

animal were found at the famous "Bone-cabin" Quarry, on the Medicine Bow River, and it was at once appreciated that it was almost the largest fossil reptile found up to date. Its hind limbs each had a length of six feet while its skull must have been very small in comparison; when standing up it had a height of fourteen feet. By using the bones of several individuals, and through the pecuniary assistance of Mr. Andrew Carnegie, and the efforts of Marsh, Dr. Holland and Dr. Wortman, a plaster cast of the skeleton of this great land reptile—which measured over 84½ feet in length—is now on exhibition in the Gallery of Reptiles in the London Museum of Natural History, while the original from which the cast was made forms a part of the collection of the Carnegie Museum at Pittsburgh.

Finally, Mr. Gilmore has made a life-restoration of *Thescelosaurus neglectus*, a new dinosaur which for twenty-three years remained in the original packing-

boxes at the United States National Museum. No wonder he named it *neglectus*! The late Mr. J. B. Hatcher collected the specimen in 1889, in Converse County, Wyoming, and he never knew that the material represented an entirely new form of these long-extinct reptiles. This species had in life a length of about 12 feet, and from the admirable restoration shown in Fig. 7 it was evidently an animal possessed of some considerable physical strength and great agility. Everything in the model indicates that it was a terrestrial species that could get rapidly over the ground—either by running or by considerable leaps. While standing or assuming other attitudes, its balance must have been well sustained by means of its long tail, which had a length equaling that of the rest of the body.

Thescelosaurus was evidently one of the larger herbivorous dinosaurs—its teeth indicating this, also its feet, which, as I say, were formed for terrestrial locomotion. Doubtless it lived upon the leaves of certain

plants of the time and upon similar foods, and was quite devoid of any carnivorous habits. In nature, *Triceratops* was one of its contemporaries in the Cretaceous geological period, not to say hundreds of other vertebrated animals of nearly every possible description. In his model, Mr. Gilmore has doubtless presented this new dinosaur in an attitude which it frequently assumed in life; indeed, the pose is most life-like and spirited, and it requires but little mental effort to picture to one's mind how *Thescelosaurus neglectus* appeared in the flesh.

It would be a difficult matter to overestimate the value of these models to science, and, fortunately, the well-equipped and painstaking palaeontologist who is the author of them is, as I write these lines, most industriously engaged in making still others, giving us forms of animal life that existed on this planet, in some instances, several millions of years ago—long before man had come into being at all.

Physiological Importance of Phase Boundaries—II*

A Consideration of the Physical and Chemical Systems Concerned in Living Cells

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I REFERRED previously to the electrical change in excitable tissues and its relation to the cell membrane. It was, I believe, first pointed out by Ostwald and confirmed by many subsequent investigators, that in order that a membrane may be impermeable to a salt it is not a necessary condition that it shall be impermeable to both the ions into which this salt is electrolytically dissociated. If impermeable to one only of these ions, the other, diffusible, ion cannot pass out beyond the point at which the osmotic pressure due to its kinetic energy balances the electrostatic attraction of the oppositely charged ion, which is imprisoned. There is a Helmholtz double layer formed at the membrane, the outside having a charge of the sign of the diffusible ions, the inside that of the other ions. Now, suppose that we lead off from two places on the surface of a cell having a membrane with such properties to some instrument capable of detecting differences of electrical potential. It will be clear that we shall obtain no indication of the presence of the electrical charge, because the two points are equipotential, and we cannot get at the interior of the cell without destroying its structure. But if excitation means increased permeability, the double layer will disappear at an excited spot owing to indiscriminate mixing of both kinds of ions, and we are then practically leading off from the interior of the cell, that is, from the internal component of the double layer, while the unexcited spot is still led off from the outer component. The two contacts are no longer equipotential. Since we find experimentally that a point at rest is electrically positive to an excited one, the outer must be positive or the membrane is permeable to certain cations, impermeable to the corresponding anions. Any action on the cell such as would make the membrane permeable, injury, certain chemical agents, and so on, would have the same effect as the state of excitation. If we may assume the possibility of degrees of permeability, the state of inhibition might be produced by decrease of permeability of the membrane of a cell, which was previously in a state of excitation owing to some influence inherent in the cell itself or coming from the outside. This manner of accounting for the electromotive changes in cells is practically the same as that given by Bernstein.

It will be found of interest to apply to secretory cells the facts to which I have directed your attention. If we suppose that the setting into play of such cells is associated with the production of some osmotically active substance, together with abolition of the state of semi-permeability of the membrane covering the ends of the cells in relation with the lumen of the alveolus of the gland, it is plain that water would be taken up from the lymph spaces and capillaries and escape to the duct, carrying with it the secretory products of the cells. This process would be continuous so long as osmotically active substances were formed. Such a process has been shown by Lepeshkin to occur in plants, and we have also evidence of increased permeability during secretory activity in the gland cells of animals. From what has been said previously, it is evident that electrical differences would show themselves between the permeable and semi-permeable ends of such cells, as has been found to be the case.

* Opening address by the president of the physiological section of the British Association for the Advancement of Science at the Manchester meeting.

As a modifiable structure, we see the importance of such a membrane as that described if it takes part in the formation of the synapse between neurones. The manifold possibilities of allowing passage to states of excitation or inhibition and of being affected by drugs will be obvious without further elaboration on my part.

Enough has already been said, I think, to show the innumerable ways in which phenomena at phase boundaries intervene in physiological events. Indeed, there are very few of these, if any, in which some component or other is not controlled by the action of surfaces of contact. But there is one especially important case to which I may be allowed to devote a few words in conclusion. I refer to the contractile process of muscle. It has become clear, chiefly through the work of Fletcher, Hopkins, and A. V. Hill, that what is usually called muscular contraction consists of two parts. Starting from the resting muscle, we find that it must have a store of potential energy, since we can make it do work when stimulated. After being used in this way, the store must be replenished, since energy cannot be obtained from nothing. This restoration process is effected by an independent oxidation reaction, in which carbohydrate is burnt up with the setting free of energy which is made use of to restore the muscle to its original state. Confining our attention for the moment to the initial, contractile stage, the essential fact is the production of a certain amount of energy of tension, which can either be used for the performance of external work or be allowed to become degraded to heat in the muscle itself. It was Blix who first propounded the view that the amount of this energy of tension is related to the magnitude of certain surfaces in the muscle fibers. But the fact was demonstrated in a systematic and quantitative manner by A. V. Hill. He showed, in fact, that the amount of energy set free in the contractile process is directly related to the length of muscle fibers during the development of the state of tension. In other words, the process is a surface phenomenon, not one of volume, and is directly proportional to the area of certain surfaces arranged longitudinally in the muscle. This same relationship has been shown by Patterson and Starling to hold for the ventricular contraction of the mammalian heart and by Kosawa for that of the cold-blooded vertebrate. It appears that all the phenomena connected with the output of blood by the heart can be satisfactorily explained by the hypothesis that the energy of the contraction is regulated by the length of the ventricular fibers during the period of development of the contractile stress. The degree of filling at the moment of contraction is thus the determining factor.

That surface tension itself may be responsible for the energy given off in muscular contraction was first suggested by Fitzgerald in 1878, and it seems, from calculations made, that changes at the contact surface of the fibrillæ with the sarcoplasm may be capable of affording a sufficient amount. The difficulties in deciding the question are great, but, in addition to the facts mentioned, there is other interesting evidence at hand. It has been shown, by Gad and Heymans, by Bernstein and others, that the contractile stress produced by a stimulus has a negative temperature coefficient. Within the limits of temperature between which the muscle can be regarded as normal, this stress is the greater the lower the temperature. The same statement was

shown by Weizsäcker (working with A. V. Hill) to hold for the heat developed in the contractile stage. Now, of all the forms of energy possibly concerned, that associated with phase boundaries is the only one with a negative temperature coefficient. Another aspect of this relation to temperature is the well-known increase of the tonus of smooth muscle with fall in temperature.

It is tempting to bring into relation with the change in surface tension the production of lactic acid. In fact, this idea was put into a definite statement by Haber and Klemensievich in 1909 in a frequently quoted paper on the forces present at phase boundaries. The production of acid is stated to alter the electrical forces at this situation. This electrical charge involves a change of surface tension, and it is this change of surface tension which brings about the mechanical deformation of the muscle. Mines also has brought forward good evidence that the production of lactic acid is responsible for the change of tension. As to how the lactic acid is set free, and of what nature the system of high potential present in muscle may be, we require much more information. The absence of evolution of carbon dioxide when oxygen is not present shows that no oxidation takes place in the development of tension. There are other difficulties also in supposing that this system present in resting muscle is of a chemical nature. If the energy afforded by the oxidation of carbohydrate in the recovery stage is utilized for the formation of another chemical system with high energy content, the theory of coupled reactions indicates that there must be some component common to both systems. It is difficult to see what component of the muscle system could satisfy the conditions required. On the whole, some kind of system of a more physical nature seems the most probable. If it be correct that the oxidation of substances other than carbohydrate, fat, for example, can afford the chemical energy for muscular contraction, as appears from the results of metabolism experiments, a further difficulty arises in respect to a reaction. But the question still awaits investigation.

On the whole, I think that we may conclude that more study of the phenomena at phase boundaries will throw light on many problems still obscure. It would probably not be going too far to say that the peculiarities of the phenomena called "vital" are due to the fact that they are manifestations of interchange of energy between the phases of heterogeneous systems. It was Clerk Maxwell who compared the transactions of the material universe to mercantile operations in which so much credit is transferred from one place to another, energy being the representative of credit. There are many indications that it is just in this process of change of energy from one form to another that special degrees of activity are to be observed. Such, for example, are the electrical phenomena seen in the oxidation of phosphorus or benzaldehyde, and it appears that, in the photo-chemical system of the green plant, radiant energy is caught, on the way, as it were, to its degradation to heat, and utilized for chemical work. In a somewhat similar way, it might be said that money in the process of transfer is more readily diverted, although perhaps not always to such good purpose as in the chloroplast. Again, just as in commerce money that is unemployed is of no value, so it is in physiology. Life is incessant change or transfer of energy, and a system in statical equilibrium is dead.