Marey, Etienne-Jules. - The work of the physiological station at Paris

In : Annual report of the Board of Regents of the Smithsonian Institution (...) to july, 1894, 1896, p. 391-412

THE WORK OF THE PHYSIOLOGICAL STATION AT PARIS.[1]

By E. J. Marey,
Member of the Institute of France.

Physiology has for its domain all organized nature. It seeks to penetrate the secret of life in all beings. It is the guide of natural history, which ought not only to describe the forms of animals and of plants, but also to ascertain the kind of life and the functions peculiar to each species.

The older naturalists understood that their science had this scope; the zoologists, for example, when they described the species of animals, noted at the same time the habitat, method of locomotion, kind of food, and manner of reproduction of each.

This way of studying and teaching the natural sciences was kept up so long as people were content to observe the exterior of animals and the external manifestations of their life; but, in proportion as the anatomy of living beings was more profoundly studied, the naturalist's task became harder; for a knowledge of the conformation of the different organs awakened a desire to understand the functions of each. From this moment a division of labor became necessary. Those who applied themselves more especially to the anatomical description of organized beings were called naturalists and those who specially studied the functions of life physiologists.

If such a separation were permanent, if the two parallel sciences were not united at certain points, both would suffer. Zoology would then be only a dry catalogue of animal forms whose meaning would be unexplained, while physiology, confined to laboratories and reduced to experimentation upon mutilated animals, would teach us less how these animals live than how to make them die.

Is it not possible to combine these natural sciences without hindering the development necessary for each? I wish to show you that this can sometimes be done and that it affords us the highest intellectual satisfaction, that of comprehending the marvelous harmonies of living

[1] A lecture delivered at the College of France. Translated from Revue Scientifique, December 29, 1894, and January 8, 1895; fourth series, Vol. II, pages 802–808, and Vol. III, pages 2–12.

nature. In order to unite zoology and physiology it is necessary that these two sciences should have methods in common and should apply them under the same circumstances, which should neither be in the gallery of the zoologist nor in the laboratory of the vivisector.

During our epoch the natural sciences have made such progress as has quite transformed them. The physiologists of to-day use new methods and instruments of precision which enable them to study the phenomena of life with an exactitude formerly obtained only by physicists. This apparatus, first intended to be used in vivisection, is undergoing a gradual change and is tending to become applicable for use upon animals and to man himself while in perfect health and in the exercise of their normal functions.

On their side the zoologists, in addition to the menageries in which they bring together living animals of all kinds and all countries, have found, in the employment of the aquarium and in the establishment of maritime zoological stations, the means of observing in its natural surroundings the fauna of the sea and even that of fresh water. The moment seems to have arrived when the natural sciences may be made to profit by these two kinds of progress, and when we may direct toward a common end efforts too long divergent.

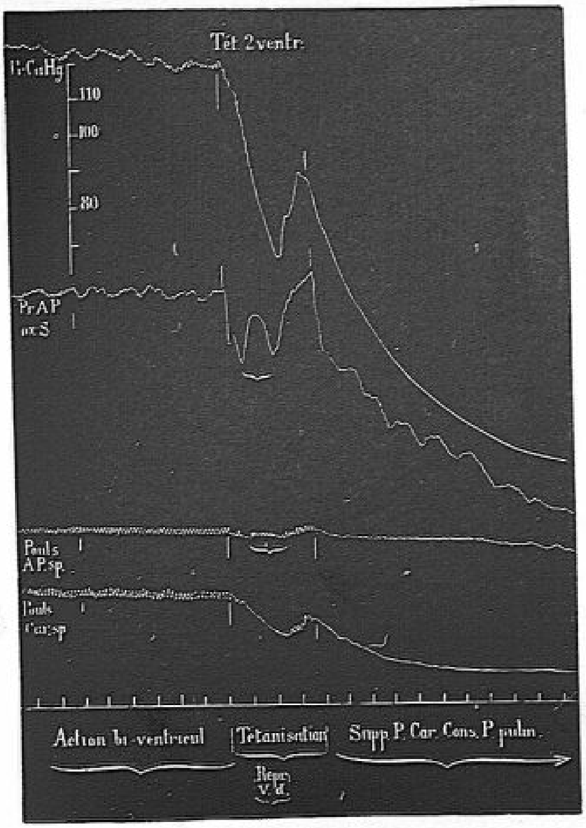
It is with this intention that the Physiological Station was established.

In order to show the resources of this institution and the developments it ought to have, permit me to first recount the evolution of the schemes of investigation for the application of which it was established.

I.

Daughter of anatomy, physiology was at first obliged to use the scalpel. It was while dissecting living animals that Asellius, Harvey, Charles Bell, and so many others made their grand discoveries. But the number of phenomena accessible to pure observation is necessarily limited, so physiologists had to borrow from the physicists their methods and their instruments in order to discover new facts. Thus the mercurial manometer was used by Magendie to measure the pressure of the blood at the different points of the vascular system; the delicate thermometers of Walferdin enabled Claude Bernard to show the unequal distribution of temperature in the organism, to recognize the effect which nerves have upon these variations of temperature, and to establish the foundations of a general theory of vasomotor nerves. M. Pasteur himself, whose discoveries have given a new impetus to physiology and medicine, would never have been able to support his doctrines by such weight of evidence had he not conceived and created new methods and appliances.

For many long years I have devoted my time to developing and perfecting physiological apparatus. Struck with the importance of movement in most of the functions of life, I wished to make it possible to



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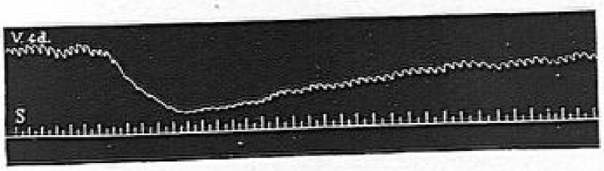

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FIG. 1.—Simultaneous tracings showing the pressure of the blood and the arterial pulsations under the action of digitaline.
FIG. 2.—Tracing showing the diminution in the volume of a finger in consequence of the contraction of its vessels.

register and measure this fugitive phenomenon, and for that purpose I had recourse to the tracing apparatus which occupies to-day an important place in our laboratories. Thus M. François-Franck, who continues with so much talent my teaching at the College of France, makes much use of the graphic method. Those of you who follow his work have often seen him examine at the same time upon the same animal, seven or eight different vital movements, registering them by tracings placed one above the other so as to make apparent the reciprocal relations of all the phenomena that occur during the course of an experiment.

Fig. 1, Pl. XLVI, taken from the beautiful memoir of M. Franck upon the action of digitalin, is an example of these multiple registrations. The five tracings shown upon this plate are, from above downward, as follows: First, that of a mercurial manometer indicating the pressure of the blood in the carotid artery; second, that of another manometer showing the variation of pressure in the pulmonary artery; third, that of a sphygmoscope giving the pulsations of the pulmonary artery; fourth, that of another giving the carotid pulse; fifth, the lower line, giving, in seconds, the time occupied by the experiment. Reference lines traced upon this sheet show the effects produced at the same moment in the four tracings by a stimulus that causes a tetanus of the heart. A simple inspection of this figure teaches us all the variations that tetanus of the heart produces in the general and in the pulmonary circulation with a precision that the most attentive observation could not attain.

In a special work[1] I have described most of the tracing instruments, paying special attention to those which do not require preliminary vivisections, but record the action of organs by their exterior manifestations. We can thus, in both man and other animals, record the pulsations of the heart and arteries, the respiratory movements of the thorax and of the abdomen, the phases in the displacement of respired air, the contractions of the muscles, with the various degrees of force which they develop, the variations of caliber occurring in small vessels, etc. Modern physiologists pay particular attention to perfecting and multiplying these apparatus already so widely applied and of a much greater range of application than had at first appeared possible.

In fact this apparatus not only records the phenomena for which it was directly invented, but permits us to ascertain indirectly other facts. Thus the myograph, invented at first for recording the movement of muscles, makes known indirectly the velocity of the transmission of force in the motor and sensitive nerves, in the columns of the spinal cord, and even in the different layers of the cortex of the brain.

For the nervous acts of organic life, such as the contraction and relaxation of vessels, of which we do not even have any conscious knowledge, physiologists also possess a veritable myograph in the graphic apparatus that records the changes of volume of organs.

[1] La Méthode graphique: Paris, G. Masson, 1885.

Many improvements have been made in this apparatus during recent years. Quite recently two pupils of M. François-Franck, MM. Hallion and Comte, have conceived a small instrument very simple and easy of application. On introducing a finger between two air-cushions connected with a graphic apparatus it is seen that this finger constantly changes its volume, swells when its vessels dilate and diminishes as they contract. Any pain felt by the subject under experiment, a simple sensation of heat or cold, any emotion, even if slight, is soon followed by notable contraction of the vessels of the finger; that is to say, by a lowering of the curve that is traced. (See fig. 2, Pl. XLVI.)

We even find that in certain maladies an excitation not perceived by the subject may give rise to a vascular contraction, which shows that the seat of production of the vascular reflex is different from that of conscious sensation.

The possibility of transmitting to considerable distances by means of air tubes the movements it is desired to record has much enlarged the field of application of the graphic method.

Thus we may in the case of a running man or a galloping horse note the succession of footfalls or the cadence of the hoofs. In a flying bird we may record the various phases of the action of its muscles, the trajectory of a point of its wing, and the reactions thus effected upon the mass of its body. But these experiments, although very carefully made, give but a partial knowledge of the complicated acts of animal locomotion. Another method, more prompt and more simple, records these movements in a much more perfect manner. This is chrono-photography.

I had the honor two years ago to make known to you the origin and developments of this method. Since then I have improved it and applied it to the study of the most varied phenomena. All these applications have been set forth in a little volume recently published.[1] It will be sufficient to say that besides the phenomena of physics and mechanics, in which chrono-photography does most valuable service, this method enables us to analyze the kind of locomotion used by most species of animals, mammals, reptiles, birds, insects, fishes, etc. It may even be used to register the movement of microscopic creatures.

Chrono-photography may therefore be considered as the most perfect form of the graphic method. It is especially important when we have to deal with very extensive or complicated movements, or, indeed, when a movement has not sufficient force to actuate the tracer of an instrument.

A record of the mechanical forces developed by animals may be obtained by other apparatus, such as dynamographs, some of which measure efforts of traction, others efforts of pressure, and these, by the way, must, like balances, be more or less strongly constructed according to the amount of force to be applied.

In order to give a complete idea of the physiological apparatus we should also cite the instruments used to measure the electric currents

[1] Le Mouvement, Paris, G. Masson, 1894.

by which nerves and muscles are stimulated, or to determine the characteristics of the electricity generated by animals. The numerous improvements introduced by M. d'Arsonval in the determination of temperatures and the measurement of the calories generated by an animal according to its height, species, and the physiological conditions in which it is placed, should be here mentioned.

All these apparatus also tend to become registers, and this makes their indications comparable with each other and permits us to assemble in a single graphic table the curves of all sorts of phenomena. All tend likewise to be applicable to man and to animals under normal conditions without disturbing in any way the functions they are intended to investigate.

The zoologist, then, as well as the experimental physiologist, may investigate in different species of animals the variation of function in an organ corresponding to its variation of form. It is here, as I have before said, that union may be effected between the two sciences, long separated from each other.

II.

Physiologists and naturalists ought to seek not only unity of method, but also a favorable field for their joint investigations. The classical physiological laboratory is not well adapted to anything but vivisections, while space, open air, and unobstructed light are indispensable for the study of living creatures. It often happens that it is difficult to secure all the conditions necessary; it is hardly possible to study the physiology of insects except in the country; marine animals must be studied at some maritime station with all the necessary instruments.

It is, however, possible to set up near cities an experimental station fulfilling the principal conditions just noted. The Physiological Station is the first establishment of this kind; it already affords many resources not elsewhere found; and is, besides, susceptible of important developments that may be made from time to time as the need for them is felt. But in bringing this establishment to its present state many difficulties were encountered which it may be useful to briefly consider.

In 1864, at the time when the graphic method of recording certain physiological phenomena seemed sufficiently developed to permit an analysis of the different kinds of movements, I attempted to use it for determining the mechanism of locomotion in different species of animals. The movement of the wings of insects was quite easy to catch, and besides, the theory of this kind of locomotion had been established by a true synthesis, using artificial apparatus, in which a motion of translation was effected by agitating mechanical wings. This first success made me think that the problem of the flight of birds, the details of which almost completely elude direct observation, might be elucidated by the same method, and that tame birds to which suitable apparatus had been fitted would, when flying in an inclosed space, record the movements of their own wings, together with the reactions which such movements produced upon their own bodies.

An artist's studio, No. 14 rue de l'Ancienne Comédie, furnished me the large room necessary for my purpose. This studio, 15 meters long by 12 wide and 8 high, was well lighted. It was easy to set up within it the workbench of a mechanic, cages for animals, and glass cases for the instruments, already so numerous, required for physiological researches. In this way, an old theater which had accommodated the Comédie Française in its early days, and was afterwards the studio in which Horace Vernet painted his great heroic pictures, became in turn a shelter for science, and was the first laboratory established by private enterprise for physiological experimentation.

Many advantages were already combined in this first establishment. They were certainly superior to those which I found later at the College of France when I entered it as professor. Much time is saved if the construction of the instruments, together with the incessant modifications of them required by this kind of experimentation, can be supervised in the same apartment in which the experiments themselves are conducted.

With carefully tamed buzzards, with pigeons, and with ducks, I succeeded in registering the movements of flight, the frequency and character of the wing strokes, the contraction of the muscles, and the reactions produced upon the body of the bird.

This study conducted me to that of the resistance of the air, which made it necessary to construct a whirling table 6 meters in diameter, in order to determine the pressure of air on different surfaces for different velocities of rotation.

This apparatus, also supplied with special registers, gives us an opportunity of analyzing the movements of walking in man, and was used in the beautiful experiments of my pupil and lamented friend, G. Carlet.

As might have been expected, the space was soon found insufficient for studying the locomotion of man. On a circular path 20 meters at most in diameter it was impossible to walk otherwise than slowly, incessantly hampered by the curve of the circle. Open roads were necessary for the study of walking and running, and horizontal or variously inclined footways were required for the determination, by means of the portable odograph, of the influences that cause variations in the cadence and length of steps. I often had to go far in order to find all the necessary conditions.

Later, attempting to determine the best means of utilizing the muscular force of man and animals, I had to compare the amount of work expended in the traction of carriages, both with rigid and slightly elastic traces, and upon different kinds of ground. In the neighborhood of the grounds of the Luxembourg there were certain avenues paved in different ways. I here experimented with carriages drawn at different velocities, following them and carrying the registering apparatus, surrounded by an importunate crowd of curious people.

At another time, wishing to ascertain the effect which gymnastic training has upon the movements of the heart and on respiration, I had to transport my apparatus to the École de Joinville, to which M. Hillairet kindly offered me access.

Finally, in order to determine the succession of the movements of the horse, I had to go to the riding schools of Paris to find the means of making the necessary experiments.

The annoyance of shifting about so continually was but slight as compared with the grave disadvantages of carrying long distances delicate instruments whose slightest derangement made the journey useless. From that time I had but one desire, that of finding a spacious ground where I might unite a workshop, a laboratory, and an experimental field. I soon thought that my wishes were about to be realized.

In 1878, the Universal Exposition had just been closed, and General Farre, then minister of war, who was interested in my experiments on the gaits of men and horses, offered to place at my disposal some ground in the Champ de Mars which was in a few months to be turned over to the war department. This was the large space where now stands the Eiffel Tower. An officer of engineers examined the place and at the end of a few weeks sent me a plan showing a perfectly level circular track 500 meters in circumference, passing through the groups of trees there planted, and touching the edges of the two lakes. At certain times of the day this track was to be given up to experiments. I yet have this plan which gave me a certain transitory joy. In a few weeks it happened that by a certain arrangement between the General Government and the city the grounds were assigned to the latter and I thought for a time that all was lost.

But the municipal council of Paris, which has given so many proofs of its interest in science, was soon to gratify my wishes beyond my hopes.

Upon the motion of its president, M. de Hérédia, the municipal council placed at my disposition a spacious ground at the Parc des Princes, and voted an annual allowance of 12,000 francs to maintain the new establishment. The General Government on its part, upon the request of M. Jules Ferry, granted the sum necessary for the construction of the buildings. Finally, to add to these resources, I transferred to the new locality the laboratory for advanced studies which I had been conducting at the College of France, as well as all the apparatus and instruments that I had made during more than twenty years.

Such was the origin of the Physiological Station, which is already known to many of you. Those who may do me the honor to visit it will not find there monumental constructions, but slight buildings which during the summer season admit of the employment of a considerable number of workers and are arranged for all sorts of studies.

I have there been able to resume, under new and quite exact conditions, my studies of the flight of birds, experimenting upon a great number of different species. By means of chrono-photography it has been possible to obtain a series of the successive phases of a wing stroke in the form of instantaneous photographs, as many as one hundred per second being recently obtained. Thus, in a wing stroke so rapid that the eye can not follow it, the apparatus shows with perfect precision more than twenty successive phases, passing from one to another by almost insensible transitions.

The gaits of the horse have been determined, not only as regards the successive beats of the feet, but in a complete manner; that is to say, by fixing the entire series of actions and reactions that are involved.

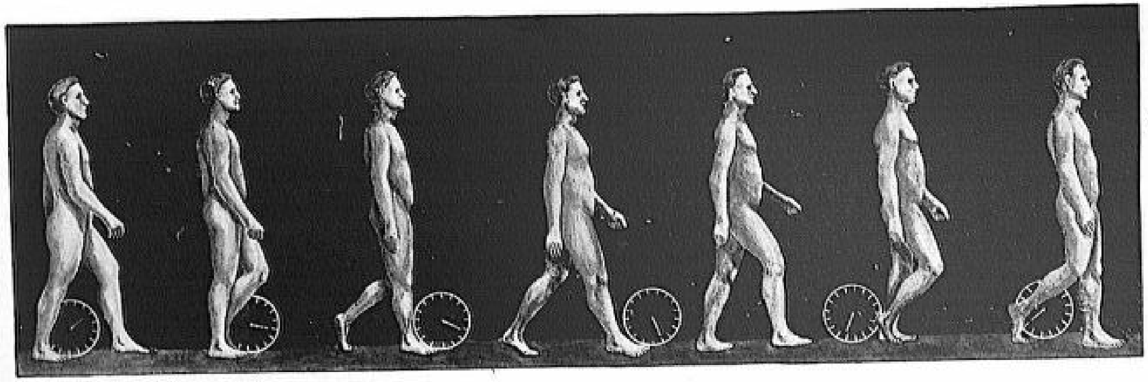
The great circular and perfectly level track permits us to analyze the walking and running paces of man as well as his various physical exercises, and to determine the conditions most favorable to the proper utilization of muscular force. These studies have been conducted with regard to their practical application, either for the amelioration of the condition of the soldier or for the improvement of the methods of physical education. In these researches I have been greatly aided by the officers of the army and by my former assistant, M. Demeny, who, up to recent years, performed his duties with much skill.

I would not speak of the experiments made at the Physiological Station on a great many physical and mechanical phenomena, such as the fall of bodies, the resistance of the air, the vibrations of strings, the movement of liquids, the measurement of forces and of work, etc., were it not that these studies are intimately connected with the physiology of movement.

In fact, in the locomotion of man and of terrestrial animals the mechanical actions of the muscles consist in displacing the center of gravity of the body, either by lifting its weight or by imparting to it a movement of translation. From these actions in various directions we can deduce the amount of work expended. In aerial locomotion the action of the muscles communicates a similar amount of movement, both to the body of the animal and to the mass of air struck by the wings. The same division occurs in different kinds of locomotion upon the ground and in the water.

The experiments already made at the Physiological Station have given the approximate value of the work expended in the different kinds of locomotion. These determinations have been checked by two different methods; on the one hand, by measuring the forces and the quantities of movement by means of registering dynamometers; on the other, by estimating the forces acting at each moment by the acceleration imparted to the mass of the body.[1] The results derived from these two sources show variations of but slight importance, that will certainly disappear when the methods of analyzing movements and forces shall be perfected.

[1] See Le Mouvement, Chapter IX.



SUCCESSIVE PHOTOGRAPHS OF A PERSON WALKING, DONE BY CHRONOPHOTOGRAPHY UPON A MOVABLE FILM.

The order is from left to right. The interval of time occurring between two successive positions may be read upon the chronometric dial whose divisions correspond to $\frac{1}{16}$ of a second. Its needle turns in a direction opposite to the motion of the hands of a watch.

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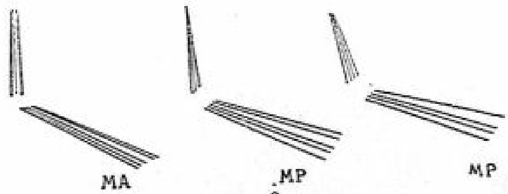

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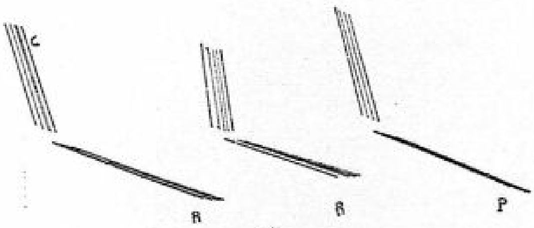

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FIG. 1.—Arrangement used to determine by chronophotography the movements of the lower jaw.
FIG. 2.—Successive positions of the lower jaw during the opening of the mouth.
FIG. 3.—Movements of the lower jaw during mastication on the incisors, MA, and on the molars, MP.
FIG. 4.—The lower jaw drawn backward, RR, and pushed forward, P.

At any rate these experiments have clearly shown that muscular forces behave in their final result like other mechanical forces.

New problems are now placed before us; let us examine them.

III.

The analysis of the movements of man and animals may be made from different points of view. It is, indeed, not sufficient to determine the external characters of the movement; the important matter is to ascertain the mechanism by which that movement is effected and to distinguish the part played by the different portions of the locomotor apparatus, muscles, articular surfaces, and osseous radii.

To adapt it for these different researches chrono-photography may be employed in different ways,[1] sometimes using a movable plate and sometimes a fixed plate.

When it is wished to record the movements as a whole, it is necessary to use chrono-photography on a movable plate, for it gives a series of entire images of the subject in action. Thus Pl. XLVII, which shows seven different attitudes of a person taking a step in walking, gives the necessary information concerning the velocity and the extent of the displacements of the body and the limbs as well as the state of contraction or relaxation of certain muscles shown in relief under the skin. But in order to be well understood these independent images should be placed in their relative positions, and this is done by means of a series of successive tracings, examples of which will shortly be given.

This laborious and delicate operation makes the analysis of movement a long process; this may, however, be shortened in certain cases. It was just because I wished to get, at a single exposure, a photographic outline of a movement that I conceived the idea of chrono-photography upon a fixed plate. With this method it is true the images of a moving man or an animal are reduced to a few brilliant points and lines, but this is generally sufficient to mark the action of the limbs in the different gaits.

It is not only in locomotion properly so called that movements occur that are of scientific interest; mastication, respiration, speech, expression of the countenance, partial movements of the limbs, hands, or feet are of no less interest.

Suppose, for example, that it is desired to ascertain the movements of the lower jaw by chrono-photography on a fixed plate.

The teeth of the lower jaw, first well wiped, are placed in one of those metallic molds full of wax, which dentists use for taking impressions. Upon this solid base there is fixed a bright metallic rod (fig. 1, Pl. XLVIII), whose angular curvature exactly follows that of the lower jaw. This rod, placed outside of the jaw, shows clearly upon a small piece of velvet that forms for it a dark background (fig. 2, Pl. XLVIII).

[1] See Le Mouvement, Chapters IV and VII.

If a series of successive photographs is taken upon a fixed plate during the act of opening or closing the mouth, the figure thus obtained gives all the positions successively occupied by the bright rod, and consequently all the displacements of the lower jaw itself. Now it will be seen that, by reason of the sliding of the condyles of the jaw in the glenoid cavities, the center of movement is found very low upon the ascending ramus near the angle (fig. 3, Pl. XLVIII).

In movements of mastication this line takes different positions according as we chew upon the incisor or upon the molar teeth. It has still other movements during speech or in displacement of the chin either forward or backward (fig. 4, Pl. XLVIII).

In these experiments chrono-photography gives us a true sketch of the movements, and as the length of the bright rod is exactly equal to that of the lower jaw its end traces out exactly the form of that part of the glenoid surface upon which the condyle slides. This experiment already shows us the necessary interdependence between the forms of organs and the forms of movements. It would be curious to follow out in a series of animal species this anatomo-physiological parallel.

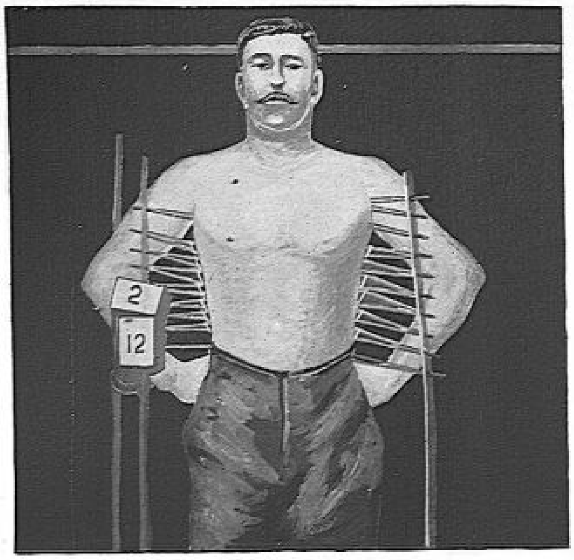
It should be noted that these experiments were made under very simple conditions and that it was not necessary to use the chrono-photographic apparatus.

In this case it was of but little importance to find the velocity and phases of movement of the lower jaw; it was only desired to determine the successive positions of the jaw at the different degrees of opening the mouth, a perfect equality in the intervals of time separating the different images being unnecessary. Besides, these experiments were made in winter, with a diffused and quite feeble light, a long exposure (about one-fourth of a second) being necessary. The procedure was as follows:

An ordinary photographic apparatus provided with a pneumatic shutter was trained upon the subject of experiment. This subject having his head firmly supported from behind so as to fix it, opened his mouth at several successive degrees of wideness, stopping an instant after each, so that a photograph might be taken. The figure thus obtained differs in no respect from that which the chrono-photographic apparatus might have given, except that the intervals separating two successive images are arbitrary.

When it is wished to determine the trajectory of a point, an ordinary photographic apparatus is also sufficient. In this case the shutter is held open during the entire movement, and if the point is brilliant and shown upon a dark background it traces its trajectory in the form of a continuous line. It is in this manner that I was able to determine the character of the movement of the atlas upon the axis, according to the trajectory made by a brilliant point fixed upon the occiput.

The movements of the ribs during respiration are determined in a similar manner. These movements are very complex because of the



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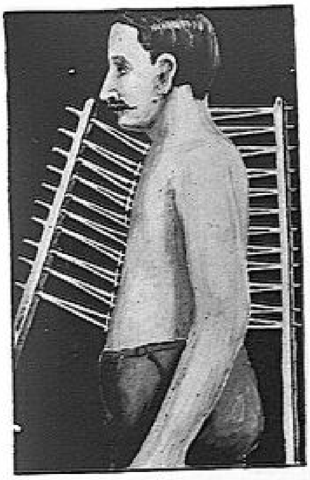

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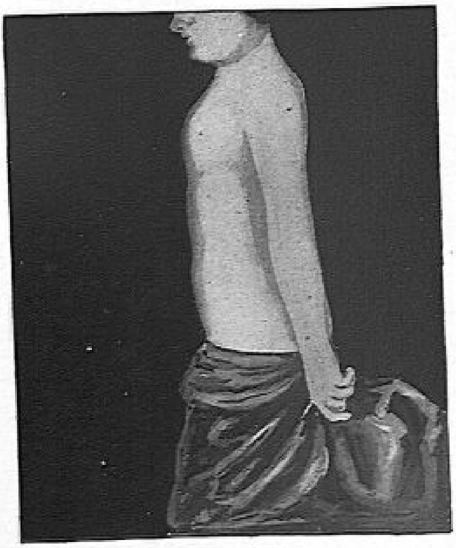

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FIG. 1.—Arrangement used to determine the trajectory made by the lateral movement of the ribs.
FIG. 2.—Arrangement used to determine the trajectory of the different parts of the anterior surface of the thorax.
FIG. 3.—Type of respiration in a woman without a corset.

curvature of the ribs, the unequal flexibility of their cartilages, and their multiple articulations both with the bodies and transverse processes of the vertebræ and with the sternum and costal cartilages. Without points of reference observation of the movements of the ribs was absolutely impossible; the nature of these displacements has therefore been heretofore determined according to certain theoretical considerations. Experimentation gives, on the contrary, very exact results.

A series of small, black rods (fig. 1, plate XLIX) presses loosely upon the walls of the chest, each resting upon a rib by one of its extremities and bearing near this point a very brilliant pearl. An ordinary photographic apparatus is turned toward the subject of experiment, who, strongly illuminated, is placed before a black background. If the exposure lasts during the entire respiratory movement we obtain fig. 1, in which each of the brilliant pearls has traced the movement of the subjacent rib. At the first glance it is seen that each rib has its own special movement.

This is not the place to analyze the mechanism of this movement. I may say, however, that among the divers opinions which have been held by authors that of Chabry accords the best with the results of the experiments.

If it is required to know the nature of the movement of the anterior wall of the chest, we apply upon that wall the series of rods and obtain the trajectory of each of the points of that wall from the epigastrium to the superior part of the sternum. We then see that the epigastrium has but a slight upward movement, while the sternum moves obliquely upward and forward.

Similar researches repeated upon different species of animals would doubtless give interesting results as to the comparative physiology of respiration considered from a mechanical point of view.

Another very important study is that of respiratory types. It has been supposed that women breathe especially by means of the upper part of the thorax (superior costal type), and men by the diaphragm (abdominal type). Hutchinson has shown these two types by tracing on a wall the silhouette of a man and that of a woman in the two extreme states of inspiration and expiration. But the hand has not time to trace the profile of the thorax and of the abdomen during the few instants in which inspiration reaches its extreme limits; besides, if the subject stops his respiratory movements a moment, nothing proves that the thorax and the abdomen keep the respective positions which they had in normal respiration.

Photography replaces with advantage the tracing of the silhouettes. An ordinary apparatus provided with a pneumatic shutter is trained upon the subject. A picture is taken during inspiration, another during expiration, and we thus obtain a double contour for all parts of the trunk displaced. We thus show that in a woman without a corset respiration occurs as it does in a man—that is to say, that the thorax and the abdomen both take part in it.

Not only does chrono-photography afford a means of studying the kinematics of movements, it also furnishes an indication of the work performed in certain muscular acts.

A distinguished engineer, M. Frémont, has just made at the physiological station a study of the work performed in hammering iron upon an anvil. On a movable film M. Frémont took the series of attitudes assumed by the blacksmith in the successive movements given to the hammer.[1] By chrono-photography on a fixed plate there was shown the trajectory of the hammer and its successive positions at definite instants, the intervals between which were measured by a chronographic dial.

By such a figure we can estimate the forces acting upon the mass of the hammer at each instant by means of the acceleration given to that mass. We also obtain a measure of the work, since it shows the velocity of the hammer at the moment it is about to strike the iron.

In most physiological acts forces and work should be measured by another method—that is to say, by the dynamograph. I have described under the name of dynamographs certain instruments that show the forces of pressure or traction applied to them by means of a stylus that traces the curve of variations of these forces.[2] I have also shown how the results obtained from these instruments may be synchronized with those obtained from chrono-photography, so that we may know at each phase of a footfall, for example, what force the foot exerts upon the soil in a vertical direction. If a traction dynamograph indicates the force developed by the same act, we may by combining these different data obtain all the information necessary to understand the mechanism of locomotion in different animals.

The number of experiments necessary may seem to you excessive, but the invention of methods, the care required to secure their precision, their first application to the analysis of movements and to the measure of forces constituted the most arduous part of the task. Already our records accumulate; the field of possible comparisons enlarges every day, and at the same time the interest in anatomo-physiological comparisons increases. I wish to give you some examples of these comparisons.

IV.

If we wish to study locomotion in different types of mammals so as to elucidate the variety of their forms by the special movements characteristic of each we must first ascertain all the anatomical and physiological elements necessary for such a comparison.

Drawings and plates will not suffice as anatomical material. It is necessary to use natural organs, skeletons, articulations, preparations, or casts of muscles. Now, thanks to the ready assistance of various

[1] These studies will shortly be published by M. Frémont.

[2] See Le Mouvement, page 142.

anatomists, I have been able to collect a portion of the specimens necessary for the study of certain common species of mammals.

I have also been able to collect, in the physiological department, chrcno-photographs and sketches of the movement of the same species.

Plates L and LI show a series of thirty-six photographs of a dog taken while making a step. For such a slow gait the number of pictures is greater than necessary, for a more rapid one all would be required. In the present case it will be sufficient to compare every four pictures to follow the phases of the movement. As the chronometric dial is used to measure the intervals of time between two successive attitudes, so the space passed over by the animal is measured by a mark fixed in the ground. This mark consists of a small white rod set up on the course. At the commencement of the experiment the dog is behind the rod, at the end he has passed it. The actual distance traversed is read off upon a metric scale.

Plate LII shows a sheep walking. The number of photographs is reduced to nine, and the time between the first and last, as shown by the chronometric dial, is twenty-five sixtieths of a second. The progression of the animal is estimated by his approach to the chronometer.

To obtain these pictures a dark background is used. This is not necessary when a movable film is employed; then a light background will answer, as shown in plate LIII, which represents a galloping horse. As this was quite a long series, it was not possible within the space of a column of text to show the entire set of movements; about half are shown from the moment when the horse leaves the ground to that when the two diagonally opposite feet are on the ground.

It is sometimes desirable to take pictures of an animal from different aspects; chrono photography upon a movable plate is easily adapted to such work. It is possible to follow in any gait of an animal the series of movements of his limbs.

But the dimensions of the pictures obtained by printing from the original negatives are too small to be directly utilized. Arrangements must be made to more easily examine and measure the displacements made by the different portions of the same limb during the step of any gait. For this we proceed as follows:

We commence by enlarging by means of a projection apparatus each of the little images which we wish to compare. Plate LIV shows one of these enlargements. It is limited to five diameters, so as to accommodate the page, but it is better to nearly double those dimensions.

If we wish, for example, to study the movement of one of the hind legs we trace the contours of that leg on a sheet of transparent paper, using as guides in applying this paper to the picture the line of the ground and a fixed point upon that line. Having traced the first image of the series we proceed to the second, placing the transparent paper exactly over the guides, and thus obtain (fig.1) the series of successive positions occupied by the hind leg of a horse while walking, from the first raising of the foot to its final return to the ground.

In this representation of attitudes the leg is supposed to occupy successive planes superposed upon each other, so that the last image covers partially those which precede it. The contours covered by the following image are represented by dotted lines.

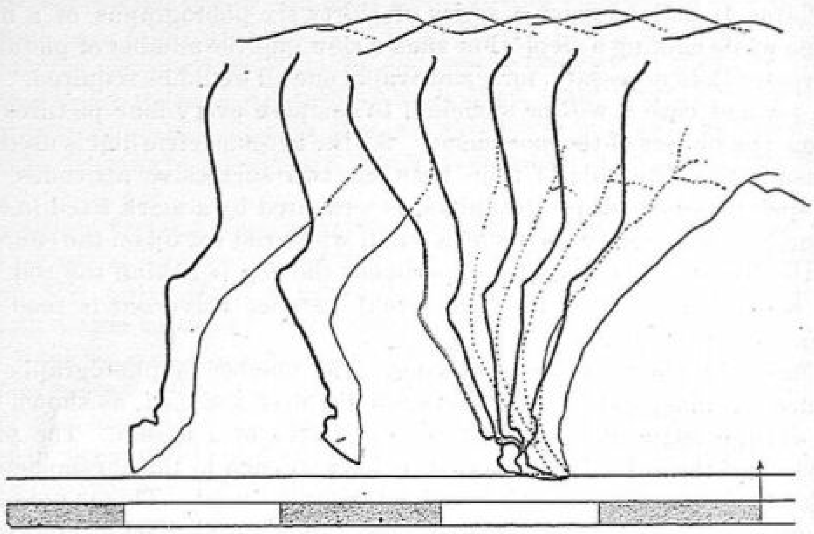


FIG. 1.—Attitudes and successive positions of the right hind leg of a horse during a step in walking.

Repeating this same operation for another species of animal, we obtain (fig. 2) the series of attitudes of the hind leg of a dog walking, and (fig. 3) a similar series for a sheep. In these last two figures an attempt has been made to represent by dotted lines the contours of the

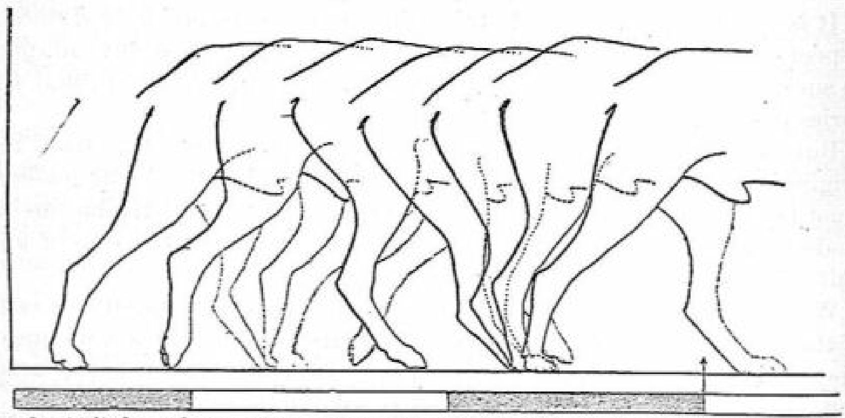
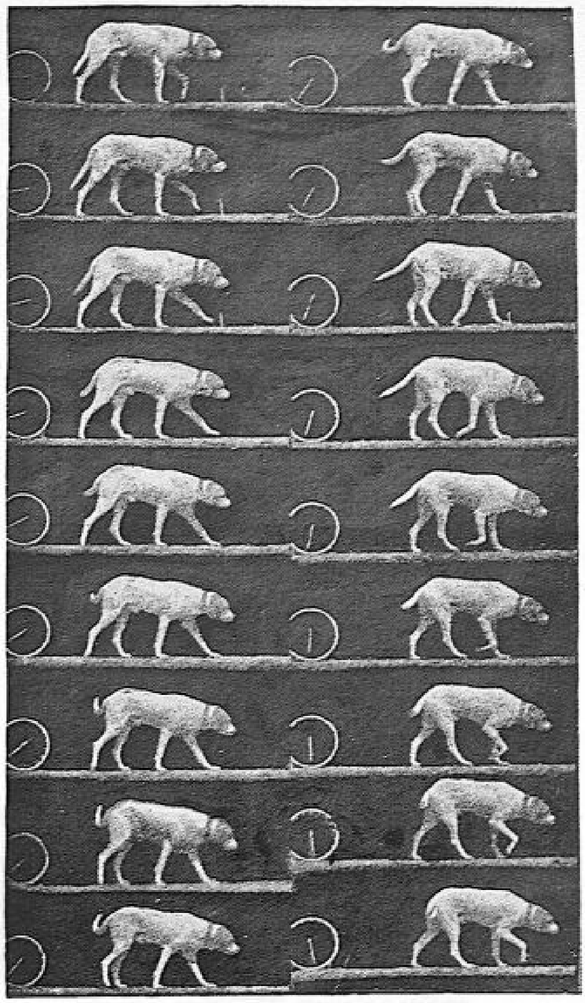


FIG. 2.—Attitudes and successive positions of the right hind leg of a dog during a step in walking. The dotted lines show the positions of the left hind leg.

left hind leg, so as to show the alternation of movements between the two legs.

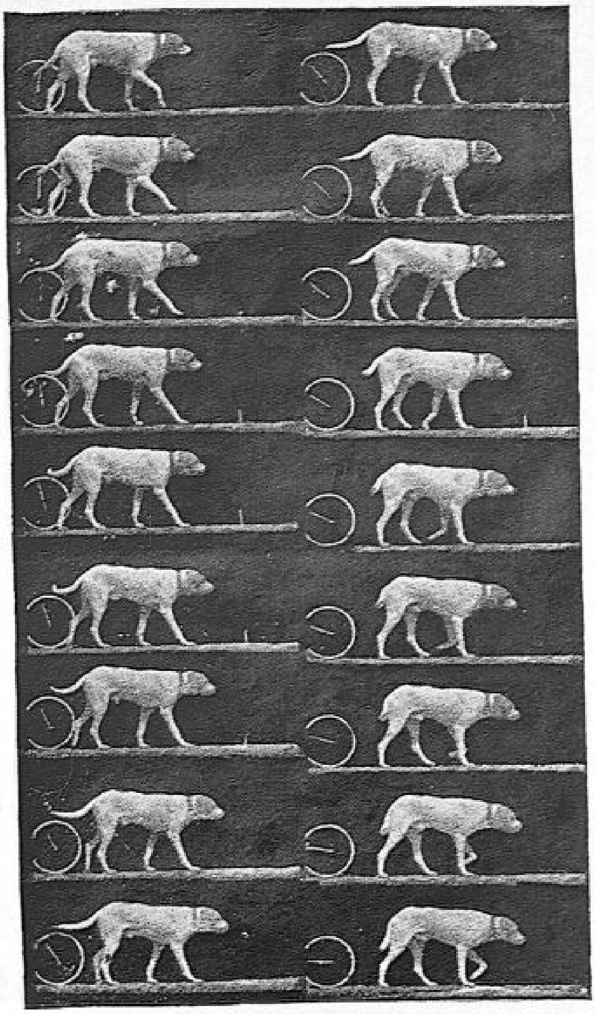
At the first glance it is seen that in different species of animals the length of the step in relation to the height is very different. This inequality is much greater in rapid gaits and in certain animals of small stature.



DOG WALKING; 36 PHOTOGRAPHS TAKEN DURING A SINGLE STEP.

The first is at the upper left-hand corner, 1st column, Plate L: the last at the lower right-hand corner, 4th column, Plate LI. Total duration of the step, [illegible] of a second.

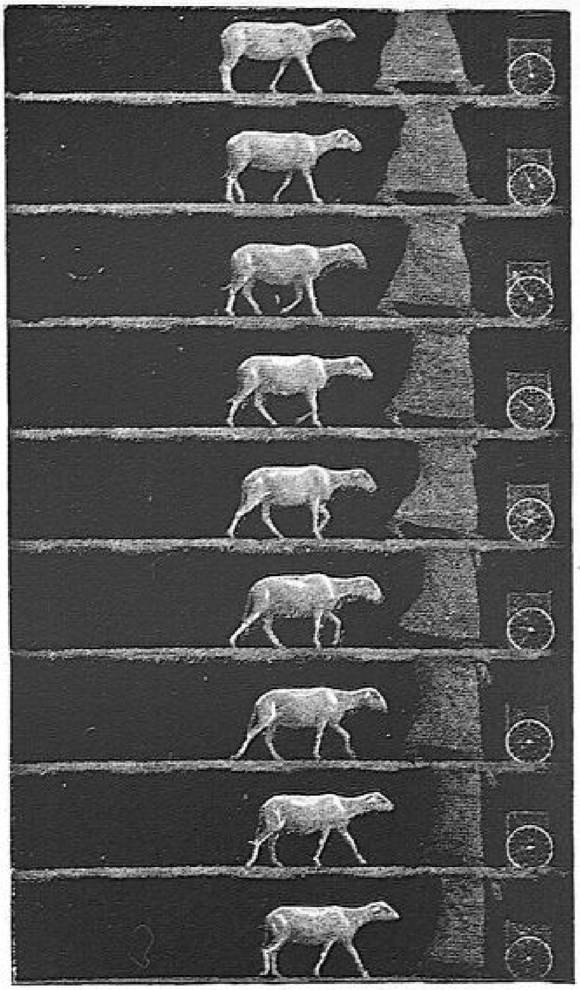
(See also Plate LI.)



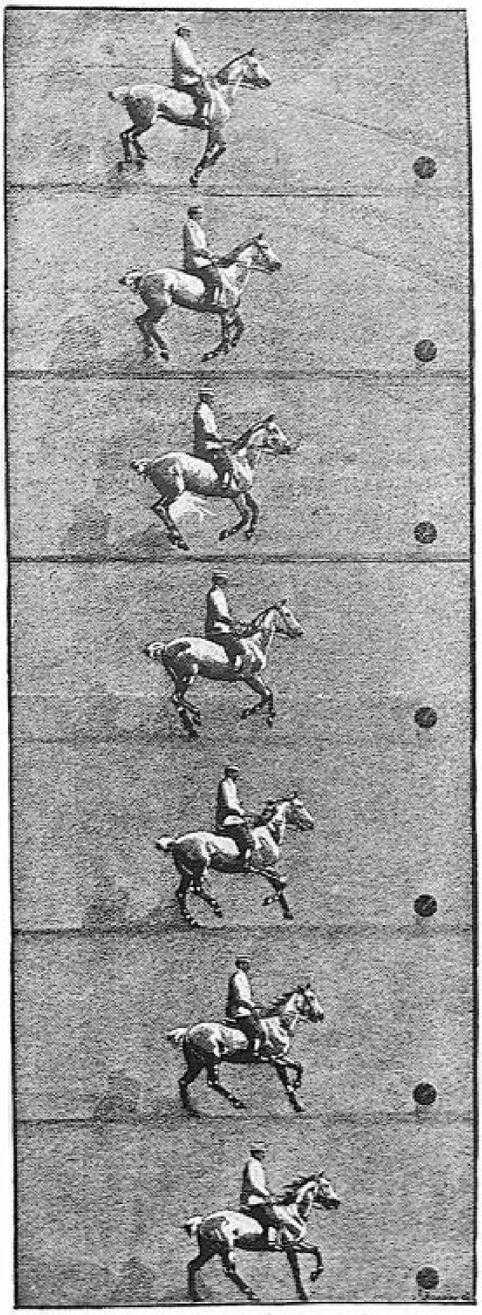
DOG WALKING; 36 PHOTOGRAPHS TAKEN DURING A SINGLE STEP.

The first is at the upper left-hand corner, 1st column, Plate L: the last at the lower right-hand corner, 4th column, Plate LI. Total duration of the step, [illegible] of a second.

(See also Plate L.)



SHEEP WALKING.



HORSE GALLOPING.
The figures follow from above downward.

PHOTOGRAPH OF A GALLOPING HORSE ENLARGED TO 5 DIAMETERS.
The picture enlarged is the last one of Plate LIII.

But I can not enter into detail regarding these special comparative studies which show analogies and differences between various species of animals in accordance with their anatomical structure.

The absolute fidelity of these chrono-photographic outlines allows us to estimate the value of certain analyses of the movements of limbs made by different authors. The most exact are certainly those of Vincent and Goiffon. We can not too greatly admire the sagacity of these authors who have given so faithful a representation of the movements of the horse in slow gaits.

Finally, these same pictures permit us to determine the action of certain muscles at different phases of the gaits. By starting from the successive attitudes of the limbs we reach the physiological mechanism of the movements under consideration.

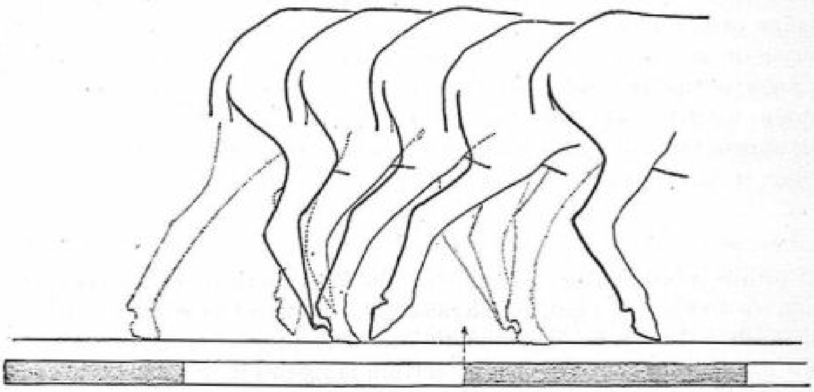


FIG. 3.—Attitudes and successive positions of the right hind leg of a sheep during a step in walking. The dotted lines show the positions of the left hind leg.

The sagacity of physiologists has often been tried by these obscure questions. Maissiat[1] more than anyone else has attempted to elucidate the part played by muscles in the walk of man. He has done in this respect all that can be done by subtle observation joined to a profound knowledge of the laws of mechanics.

But in questions of this kind the keenest intelligence can not attain the precise results that are obtained by an exact method. Already, by using localized electrization, Duchenne, of Boulogne, has shown in man the special functions of the individual muscles; he has shown that in the various acts of locomotion the muscles are associated by groups, synergistic or antagonistic, and that each movement is a resultant of these combined forces.

More powerful methods allow us to now elucidate these questions.

Upon the photographs of an animal in motion we may mark the origin and insertion of muscles which we have learned from our anatomical specimens, and, joining these insertions by one or more marks,

[1] Jacques Maissiat, Études de physique animale, 4°, Paris, 1843.

we will have for each attitude of a limb the length shown by each muscle visible in the figure under consideration. We can easily follow upon the series of photographs the phases of the shortening or lengthening of these muscles—that is to say, their contraction or their relaxation. We may finally trace the curve or change of length of these different muscles according to time, and compare the relations which exist between certain muscular acts and the reactions imparted to the body of the animal.

As soon as we know the action of the different muscles during the different phases of movement of an animal, we shall have the greater part of the data necessary for understanding the mechanism of locomotion. Now, this knowledge can not be acquired by simple observation, for the most sustained attention concentrated on the action of a single muscle, can with difficulty catch the phases of activity and of repose even for the slowest gait. How, then, can we hope to catch the action of all the muscles of the limbs at all phases of a rapid gait?

Such is the general plan for the study of comparative locomotion which I have just undertaken. This long task is as yet but little advanced, but the results which it promises are worth all the efforts which it will cost.

V.

Certain minds value science only for its practical application. To such we may recall what the Physiological Station has already done and show what it may be expected to do. The physician may seek there new means for the diagnosis of certain maladies and for investigating the effects of their treatment; the soldier may study there the proper regulation of marching so as to diminish fatigue and use to greater advantage the bodily forces; the educator of youth may learn how to logically direct gymnastic exercises; the artist, how to represent more truthfully the scenes that he wishes to depict; the agriculturist, how to use to the best advantage the strength of animals; the artisan, how to more quickly acquire the skill necessary for his professional labors. It seems that the utilitarian side of physiology has up to the present time been the best appreciated.

But science has also other functions; it gives a lofty satisfaction to the mind by causing us to comprehend the marvelous harmonies of nature. The astronomer who knows how to calculate the movement of the stars, to measure their distance, estimate their masses, and even determine their chemical composition, must have a more lively intellectual pleasure than the ordinary contemplator of the starry vault. There is no doubt that zoology and physiology, mutually elucidating each other, give us a grander conception of the animal kingdom by showing its action in all its beauty.

I imagine that this evolution of the natural sciences will be effected, as may be said, of itself, by the patient and methodical collection of anatomical facts and experimental determinations. And since we are considering here only the comparative physiology of animal locomotion, I believe that it is easy to point out the successive stages which ought to lead to this result.

First, the animal forms should be grouped according to the type of motion peculiar to them, so as to bring into notice their general anatomico-physiological relations. This we have now begun to do, and it is already evident that many of these relations depend upon ordinary laws of mechanics. These relate to muscles, bones, and articular surfaces. As regards this I can only summarize here what I have given elsewhere with more detail.[1]

The relation existing between the form and the functions of muscles is as follows: The extent of the movement of a muscle is in proportion to the length of its red fibers; its force is proportional to the cross-section of such fibers; the work it can perform is proportional to its weight.

These relations, the first of which was established by Borelli, can easily be verified upon the muscles of a single animal. They explain also why, in two different species, homologous muscles have different anatomical characters; it is because the functions of the muscles differ in the two species.

It will be seen that in order to carry further the anatomico-physiological relation it will be necessary to determine with great precision the functions of each muscle and the peculiarities of its movements; it is precisely for that purpose that the experiments have been undertaken which I have cited above.

The form and length of the bones correspond to that of the muscles attached to them, and to which they seem subordinated, as is shown by the beautiful experiments of Fick; the configuration of the articulations shows the character of the movements which they permit.

Let us consider, for example, the form of the head of the humerus in different animals. We see that it has a spherical curvature in man, monkeys, and lemurs, in which animals movements in every direction are allowed; that it is cylindrical in ruminants and pachyderms whose anterior limbs move backward and forward, parallel to the axis of the body; elliptical in birds whose wings move with unequal amplitude in two directions perpendicular to each other. It is impossible not to see that there is, between the form of the articular surfaces and the movements, a necessary relation which permits us, when we know the characteristics of the movement, to predict what will be those of the organ, and vice versa.

A long habit of comparing with each other the skeletons of different animals enabled Cuvier to recognize among the different bones of an animal certain relationships which he called the subordination of characters. A bone of a certain form implied the existence of certain

[1] La Machine Animale, Chapter VIII.

characteristics in the other pieces of the skeleton. Our great naturalist could therefore, to repeat an expression that has become classical, restore from a single bone the entire skeleton of the animal to which that bone belonged.

Without the long practice of a Cuvier, we may, by taking for our guide anatomico-physiological relations, arrive at determinations of a similar kind which may seem astonishing to those who do not know the theory by which they are reached.

I have shown that it is sufficient to see the wing of a bird, or even the bones of the forearm of that wing, to deduce the dimensions of the sternum.[1] These relations have not, as far as I am aware, been indicated by anatomists. They are as follows: Birds with small wings have the sternum long and narrow; those with the large wings have that bone broad and short. This relation is easy to verify on the skeletons of birds in zoological collections. The considerations which led me to predict this are as follows:

In watching the flight of birds it is seen that large-winged species have wing beats of but slight extent. This is because the large surface of their wings finds a strong resistance in the air. Species that have but little wing surface have, on the contrary, wing beats of great amplitude in order by motor work and by the length of the path described to make amends for the feeble resistance. Having such dissimilar movements, these two kinds of birds ought to have corresponding differences in the great pectoral muscles that lower the wings. In the first these muscles are large and short; in the second, long and slender. But the sternum, in the lateral fossæ of which these muscles are inserted, must correspond in its form to that of the muscles themselves. It must therefore be broad and short in the first type of birds, long and narrow in the second. All sorts of intermediate forms exist between these two extremes.

A comparison of the skeletons of birds shows that it is really so. Still, gallinaceous birds seem to offer an exception to the rule; they have a sternum too short for the small surface of their wings. But in these species the great length of the coracoid bones really prolongs the sternum, so that the exception to the general rule is only apparent.

The same kind of relations led me to predict, from the conformation of the muscles of the calf, a curious peculiarity of the skeleton of the negro. Comparing the calves of the negro with those of the white man it is seen that in the first the gastrocnemii are much longer and more slender, which allows us to conclude that the muscles have less force but more range of motion in the black race. Now, to get the same results of work expended in walking, it is necessary that the muscles should act upon a longer lever; or, to state it otherwise, that the distance should be greater between the end of the calcaneum and the center of movement in the ankle joint. Measurements show that this predic-

[1] La Machine Animale, Chapter VIII.

tion is correct; the difference in the length of the calcaneum in the two races is enormous, the ratio being as 7 is to 5.

The constant examination of the physiological relations existing between the form of the locomotor organs and the type of locomotion in the different species of animals is the directing idea of the studies that are pursued at the Physiological Station. There is no doubt that every advance in our knowledge of the movements of locomotion will bring out more clearly the perfect harmony that exists between an organ and its function.

VI.

I have tried to show by examples the happy effect of a union between comparative anatomy and physiology. Anatomy alone may reveal certain unexplained relations between organs—the law of the subordination of characters is of this nature—but the law of harmony between organs and their functions is deduced from acquaintance with the physiological activities of each part of the body; it does not content itself with simply stating the fact, but explains it, and thus completely satisfies the mind.

This is not yet all. Naturalists have always sought to ascertain how the conformity between an organ and its functions is actually brought about. From this research originated the doctrine of final causes which has, in our days, been replaced by more satisfactory hypotheses tending to show that the different types of animals have been evolved during the progress of ages by the action of forces effecting a closer and closer adaptation to the varying conditions in which they are placed. This is the doctrine of transformism or evolution.

But how shall we explain, in its turn, this evolution by the action of natural forces? Certain zoologists, like Buffon and Lamarck, admit that exterior influences may, in a more or less direct way, induce modifications of organs; others, such as Darwin and Wallace, hold that certain variations are transmitted by heredity when their effect is such as to better adapt the beings that possess them for living in the conditions in which they are placed, and to better fit them to resist agencies that cause their destruction.

Twenty years ago, in discussing these two hypotheses,[1] I ventured to hope that experimentation might decide this question, or at least assign an equitable part to the different factors of evolution. The eminent surgeon, J. Guérin, struck at seeing, after luxations, a tendency to the formation of a new joint with cartilages, synovial membrane, and ligaments, said "Function makes the organ." This aphorism expresses the ideas of Lamarck and Buffon; certain pathological cases amount, indeed, to actual experiments, and show that, in a living being, mechanical forces may bring about an adaptation of organs resulting in a change in their functions.

[1] La Machine Animale, page 105.

Guided by certain theories it occurred to me that the muscular system might also be modified and the form of a muscle changed by altering the range of its movements. The result, as we shall see, has confirmed my anticipations.

Let us take up again the well-marked example of the unequal length of the gastrocnemii muscles in the white man and in the negro. If the white man, as we have said, has the shorter calf, it is on account of the shortness of his calcaneum. Suppose that the length of the calcaneum in an animal is diminished. If the muscle adapts itself to the new conditions of work it ought to diminish in length.

The rabbit is well adapted for such an experiment. It has a very long calcaneum, and consequently the extensor muscles of the foot have very long, red fibers. I resected in a rabbit a third of the length of the calcaneum, and placed the limb operated upon in a plaster cast until the bone was entirely united. The animal was then set free in a large yard, where soon it was running about with as much agility as its companions. At the end of a year the rabbit was killed and it was seen that upon the side operated upon the muscles had become modified in accordance with the theory. The red fibers were reduced to about a third of their length and replaced by tendon. A comparison of the sound limb with that operated upon showed this change in a striking manner.

I made an experiment which was the converse of this by an operation upon a kid. In this species only the ungual extremity of the foot strikes the ground, and the calcaneum, always raised, moves but slightly in walking. The resection of this bone had, therefore, but little effect either upon the mode of locomotion of the animal or upon the character of its muscles.

Finally M. W. Roux has given numerous examples of the modifications of the muscles of man after partial anchyloses which reduced, more or less, the range of movements. He has shown in a great number of autopsies a diminution in the length of the red fibers and their replacement by tendon. This diminution in length was always proportional to the reduction which had occurred in the range of movement.

The adaptations of muscles to mechanical conditions experimentally created by mutilations is then well established. It is more than probable that similar adaptations may be obtained in the length of the muscles of animals by placing them in conditions where they would be forced to make movements more extensive than those of their normal life, by obliging them, for example, to leap or climb to get their food. I will shortly cite some facts of this kind.

But even if it is shown that in an individual the muscles and the skeleton become adapted to conditions of work, this would not be sufficient to explain transformism. It is, in fact, necessary, in order to cause a variation of species, that the modification acquired by individuals should be transmitted to their descendants by heredity.

Now, except in certain rare cases, the effects of the mutilation of peripheral organs are not transmitted to the offspring. But it is not the same with lesions that affect the nervous system. This fact has been well established by the experiments of Brown-Sequard. In guinea pigs this eminent physiologist saw curious deformations of the limbs and exophthalmia produced as a consequence of nervous lesions; and these modifications may be transmitted hereditarily throughout a long series of generations. It seems that in such cases the traumatism has affected function at its very origin; that is to say, in the organ placed at the head of the physiological hierarchy.

There is, indeed, an evident subordination among the different parts of the organism; the nervous system conceives acts and directs them to be carried out; the muscles perform these acts; the bones and the articulations bear the strains. May we not suppose that some new exterior circumstances excite in an unaccustomed manner the nervous system of an animal so that new conditions bring about new acts and consequently lead to a modification of organs? The modifications thus produced would be transmissible by heredity as in the experiments of Brown-Sequard. We might thus explain the transformation of animals during the lapse of ages: The variations of the environment create new needs and excite to new acts, affecting first the nervous system, which gradually modifies the organs subordinate to it.

Thus in the course of the past two centuries the breed of race horses has diverged markedly from its primitive form. The excitation to more rapid and more energetic muscular action is the cause of the modifications revealed by comparative anatomy, which are in great part hereditarily transmitted.

Jonathan Franklin states that kangaroos bred in captivity, having no longer as in their natural habitat to bound over the tall grass, begin to use their fore limbs for walking and running, while they lose in part the robust character of their tails and the power of their hind legs. M. Tegetmeier[1] states that rabbits, although imported into Australia in quite recent times, have already shown notable modifications, and have acquired by climbing trees habits which they did not have in the country of their origin. These facts and other similar ones should be rigorously investigated. The physiological and anatomical modifications of all such cases should be determined with precision, so as to ascertain if they correspond. If these modifications are real and their hereditary transmission is well established the theory of evolution will be experimentally demonstrated.

You see how many questions present themselves and how vast is the experimental field in which the Physiological Station may be used. I hope that I may have inspired you with a desire to seek a solution to all these problems. The task is long and difficult, but it is not beyond the scope of the experimental methods at our disposal.

[1] In Land and Water, London, 1892.

As for myself, I am no longer at an age when great projects are possible. It is my desire to associate in my enterprise those who may have the time and the necessary force to continue it. For this reason I ask you to make use of the resources of the Physiological Station. You will find there means of study applicable to the most varied subjects and sometimes even pecuniary subsidies, too often wanting to workers.

Nothing conduces more to the development of science than the association in the same work of men whose knowledge and aptitudes differ. Physicists, machinists, anatomists, and physiologists mutually enlighten and supplement each other. The animal organism will offer to them a valuable field of study, for in its physical and mechanical phenomena it gives simple and admirable solutions of an infinity of problems.

This idea that different branches of knowledge should be brought together is not a new one; it has been considered in the organization of our great establishments for superior instruction, but the combination is not made in an effective manner; physicists, chemists, and mathematicians work near each other, but they do not work together. And this results from the very necessities of teaching, which, in order to secure clearness of exposition and good methods, must necessarily present each branch of science as isolated from the others and sufficient unto itself.

The fusion of different sciences can not be effected at this time except in matters of research; this promises important discoveries, but we must not ask of it the material for regular teaching. The Physiological Station is simply an establishment for original research, where I invite you to unite your efforts and your learning for the resolution of the problems that I have just concisely placed before you. If you respond to my appeal, each of you, I am sure, will find it to his profit.

As for myself, I shall owe you the gratification for which I am most ambitious, that of having been useful.