The Function of Hormones in regulating Metabolism.¹

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IT has long been known that a variety of substances which are generally regarded as chemically neutral are powerful stimulants of vital activity if used in very minute proportions but potent lethal agents if allowed to operate in larger amounts. Few botanists are unaware of the destructive effect that is exercised on plant tissues by the common anaesthetic chloroform and of the use that is made nowadays of hydrocarbons, such as toluene and naphthalene, as 'sterilizing' agents; the acceleration of the flowering processes in plants and of the ripening of fruits by means of ether vapour may also be cited as familiar cases of stimulative action: we have been led to study the effects produced by such neutral substances in the hope of arriving at an explanation of their phenomenal activity. In a recent communication to the Royal Society we have described and discussed experiments made with *Prunus Laurocerasus* in which leaves of this shrub were exposed to a variety of vapours and solutions in presence of Guignard's alkaline picrate paper; this test affords a means of detecting minute quantities of hydrogen cyanide, the yellow paper becoming orange and ultimately brick-red under the reducing influence exerted by this compound.² When a substance enters the leaf and conditions hydrolysis of the cyanophoric glucoside *Prulaurasin* ($\text{PhCH}(\text{CN})\cdot\text{O}\cdot\text{C}_6\text{H}_{11}\text{O}_5$), which the leaf contains, the intrusion is indicated by an escape of hydrogen cyanide. As the change that is initiated by the entering substance is cumulative, for reasons that will be apparent later on, a minute proportion of substance produces a relatively large effect; the test, therefore, becomes one of extraordinary delicacy.

The title of our communication³ may be referred to as an indication, in our opinion, that the inquiry is one in which many issues are to be considered.

¹ Studies in Enzyme Action XIV; for XIII, see Roy. Soc. Proc., B., lxxxii, 1910, pp. 349-67.

² Cp. A. C. Chapman, *The Analyst*, 1910, with reference to limitations, pp. 35, 269.

³ The Origin of Osmotic Effects. III. The Function of Hormones in stimulating Enzymic Change in relation to Narcosis and the Phenomena of Degenerative and Regenerative Change in Living Structures. Roy. Soc. Proc., B., lxxxii, 1910, pp. 588-602.

It is obvious that the leaf, like the seed, must be provided with a protective mechanism preventing both escape and entry of all but a very limited number of substances. The invaluable series of observations made by Adrian J. Brown¹ with blue barley, *Hordeum vulgare*, var. *caerulescens*, have shown that the grain is surrounded with a membrane of extreme tenuity, which is penetrable by but few mineral substances and also not by sugars, &c.; our observations show that the leaf is protected in a precisely similar manner. The protection is obviously afforded by what is perhaps best termed a *differential septum*, the term semipermeable membrane being far too narrow and misleading as an indication of the functional significance of the membrane. As it appeared to be desirable to give a special name to the class of substances that pass through differential septa such as are met with in the barley grain and laurel leaf, exciting activity within the cells when they have thus gained an entry, we have proposed that the term *Hormone*—given by Starling to certain excitants of functional activity in the animal organism (including carbon dioxide)—should be applied to all such substances. The hormones as a class are substances which have but slight attraction for water and may therefore be spoken of as '*anhydrophilic*'; hydrophilic substances generally fail to penetrate septa which are selective to the degree manifest in cereal grains and the laurel leaf. We believe this criterion to be one of special importance.

In all our experiments freshly-picked leaves were either exposed to the vapour of the substance to be tried in corked tubes or nearly immersed in solutions. The tests were made both at room temperatures and at 37° with leaves picked at different periods throughout last year (1910). Young leaves picked in the spring responded far more rapidly to stimulation than older leaves collected in the late summer and autumn.

As in the case of the laurel leaf, the substances found to be inactive were: *weak* solutions of mineral acids, caustic soda and most metallic salts; the active salts were mercuric chloride (not nitrate nor sulphate), cadmium iodide (not chloride), sodium and potassium fluoride. Iodine, carbon dioxide and hydrogen sulphide act slowly, ammonia very rapidly.

Acids of the acetic series were found to be effective in the order observed by Loeb and others, activity being most marked in the case of the least soluble acids of highest molecular weight.

The same may be said of the alcohols of the methylic series. Lactic, benzoic, picric and salicylic acids act slowly, oxalic, tartaric and citric acids are inert.

Volatile hydrocarbons, especially benzene and toluene, carbon bisulphide, chloroform, ethers and ethereal salts, aldehydes, acetone, camphor, piperidine and phenols are all very active excitants; paraldehyde in aqueous solution is also very active.

¹ Annals of Botany, vol. xxi, 1907, p. 790; Roy. Soc. Proc., B., lxxxix, 1909, p. 82.

Not only does the colour change when the leaf is exposed to these various substances but the leaf becomes flaccid and the amount of reducing sugar in it is largely increased.

Mirande, in a recent communication to the French Academy,¹ has given a long list of organic substances of various classes which will penetrate into the leaf but has been unable to draw any definite conclusion as to the existence of a relationship between structure and activity. In our opinion, the difference is not one of structure, except in so far as structure determines the degree of affinity of the substance to water and its solubility relationships.

The picture that we have formed of the mode in which hormones gain an entry involves the conception that the surfaces of the intermolecular spaces in the differential septa are coated with a protective sheath of molecules of 'hydrone', OH_2 —the fundamental molecule of water.

Anhydrophilic substances are able to escape the gauntlet and pass through almost without hindrance, whilst those to which the molecules cling are unable to run the blockade, because the hydrone molecules attached to them are so much attracted by and attractive of those attached to the passages in the septum, so much under the influence of the water in which they are dissolved, perhaps also too heavily laden with hydrone and therefore too big to get through, although not too big in themselves.

The hypothesis on which this conclusion is based has been developed in a communication made by one of us to the Royal Society² and also in two articles in 'Science Progress', Nos. 11 and 12, January and April, 1909. The chief contention, on which stress is laid, is that the unit molecule OH_2 is eminently unsaturated and active; consequently that water itself is probably a mixture of complex molecules formed by the union of hydrone molecules in various proportions—perhaps in twos, threes, fours and fives—this mixture being saturated with hydrone in proportions which must be supposed to vary with the temperature; hence, perhaps, the increase in the rate of change in aqueous solutions as the temperature rises. Foreign molecules, when dissolved in water, are supposed to have the effect of interfering with the formation of the various polyhydrones, the consequence being that solutions are richer than water in hydrone the larger the proportion of the solute: the attraction which the hydrone molecules have for each other is supposed to condition the so-called osmotic pressure effects.

The main effect produced by hormones when they gain entry into the living cell is the stimulation of enzymic activity. In our communication to the Royal Society we have pointed out that it is to be supposed that they exercise a determining influence in regulating metabolism in plants as well as in animals; as the section dealing very briefly with their influence on

¹ Comptes rend., t. cli, 1910, p. 481.

² Roy. Soc. Proc., B., lxxxi, 1908, p. 80.

plants was omitted from the communication we may be allowed to reproduce it verbally as presented to the Royal Society:—

‘It is the common practice among gardeners in the afternoon, after watering the plants in a glass house, to spray the leaves more or less heavily with water and then to close the house. During the daytime, while regenerative changes prevail, the proportion of diffusible hormones in circulation must be relatively small and water will have little tendency to pass in through the leaf surfaces; as the light diminishes, degenerative changes set in and gradually increase in intensity—these undoubtedly give rise to carbon dioxide and other hormones which serve to induce the entry of water at the leaf surface. The development of perfume by flowering plants, &c., in the evening, is clearly an external manifestation of the beginning of the degradation process; flowering, in fact, marks the onset of the period when degenerative processes begin to prevail and the accumulated stores of material are set in circulation to develop the reproductive organs and seed. The perfume itself must exercise a stimulative influence on the plant in which it is produced.

‘Attention has been directed to the effects produced by sterilizing soils more or less completely through recent work done in the Rothamsted laboratory by Russell and others. Partially sterilized soils are more rapidly oxidizable than unsterilized and the fertility of a soil is greatly increased by partial sterilization. These results are attributed with reason to the destruction of protozoa, which normally fatten on the Bacteria and prevent these latter from determining the gradual break-down of organic matters in the soil into the materials which serve as plant food. The nitrifying Bacteria are killed off but other Bacteria survive and these tend to produce ammonia among other things—so that partially sterilized soils are rich both in carbon dioxide and ammonia in comparison with the unsterilized. We are inclined to believe that these two factors are of prime importance in facilitating plant growth by affording the stimuli required to determine the degenerative changes involved in the translocation of nutritive materials.

‘Mr. Pickering has shown that, in soils which have been more or less effectually sterilized by heating, the germination of seeds takes place much less rapidly than in unsterilized soils, if at all. He attributes this result to the production of a substance or substances which have a directly toxic effect. We are inclined to think that in such soils the necessary stimulus to the inhibition of water and germination is lacking, chiefly because carbon dioxide and ammonia—the latter especially, perhaps—are produced only in abnormally small amounts, if at all. We doubt if seeds would germinate in pure sterile water.¹

¹ It is well known that it is difficult to sterilize the exterior of seeds. Our observations show that ordinary sterilizing agents should not be used, as these will penetrate into the seed. Taking into account Adrian J. Brown’s observations, it is clear that one of the best ways to sterilize cereal

'The experiments made at the Woburn Fruit Farm by the Duke of Bedford and Mr. Pickering have brought into prominence the highly deleterious effect of grass on the growth of trees and the earlier annual maturity of trees the roots of which are covered with grass.

'Mr. Pickering, after testing various possibilities, has been led to assume that toxic substances are formed by the growth of the grass and that these affect the underlying roots of trees. Here, again, taking into account the pronounced aminophilic habits of the Graminae, we are inclined to think that the roots of trees under grass suffer because they are more or less completely deprived of the stimulus afforded by the greater proportion of ammonia and carbon dioxide in bare soils.

'It has long been known that under certain conditions sulphate of ammonia has advantages over nitrate of soda as a nitrogenous manure. It is customary to attribute the difference to the fact that ammonia salts are less easily washed out of the soil. We are inclined to think that the stimulative influence of ammonia should also be taken into account. It is possible that the value of ammonia in comparison with other forms of nitrogenous fertilizer has been somewhat overlooked and attention concentrated too much on nitrification in soils.

'Lastly, we may refer to the nodular growths on the roots of leguminous plants; these are known to be most essential to the proper growth of the plant but their function is by no means clear; it is well known that they are the seat of bacteroids and it may be that these function as assimilators of atmospheric nitrogen gas and convert it into ammonia; or it may be that they exercise digestive functions and serve to "deamidate" amino-compounds. At all events, they are distinctly alkaline, whereas the root sap is acid. Moreover, it has been shown by Hutchinson and Miller that, when distilled with magnesia under reduced pressure, the nodules furnish more ammonia than do the roots (0.043 per cent. against 0.016 per cent.). We suggest that some part at least of the influence exercised by the nodules may be due to their aminogenetic power. We propose to make this assumption the basis of experimental inquiry.'

Most leaves become more or less brown when exposed to the action of either chloroform or toluene; the most striking exemplification of this change that we have met with is afforded by *Aucuba Japonica*, the common spotted Japanese laurel; when subjected to the action of substances which

grains, at all events, would be to steep them in sulphuric acid and then to wash thoroughly with sterilized water under antiseptic conditions.

At a recent meeting of the Institute of Brewing (Journ. Inst. Brewing, No. 3, vol. xvi, 1910, pp. 253, 259), when German brewing practice was under discussion, surprise was excited by the statement that it had been found advantageous to steep barley for malting in weak sulphuric acid; it was suggested that sulphurous acid was meant but this was denied and reference was made to Adrian Brown's observations as showing that the acid would not enter the grain; but the obvious value of such treatment was in no way emphasized.

determine the liberation of hydrogen cyanide from the cherry laurel, the leaf of this shrub changes in colour from green, not merely to brown but to a rich chocolate brown-black and ultimately to black. On this account, as it carries its own indicator, it may be used even more effectively than the laurel leaf and with less trouble; otherwise its behaviour is precisely similar to that of the laurel leaf.

It has been shown by Bourquelot and Hérissé¹ that all the organs of *Aucuba*, the seed kernel especially, contain a crystalline glucoside, aucubin, $C_{13}H_{19}O_8$, which is resolved by 'emulsin' into glucose and aucubigenin, $C_7H_9O_3$ (?). This latter, however, is so unstable a compound that it has not been isolated; as it is liberated it undergoes decomposition spontaneously into a black substance that is insoluble in water, alcohol, ether and even in a solution of caustic soda. According to Bourquelot and Hérissé, the change takes place in absence of oxygen; Maquenne and Demoussy,² who have used *Aucuba* together with other leaves in studying the effect of ultra-violet light in comparison with that of heat and chloroform, have arrived at a similar conclusion.

Maquenne and Demoussy have stated that if the leaf be kept in boiling water sufficiently long to destroy the enzyme, it nevertheless blackens subsequently; they have attributed the change to the slow hydrolysis of the glucoside under the influence of acid present in the leaf. We have not observed this effect when the leaf has been kept sufficiently long in boiling water; neither the leaf nor the aqueous extract in contact with it has changed in colour, although this latter has blackened rapidly after emulsin has been added to it.

Several varieties of *Aucuba Japonica* are in cultivation—most of these, especially the *longifolia* variety, behave precisely like the common form; but one (*A. Japonica*, var. *vera*) which we owe to the courtesy of Mr. L. R. Russell, of Richmond, does not blacken to any appreciable extent. Berries of this variety obtained by fertilizing with pollen from the male of the common form evidently contain much aucubin, as they blacken quite readily; it is not improbable, therefore, that *Aucuba* may furnish an interesting subject of study from a Mendelian standpoint and we hope to carry out experiments from this point of view.

Aucubin has been separated from a number of varieties of *Aucuba* by C. Lebas.³

The only other shrub we have met with that is at all comparable in its behaviour with *Aucuba Japonica* is *Azara microphylla*; the leaves of this shrub become a rich brown when exposed in chloroform vapour. We have not succeeded in obtaining from this an extract which changes colour when

¹ Ann. Chim. Phys., 8^{me} sér., t. iv, pp. 289-318.

² Comptes rend., t. cxlix, 1909, p. 957.

³ Journ. Pharm. Chim., t. xxx, 1909, p. 385.

mixed with 'emulsin'. Dogwood, the only English ally of *Aucuba Japonica*, does not blacken.

The leaves of the well-known shrub *Garrya elliptica*, the male of which is grown on account of its decorative green catkins, change to an ugly grey colour in chloroform. The colourless extract obtained on boiling the leaves in water assumes a beautiful blue colour when digested with 'emulsin'. We shall endeavour to extract the β -glucoside which is indicated by this behaviour.

Two other species of *Garrya*, *G. macrophylla* and *G. Thureti*, that we have tested behave similarly, although the latter gives but a weak effect. [Since this account was written, Hérissé and Lebas have recorded the isolation of aucubin from these two species and also from *G. elliptica*.¹] Aucubin has also been separated from several species of *Plantago* (Bourdier²).

It is well known that the seed-pods of many leguminous plants ultimately become black. Apparently, in most cases, the effect cannot be much hastened by means of chloroform—as a rule, the effect can only be produced 48–24 hours before the seed is ripe; it would seem that either the enzyme or the substance which affords the black product comes into existence only at a late stage of growth. In the case of the ordinary Broad-bean, however, the pod can be caused to blacken at any time by exposure to chloroform. It is well known to botanists that the leaves of parasitic plants generally blacken with extreme readiness. We have found that the leaves of *Drosera* become intensely black when placed in toluene vapour.

The last case to which we will refer is that of Mangel-wurzel. It is well known that when the root is pulped it changes colour; if exposed in chloroform it soon blackens but the blackening is at first local. The blackening is shown also by sugar-beet but far less intensely. If a slice of the root, cut horizontally, be taken, the blackening takes the form of more or less circular rings of black dots; in slices cut vertically, the whole vascular system is seen outlined in black. Gradually the colour spreads to the soft tissue outside the vascular system—whether because of the diffusion of the colouring matter or because the action actually extends into this region, we cannot say at present. We are inclined to think that in this case the localization of the colour in the vascular system is due rather to the localization of an enzyme than to that of a colouring material. We intend, if possible, to study these and other cases of melanism induced by anaesthetics during the coming season, in the hope of deciding an issue that has already received attention at the hands of various observers several of whom have correlated the change with that occurring in cases of alkaptonuria in the human subject.

It would seem probable that in the case of many fruits the final

¹ loc. cit., 7^{me} série, t. ii, 1910, p. 490.

² Journ. Pharm. Chim., t. xxvi, 1907, p. 254.

appearance assumed by the fruit may be conditioned from within rather than by any environmental influence.

As the banana ripens, the green outer skin becomes yellow and finally a deep brown, if not black; the fruit is then fully ripe. The brown-black colour is easily produced by exposing the fruit to an anaesthetic. Moreover, if the interior edible part of the fruit be corked up in a test-tube together with an *Aucuba* leaf, the latter blackens sooner or later, especially if the temperature be raised to 35–37°. There can be little doubt that under natural conditions the blackening of the outer skin is due to the escape of an ethereal salt produced within; a signal is thus given that the fruit is ripe.

The autumn coloration of leaves and their fall may well, at least in part, be conditioned by processes of a similar order—by a sudden outburst of hormones which either determine the occurrence of special enzymic changes or hasten such changes. Similar considerations may apply to the ripening of seeds.

This last autumn, when green leaves of Mangel-wurzel taken from the various plots at Rothamstead were exposed to the action of toluene, those obtained from plots which had been highly manured with nitrogenous materials retained their green colour more or less completely; those from roots grown on other plots became yellow, resembling in this respect those grown under ordinary farm conditions and judged to be about ripe.

Much discussion has taken place as to the physiological significance of glucosides.¹ Dunstan and Henry,² in summing up the position with reference to cyanophoric glucosides, speaking of the value of hydrogen cyanide to the plant, remark: 'At first it was regarded as merely a waste product of no metabolic importance; later the view that it was possibly a means of protection was suggested; and more recently a small number of botanists and chemists have put forward the idea that the acid is an intermediate product in the synthesis of proteids.' We are inclined to take the view that, in not a few instances at all events, the compound associated with glucose functions simply as a hormone. In some cases the cyanophoric glucoside disappears as the seed ripens—in *Linum*, for example; maybe, hydrogen cyanide is of special service in hastening ripening; or when present in the seed, as in mustard, the glucoside may undergo hydrolysis during germination and furnish a hormone which serves to stimulate the growth of the seedling. The extent to which hormones are producible may have something to do with the various degrees of readiness with which seeds germinate. It is well that we should point out that, from our point of view, it is improbable that hydrogen cyanide is ever present as such except in minimal amount, unless perhaps at certain special times; it would necessarily escape at a rapid rate if it were thrown into circulation.

¹ Cp. E. F. Armstrong, *The Simple Carbohydrates and Glucosides*, p. 89.

² British Association Report, 1906, p. 145.

Again, the attack of plants by fungoid growths may be made possible by the excretion of hormones by the fungus. The behaviour of *Drosera* appears to us to be significant from this point of view. Before it will be possible to appreciate and interpret the whole of Darwin's wonderful observations on this plant, it will be necessary to repeat many of the experiments, taking into consideration our modern knowledge of enzymic changes. It is already clear, however, that most of the substances which Darwin found to be capable of inciting the digestive activity of the plant are substances that we class as hormones. Apparently the enzyme and the accompanying acid are not secreted until the glands are excited by the absorption of some soluble matter. The fact that acids generally do not act as excitants but only certain acids appears to us to be clear proof that the glands are provided with a differential septum which loses the differentiating power and then permits of the excretion of the enzyme *only after it has been sufficiently thinned by enzymic attack from within*. Darwin himself remarks: 'It is strange that allied acids act very differently; formic acid induces very slight inflexion and is not poisonous, whereas acetic acid of the same strength acts most powerfully and is poisonous. Lactic acid is also poisonous but causes inflexion only after a considerable lapse of time. Malic acid acts slightly, whereas citric and tartaric acids produce no effect.'¹

The order given is precisely that which we find to be the order of the activity of acids towards laurel and *Aucuba* leaves and that which Adrian Brown has deduced as the order of permeability in the case of the barley grain. Our observations as to the activity of hormones generally, it may be remarked, are also in complete harmony with those made by Overton and by Fühner and Neubauer using blood corpuscles and with Loeb's remarkable studies of artificial parthenogenesis.

That one effect is to thin the leaf membrane and deprive it of differentiating power there can be little doubt—the enzyme could not well escape otherwise. We have had ocular demonstration of such an effect in experiments made with young *Rhododendron* leaves with the object of ascertaining to what extent the leaves increased in weight—(a) when kept in water alone, (b) when kept in water to which toluene was added. In the course of several days a considerable increase took place only in the latter case. It so happened, moreover, that the bottles in which the leaves were immersed in water were left on the bench perhaps a couple of months. During the whole time, in the bottle in which water alone was used, the leaves remained green, only a few brown spots appearing here and there; no appearance of colour in the water was noticeable and no fungoid growth. In the other bottle, in which the leaves were brown, the solution soon became brown in colour and full of a mycelial growth; evidently sugar had passed out from the leaf in the one case but not in the other.

¹ Insectivorous Plants, 1875, p. 273.

If, in the case of *Drosera*, thinning and repair of the leaf are possible alternately, the leaf must vary in 'sensitiveness' according as it has been stimulated or not more or less recently; this indeed appears from Darwin's statements to have been the case.

Salts generally, with few exceptions, have but little effect on leaves of cherry-laurel and *Aucuba*. It will be remembered that many salts were found by Darwin to cause inflexion of the tentacles of *Drosera*—sodium salts, for example; yet the corresponding potassium salts were without effect. It is noteworthy that the effect of sodium salts was transient and that recovery usually took place when the leaves were placed in water. We are therefore inclined to think that such salts may have produced an exosmotic effect. In our experience, in cases in which a substance penetrates into the cell, if the action be sufficiently prolonged, necrosis inevitably follows; the quick recovery of *Drosera* leaves in water appears therefore to be evidence that the salt does not penetrate into the cells of the glands.

The greater activity of sodium salts may therefore be due to the greater osmotic tension of the solution. Darwin, as a rule, used a solution of one part of the salt to 437 parts of water; the solutions of potassium salts he used were weaker therefore than those of the corresponding sodium salts, both because the molecular weight of the former is greater and because sodium salts appropriate a larger proportion of water in solution.

Cadmium chloride, according to Darwin, caused inflexion but without discolouring the glands; mercuric chloride not only acted very rapidly but caused discoloration. This order of difference corresponds very closely with that observed by us.

Darwin has laid much stress on the extraordinary sensitiveness of *Drosera* to ammonia and many ammonium salts, especially the phosphates, which were the most active of all the salts he tried and much more powerful even than the carbonate, which was more powerful than the nitrate. This result was intelligible, he thought (p. 171), from the difference of the amount of nitrogen in the carbonate and nitrate and from the presence of phosphorus in the phosphate; the inflexion produced by other salts of ammonia, he suggested, was due to their nitrogen.

We are inclined to think that in all cases the stimulating effect is due to ammonia and that the activity of the salts in solution is conditioned by the extent to which ammonia is liberated by the hydrolysis of the salt. If an *Aucuba* leaf be partly immersed in a weak solution of ammonium carbonate, the part immersed is somewhat less rapidly and less intensely coloured than that which is not in contact with the liquid, the ammonia penetrating more rapidly from the atmosphere than from the solution; the difference is not improbably due to the fact that the film on the leaf surface is a more concentrated solution of ammonia than the solution itself.

At first our results with ammonium salts appeared to be in harmony

with Darwin's conclusion that they are very active ; but the experiments were carried out in ordinary soft glass tubes and, suspecting that ammonia might be liberated, we were led to repeat them carefully in hard glass vessels. At room temperatures the chloride, nitrate, phosphate and sulphate were practically without effect, although as the temperature was raised they became slightly active ; the ammonium salts of weak organic acids were more active.

Although we are not yet prepared to grade ammonium salts in their order of activity, we are convinced that the salts of the strongest acids are the least active and that the activity is consequent on the liberation of ammonia by hydrolysis.

Whatever explanation be given ultimately of Darwin's observations, a sense of wonderment at the perfection of the inquiry must be felt by all who study the record in the light of modern knowledge. The stimulus that 'Insectivorous Plants' gave to the study of the process of digestion is probably far greater than is realized ; inspiration is still to be found in its pages ; indeed, not a few of the problems to which attention was called by Darwin now deserve reconsideration in detail.

The information given by Loeb in the various accounts of his experiments on artificial parthenogenesis in some respects supplements that to be derived from Darwin's account of the behaviour of *Drosera* and from the behaviour of leaves such as that of *Aucuba*. The characteristic feature in the development of the sea-urchin egg by artificial means appears to be the formation of a 'fertilization membrane' at an early stage in consequence of an inflow of water which determines a growth in size of the egg.

A similar effect may also be produced by placing the eggs in distilled water instead of in a solution of the hormone in sea-water or some similar liquid. If the action either of water or of hormone be allowed to continue, the cell breaks down entirely.

One effect of the hormone on the leaf, as we have shown, is that it conditions the entry of water ; it is clear that this effect is also produced in the case of the sea-urchin egg. As the egg must be in equilibrium with the sea-water from which it is taken, it is to be expected that water would diffuse into it when distilled water is substituted ; what is surprising is that so much water should be absorbed as a consequence of the entry of the spermatozoon or the introduction of a minute proportion of some hormone. Ovum and spermatozoon are reciprocally affected as soon as the contact is effective. It is obvious that the spermatozoon is affected as it soon merges in the ovum ; and not only do changes become apparent within but also without the egg-cell—the superabundant spermatozoa in its neighbourhood being not merely warned off but even slain. Obviously, some hormone is produced which passes out rapidly into the medium surrounding the ovum.

The effect produced by the spermatozoon apparently is never exces-

sive; any hormone that is added incautiously and even distilled water will cause the ultimate break-down of the cell if the action be continued long enough.

We have contended in our communication to the Royal Society that one effect of the entry of a hormone is to condition the introduction of water and that the consequent dilution of the cell contents would determine the occurrence of down-grade changes. In the living cell, at any moment, the changes taking place forward (synthetic) and backward (analytic) must necessarily be in equilibrium; in the egg, presumably, the state is one of almost restful equilibrium. The effect of dilution should be to disturb the equilibrium previously existing in the analytic rather than in the synthetic direction. Loeb's observations show clearly that such an effect is produced. But the increase of katabolic activity cannot well be the only effect produced by the hormone; probably the protoplasmic structure is also affected by it. Darwin has called particular attention to the visible changes effected within the cell; Loeb's observations afford further proof that internal turmoil, eventually amounting to complete disaggregation of structure, is conditioned by the entry of foreign matter.

It appears to us probable that a primary effect of the hormone is to condition the separation from each other of *the successive layers* which may be supposed to constitute the protoplasmic complex; although deposited in close contact, these are perhaps sheathed with thin layers of hydrone molecules and disintegration sets in when the aqueous layers are penetrated by the hormone. A similar effect would be produced by freezing. Assuming such changes to happen, enzymes previously stored in the cells would be set at liberty and by their action the proportion of molecules in solution would be rapidly and largely increased—in other words, the osmotic tension would be raised and a flow of water determined to the region in which the hormone is active.

Waller has contended that the effect studied by us is a death phenomenon. This appears to us, however, to be merely a Wallerian *façon de parler* based on a definition of death peculiar to himself. Whether or no the action of a hormone be followed by death is apparently entirely a question of the amount administered—Darwin's observations and horticultural practice disprove Waller's statement. According to Loeb, benzene, toluene and a great number of other substances at once condition the formation of the fertilization membrane in sea-urchin eggs but this is rapidly followed by necrosis unless care be taken to initiate the change by a minimal dose. If the eggs are immersed in sea-water containing amylene or benzene, the membrane is formed at once while they are in the liquid; if fatty acids are used, the membrane is formed only when the eggs are taken out of the mixture and restored to fresh sea-water.

The process of alternate 'decay' and repair, obvious in *Drosera*, is

manifestly a phenomenon of supreme importance if it be of general occurrence. It is worth while to inquire whether, for example, the absorption of salts by plants may not be in part at least conditioned by such a process ; whether the translocation of diffusible matter may not be dependent largely upon such a process ? Obviously, the conditions are very different at different times of the day ; it is to be supposed that up-grade changes are ascendant at one time (whilst light is active) and down-grade changes at another : during the latter period it may be well that the tissues are far more easily permeable than during the former. The degree of immunity under various conditions and at various ages, the occurrence of latent diseases at certain seasons, may be largely a question of the resistance afforded by septa to penetration—to their liability to become thinned under certain conditions. For such reasons, some hesitation may be felt in accepting all the results that have been obtained with blood corpuscles in ordinary glass tubes, for example ; under such conditions they may well have properties somewhat different from those they possess in the body.

Armstrong, Henry E. and Armstrong, E. Frankland. 1911. "The function of hormones in regulating metabolism." *Annals of botany* 25, 507–519.
<https://doi.org/10.1093/oxfordjournals.aob.a089339>.

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DOI: <https://doi.org/10.1093/oxfordjournals.aob.a089339>

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