird carries upon its back a light metallic drum, like the one already described; that the membrane of this drum be turned upward, and that this instrument be put in communication with the registering apparatus by means of a long tube. If the membrane of the drum freely partakes of the motions of the bird it will not produce any displacement of the air in the apparatus, and the registering lever will remain motionless. But if we prevent the membrane from partaking of all the motions of the bird, if we can give it a tendency to remain at rest while the drum is moved, motion will be produced in the air with which the drum is filled, and the signals will be registered by the lever. Now, we can produce this tendency to remain at rest upon the membrane by loading it with an inert body, such as a disc of lead.

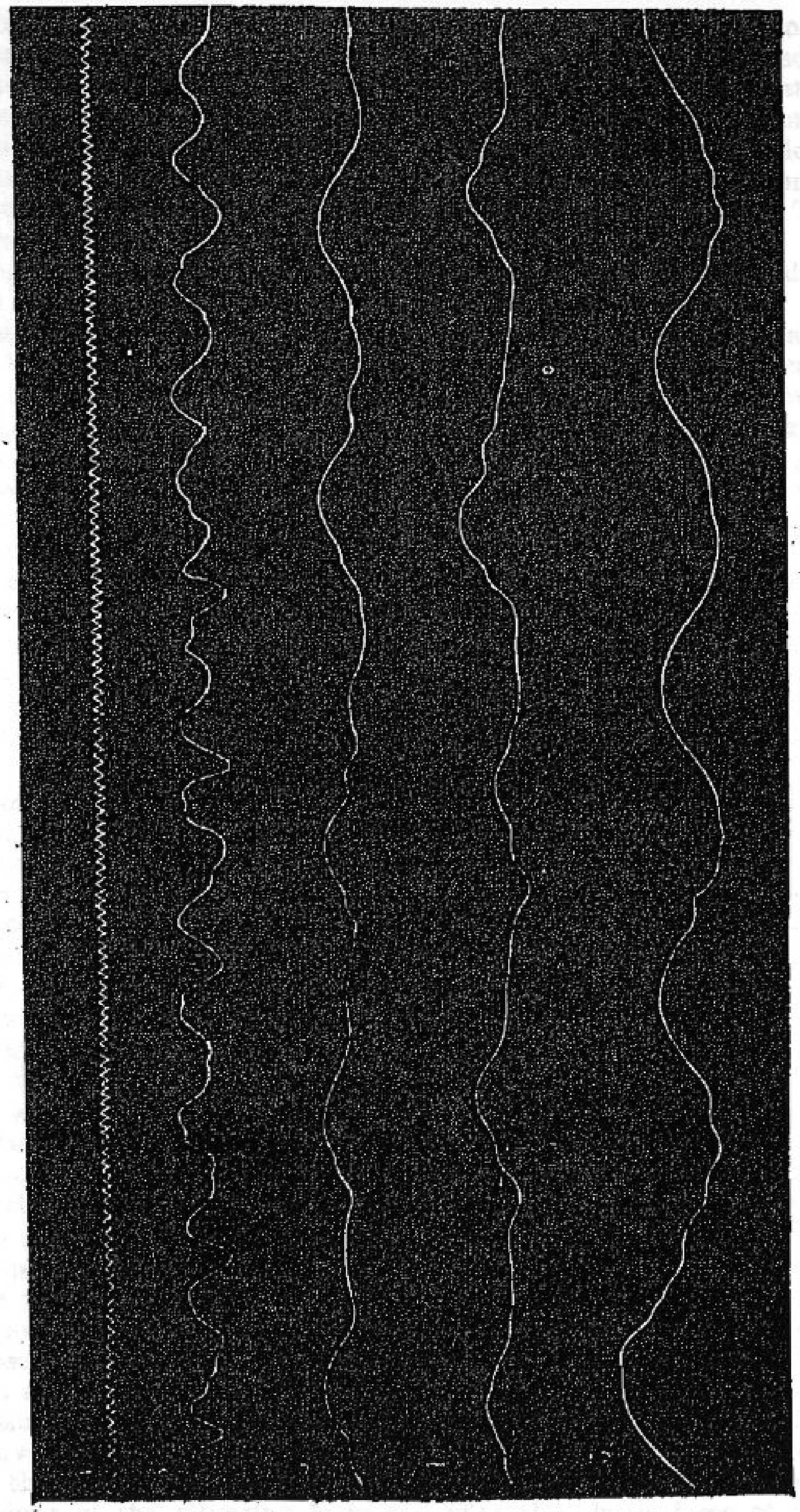
Fig. 29 shows the drum with an inert mass upon its membrane. This mass is formed of discs of lead, of which a certain number can be added or taken off, until the apparatus responds satisfactorily to the motions of vertical oscillation imparted to it. In this arrangement the movements in the horizontal plane are without influence upon the apparatus. If the drum is suddenly raised, the inert body, not participating in this elevation, depresses the membrane exactly as if the mass itself had been depressed and the drum had remained motionless. Conversely, when the drum descends, the inertia of the mass resists the motion as if it or the membrane had been raised and the drum had remained motionless. We may remark that the movement of the lever is in the same direction as that of the drum; that is to say, if the drum be raised the lever also raises itself. It may happen with an apparatus of this kind, that in the motion of the wings rubbing may be produced on the membrane of the drum which will make confusion in the signals. To avoid this I cover the upper part of the apparatus with a metallic network, as seen in Fig. 29. The drum is there represented in the hand, held by the transmitting tube connecting with the registering apparatus. If the drum is moved in the vertical plane the lever is seen to move in the same direction, at the same instant of time, and with an amplitude proportionate to the motions of the hand. If, on the contrary, we give the mass a lateral motion, no effect is produced upon the lever and no signal is made. But it may be said that an inert mass placed on an elastic membrane tends to execute vibrations peculiar to itself, and that the apparatus will transmit these vibrations of the mass of lead and the membrane which carries it independently of the oscillations of the bird. How shall we get rid of this complication? The law of vibrations teaches us that the duration of the double period of each of them varies with the weight of the vibrating body and with the elastic force of the lamina which carries it. The greater the mass and the feebler the elasticity the longer will be the period of vibration. Now, the motions which we are studying are rather frequent, some birds making eight or ten strokes of the wing per second. If we arrange it so that the period of oscillation of the mass of lead itself is much longer than that of the bird, we shall no longer be troubled by the complication of these interfering motions. By employing a heavier mass and a less tense membrane, a good trans-

Fig. 29.



Apparatus for transmitting to the registering lever all the oscillations imparted to it in a vertical plane.

Fig. 30.



Line 1. Chronographic trace of a tuning-fork vibrating 100 times a second. 2. Vertical oscillations of the wild duck during flight. 3. Oscillations of the hen-hawk. 4. Of the screech-owl. 5. Of the harrier.

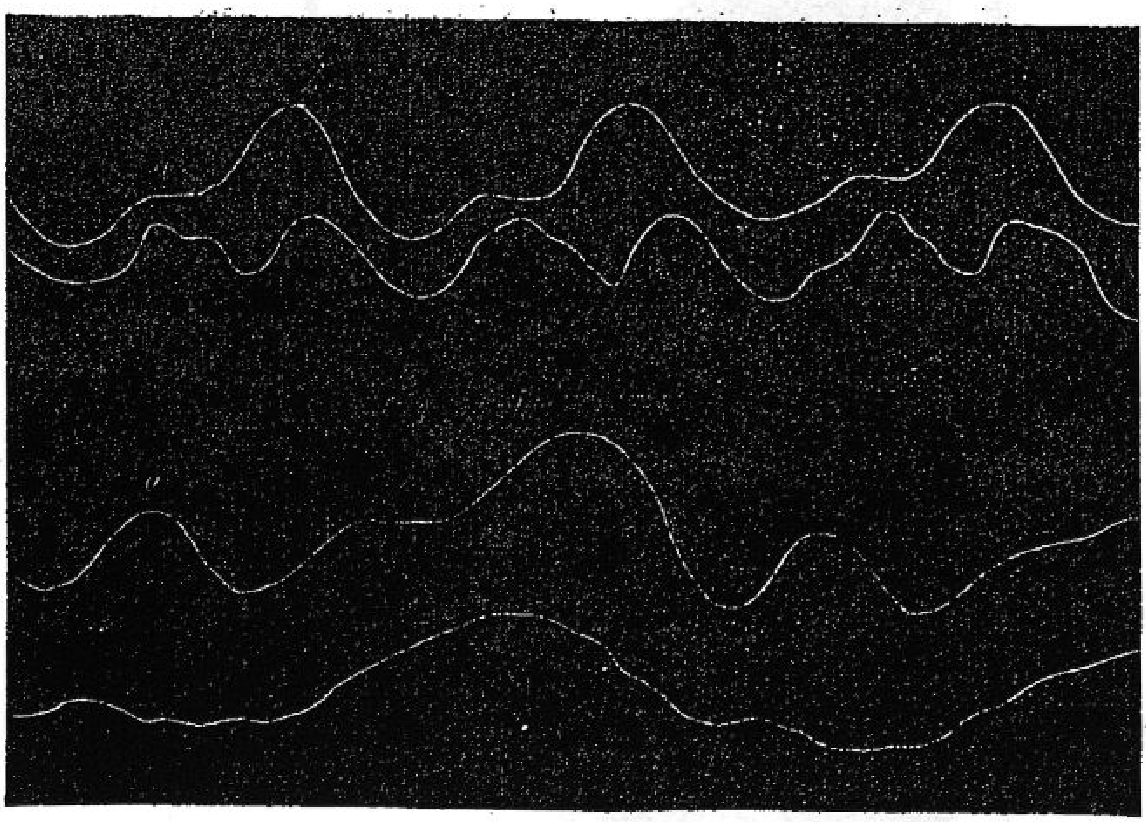
mission of motions, which are not too slow, may be obtained, for instance, such as last less than half a second. It is not necessary, either, that the instrument should be applied to the study of the oscillations of all species of birds.

But to make sure of the accuracy of the apparatus it should be verified by the method much like that which I have used to correct all my apparatus. This consists in making directly, by hand, the tracing of the motion which I have imparted to the weighted drum, and observing whether the registered motion was the same as the first.

Experiments made upon different kinds of birds, ducks, harriers, hen-hawks, and owls, have shown me that, in relation to the intensity of the oscillations in the vertical plane, very varied types of flight exist.

Fig. 30 shows tracings, furnished by different kinds of birds, upon a cylinder turning at a uniform rate, and contrasted with a tracing produced by a tuning-fork making 100 vibrations per second. These tracings enable us to estimate the absolute and relative duration of the oscillations of flight in these different birds. It follows from these figures that the frequency and amplitude of the vertical oscillations vary a good deal with the kind of bird under consideration.

Fig. 31.



In the upper half is seen superposed the muscular tracing and that of the vertical oscillations in a wild duck. Below the undulation *a*, which indicates the elevation of the wing, is seen a vertical oscillation; and another, below *b*, which indicates the lowering of the wing. In the lower portion are the same tracings obtained from a harrier; here the oscillation at *a*, which corresponds to the elevation of the wing, is less marked than in the duck.

To better comprehend the cause of these variations, let us register at the same time the vertical oscillations of the bird and the action of the muscles of its wing. If we make this double experiment upon two birds, differing in their manner of flying, such as the wild duck and the harrier, the tracings represented by Fig. 31 will be obtained.

The duck presents two energetic oscillations at each revolution of its wing; the one at *b*, at the moment when the wing relaxes, is easily understood; the other, at *a*, at the moment when the wing rises. To explain the ascension of the bird, during the time of elevation of the wing, it seems to me indispensable to call in the action of the boy's kite, previously alluded to. The bird, moving forward with acquired velocity, presents its wings to the air in an inclined position similar to that of the kite, and thus transforms its horizontal force into an ascending one.

The flight of the harrier presents the ascension which accompanies the elevation of the wing in a smaller degree. May not the cause of this difference be recognized as a smaller relative inclination of the wing toward the horizon?

Determination of the different phases of the evolution of the wing to which the vertical oscillations correspond.—The interpretation of these curves throws light at once upon the experiments made on the variations of the transformation of velocity in the bird, at different moments, during the evolution of the wing.

But, before going further, we may remark that the preceding experiment furnishes a very precious lesson in the theory of flight. In fact, if the bird excutes a series of ascents and descents, the duration of the descending period will approximately inform us of the amount of the positive work which the bird must perform to rise again to the height from which it fell, and we see that the duck, which makes nine vibrations of the wing per second, executes two vertical oscillations during each vibration, or eighteen in a second. Each oscillation is composed of a rise and fall, so that each descent of the bird cannot last more than one thirty-sixth of a second. Now, if we subtract the effect produced (as in a parachute) by the outspread wings of a bird, we find that a body which falls during one thirty-sixth of a second traverses only fifty-two millimetres. This fall repeated eighteen times a second constitutes a total rise of 9·36 centimetres, necessary to maintain the bird in the same horizontal plane during one second.

In the tracing of the harrier, the descents are less than in the wild duck, probably on account of the large surface of the wings of this bird.

Determination of the variations of the rapidity of flight.—The second question to be solved relates to the determination of the various phases of rapidity of flight. The solution can be found in the following manner: If the weighted drum be placed upon the bird's back in a vertical plane perpendicular to the direction of flight, it will be insensible to vertical oscillations, and will only indicate those of forward and backward; also, by turning the membrane of the drum forward it is clear that if the advance of the bird is accelerated, the retardation of the weight on the translation of the apparatus will produce a crowding of the air in the second drum, and an elevation of the registering lever, while a relaxation of the effort of the bird will bring about a descent of the registering lever. Experiments upon the kinds of birds previously mentioned furnish tracings analagous to those of the vertical oscillations. If it is true, as I suppose, that the vertical oscillation of the bird at the moment of raising the wing be due to the upward transformation of velocity, by obtaining, simultaneously, the tracing of the vertical oscillations and those of the variations of velocity, we shall have the means of confirming this theory. When obtaining at one time the two kinds of oscillations in the flight of a harrier, I have seen that the phase of descent of the wing resulted both in the elevation of the bird and the acceleration of its speed. This effect is the necessary consequence of the inclination of the plane of the wing at the moment of its descent, as we have previously shown in the flight of insects. As for the phase of elevation of the wing, it is proved that during the slight ascension which it produces the speed of the bird is diminished. In fact, the curve of the variations of rapidity falls as soon as the bird begins to rise. This is, then, a confirmation of the previously suggested theory of the upward transformation of the speed of birds. Thus by this mechanism the descending stroke of the wing creates the force which produces the two oscillations of the bird in the vertical plane. The downward stroke directly produces the ascent which is synchronous with it, and indirectly by creating the velocity which prepares for the second vertical oscillation.

Simultaneous tracing of the two kinds of oscillation of the bird.—Instead of representing each kind of oscillation separately, I have thought that it would be more instructive to obtain a single line which, by its curves, should represent both of the movements which the body of the bird executes in its course through space. The method which has been used to obtain the curve of the point of the wing, with some modifications, can be made to furnish a simultaneous tracing of both kinds of motion. For this both drums must be connected with the same inert mass, and placed at right angles to each other. Turning back to Fig. 23, which shows the two levers connected by tubes which transmit to the one all the motions executed by the other, when any motion is imparted to the first lever, the second lever reproduces the same motion in the same direction. Now, let us charge one of the levers with a mass of lead, and, taking the support of the apparatus in the hand, make it describe some motion in a plane perpendicular to the direction of the lever. We see that the lever No. 2 executes directly opposite movements. In fact, since the motive force which acts on the membranes of the drums is simply the inertia of the mass of lead, and since this mass is always behind the motion given to the apparatus, it is clear that if the whole be raised the mass will keep the lever down; if the whole be lowered, the mass will raise the lever; if it be carried forward, the mass will hold back the lever, &c. Now, the second lever, executing the same motions as the first, will give curves which are directly the opposite of the motion which has been given to the support of the apparatus. This being settled, now for the experiment:—For this I take the apparatus represented on the back of the harrier in Fig. 25; I remove the rod which receives the motion of the wing, and the parallelogram which transmits it to the lever. I keep only the lever connected with the two drums and the mounting which attaches it to the bird's back. I fix a

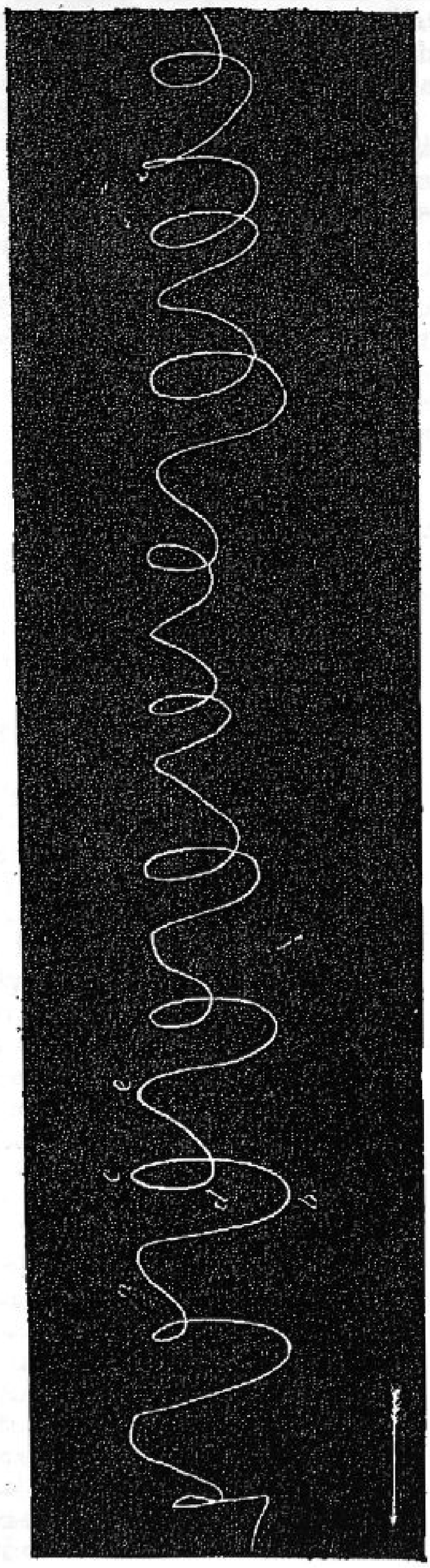


Fig. 32.

Simultaneous tracing of both kinds of oscillations executed by a harrier during flight.

mass of lead on this lever and let the animal fly. The tracing obtained is represented by Fig. 32.

The analysis of this curve is at first sight extremely difficult. I hope, however, to succeed in showing its signification. It is traced on the cylinder under the same conditions as Fig. 26, showing the different motions of the point of the wing. The glass plate moves from the right to the left; the tracing is read from left to right. The head of the bird is toward the left; this flight is in the direction of the arrow. We can divide this figure by vertical lines passing through homologous points, cutting it either at the top of the loops or at the summit of the simple curves, as represented at the points *a* and *e*. Each of these divisions encloses similar elements, although their development is unequal in different parts of the figure. For the present we shall neglect these details.

It is evident that the periodical return of similar forms corresponds to a return of the same phases in an evolution of the bird's wing. The division *ae* thus represents the different motions of the bird during an alar evolution.

Let us recollect that in the curve which we are analyzing all the motions are the reverse of those which the bird really executes. The two vertical oscillations, the great and the small, should then be represented by two downward curves. It is easy to recognize them in the great curve *abc* and the small curve *cde*. Thus the bird rises from *a* to *b*, falls from *b* to *c*, again rises from *c* to *d*, and re-descends from *d* to *e*; but these oscillations encroach on each other, producing the loop *cd*. The oscillation *cde* partly covers the first anteriorly. This is a proof that the indications of the curve are the reverse of the true motion; for, at this moment, the bird recedes, or at least relaxes its course. As the apparatus is only sensible of changes of velocity, it is clear that the tracing does not take the uniform rapidity of the bird into account, but indicates acceleration as a forward movement and retardation as a retrograde movement. This figure, then, sums up all the preceding experiments which we have made on the motions of the bird in space. It is here seen that the bird at each evolution of its wings rises and falls twice successively; that these oscillations are unequal; the larger, as we know, corresponding to the depression of the wing, the smaller its elevation. It is also seen that the ascent of the bird during the raising of the wings is accompanied by a retardation of its speed, which justifies the theory by which this ascent has been considered as made at the expense of the bird's acquired velocity. But this is not all; this curve also shows us that the motions of the bird are not the same at the beginning and end of flight. We have seen already (Fig. 20) that the first strokes are more extended than the others; we now see that at first—that is, at the left of the figure—the oscillations produced by the descent of the wing are also more extended. But theory foretold that the oscillation of the elevation of the wing being derived from the acquired speed of the bird should be very feeble at the beginning of flight when the animal has acquired but little impetus. The figure shows us that this does happen, and that at the beginning of flight the second oscillation (which forms the loop) is very insignificant.

At last, then, we are in possession of the principal facts upon which the study of the mechanical power developed by the bird during flight can be established, and we see that it is during the descent of the wing that the entire motive force which sustains and directs the bird in space is created.