

## THE BRITISH ASSOCIATION.

## SECTION I.

## PHYSIOLOGY.

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*Correlation of Reflexes and the Principle of the Common Path.*

It has been lightly said that this Association meets to cultivate less muses than amusements. The two are compatible, and here happily the muses not merely nine, but ten; for we surely include among the muses "Physiologia." Here in Cambridge our muse admits frankly that a mistake has been made about Parnassus—it is not a mountain but a flat place, almost fenny, once worried by mosquitoes, and now immune from all worries.

Perhaps the confusion between Parnassus and a mountain was due to the Gog-Magog hills. Those hills our muse has haunted and still haunts. She has votaries there; among them one who instituted her worship in this place, a teacher whose powerful appeal attracted disciples from all sides, one whose enthusiasm was, moreover, never narrowed to a single science alone, but floods all biology. With Cambridge and Physiology the name of Sir Michael Foster rises to the lips as an indissoluble sequence. So it will ever be; and it must give him pleasure, as it gives us, to have for his successor here one of his first pupils, one associated far and wide with that which Physiology treasures as always golden, the discovery of imperishable facts.

When this Section last met, two years ago, its President, Prof. Halliburton, reviewed for us the existing position of chemical physiology. We cannot from the nervous system draw themes of such general attractiveness as the new biochemistry, with its startling reactions, its varied hypotheses, its *toxophores*, *haptophores*, *amboceptors*, and other fairy-like agents.

Physiology studies the nervous system from three main points of view. One of these regards its processes of nutrition. Nerve-cells, as all cells, lead individual lives, breathe, dispense their own stores of energy, repair their own substantial waste, are, in short, living units, each with a nutrition more or less centred in itself. The problems of nutrition of the nerve-cell and of the nervous system, though partly special to this specially differentiated form of cell life, are, on the whole, accessible to the same methods as is nutrition in other cells and in the body as a whole.

But beside the essential functions common to all living cells, the cells of the nervous system present certain which are specialised. Among properties of living matter, one by its high development in the nerve-cell may be said to characterise it. I mean the cell's transmission of excitement spatially along itself and thence to other cells. This "conductivity" is the specific physiological property of nerve-cells wherever they exist. Its intimate nature is, therefore, a problem coextensive with the existence of nerve-cells, and enters as a factor into every question concerning the specific reactions of the nervous system.

Thirdly, physiology seeks in the nervous system how by its "conductivity" the separate units of an animal body are welded into a single whole, and from a mere collection of organs there is constructed an individual animal.

This third line of inquiry, though greatly needing more data from the second and the first, must in the meantime go forward of itself. It is at present busied with many questions that seem special—hence its work is generally catalogued as Special Physiology. But it includes general problems. In the time before us I would venture to put before you one of these.

When we regard the nervous system as to this, which I would term its *integrative* function, we can distinguish two main types of system according to the mode of union of the conductors—(i.) the *nerve-net* system, such as met in Medusa and in the walls of viscera, and (ii.) the *synaptic* system, such as the cerebro-spinal system of Arthropods and Vertebrates. In the integrative function of the nervous system the unit mechanism is the *reflex*. The chain of conduction in the reflex is a nervous arc, running from a receptor organ to an effector organ, e.g. from a sense-organ to a limb-muscle. We may still, I think, conveniently

accept the morphological units termed neurones as units of construction of the reflex arc. It may be that these neurones are in some cases not unicellular but pluricellular. That question need not detain us now. Accepting the neurone as the unit of structure of the reflex chain, the characteristic of the synaptic system is that the chain consists of neurones jointed together in such a way that conduction along the chain seems possible in one direction only. These junctions of the neurones are conveniently termed synapses. The irreversible direction of the conductivity along the neurone chain is probably referable to its synapses. This irreciprocity of conduction especially distinguishes the synaptic nervous system from the nerve-net system.

The first link of each reflex chain is a neurone which starts in a receptor organ, e.g. a sense-organ. A receptive field, e.g. an area of skin, is always analysable into receptive points, and the initial nerve-path in every reflex arc starts from a receptive point or points. A single receptive point may play reflexly upon quite a number of different effector organs. It may be connected through its reflex path with many muscles and glands in various parts. Yet all its reflex arcs spring from the one single shank, so to say; that is, from the one afferent neurone that conducts from the receptive point at the periphery into the central nervous organ. This neurone dips at its deep end into the great central nervous organ, the cord or brain. There it enters a vast network of conductive paths. In this network it forms manifold connections. So numerous are its potential connections there, that, as shown by the general convulsions induced under strychnia-poisoning, its impulses can discharge practically every muscle and effector organ in the body. Yet in normal circumstances the impulses conducted by it to this central network do not irradiate there in all directions. Though their spread over the conducting network does, as judged by the effects, increase with increase of stimulation of the entrant path, the irradiation remains limited to certain lines. Under weak stimulation of the entrant path these lines are sparse. The conductive network affords, therefore, to any given path entering it some communications that are easier than others. This canalisation of the network in certain directions from each entrant point is sometimes expressed, borrowing electrical terminology, by saying that the conductive network from any given point offers less resistance along certain circuits than along others. This recognises the fact that the conducting paths in the great central organ are arranged in a particular pattern. The pattern of arrangement of the conductive network of the central organ reveals somewhat of the integrative function of the nervous system. It tells us what organs work together in time. The impulses are led to this and that effector organ, gland or muscle, in accordance with the pattern. The success achieved in the unravelling of the conductive patterns of the brain and cord is shown by the diagrams furnished by the works of such investigators as Edinger, Exner, Flechsig, van Gehuchten, v. Lenhossek, v. Monakow, Ramon, and Schäfer. Knowledge of this kind stands high among the neurological advances of our time.

But we must not be blind to its limitations. The achievement may, though more difficult, be likened to tracing the distribution of blood-vessels after Harvey's discovery gave them meaning, but before the vasomotor mechanism was discovered. The blood-vessels of an organ may be turgid at one time, constricted almost to obliteration at another. With the conductive network of the nervous system the temporal changes are even greater, for they extend to absolute withdrawal of nervous influence. Our schemata of the pattern of the great central organ take no account of temporal data. But the pattern of the web of conductors is not really immutable. Functionally its details change from moment to moment. In any active part it is a web that shifts from one pattern to another, from a first to a second, from a second to a third, then back perhaps to the first, and then to a fourth, and so on backwards and forwards. As a tap to a kaleidoscope, so a new stimulus that strikes the central organ causes it to assume a partially new pattern. The pattern in general remains, but locally the patterns are in constant flux of back and forward change. These time-changes offer, I venture to think, a study important for understanding the integrative function of the nervous system.

If we regard the nervous system of any higher organism from the broad point of view, a salient feature in its architecture is the following. At the commencement of every reflex arc is a receptive neurone, extending from the receptive surface to the central nervous organ. That neurone forms the sole avenue which impulses generated at its receptive point can use whithersoever may be their distant destination. That neurone is therefore a path exclusive to the impulses generated at its own receptive points, and other receptive points than its own cannot employ it.

But at the termination of every reflex arc we find a final neurone, the ultimate conductive link to an effector organ, gland or muscle. This last link in the chain, e.g. the motor neurone, differs obviously in one important respect from the first link of the chain. It does not subserv exclusively impulses generated at one single receptive source alone, but receives impulses from many receptive sources situate in many and various regions of the body. It is the sole path which all impulses, no matter whence they come, must travel if they would reach the muscle-fibres which it joins. Therefore, while the receptive neurone forms a private path exclusive for impulses of one source only, the final or efferent neurone is, so to say, a public path, common to impulses arising at any of many sources in a variety of receptive regions of the body. The same effector organ stands in reflex connection not only with many individual receptive points, but even with many various receptive fields. Reflex arcs arising in manifold sense-organs can pour their influence into one and the same muscle. A limb-muscle is the *terminus ad quem* of nervous arcs arising not only in the right eye but in the left, not only in the eyes but in the organs of smell and hearing; not only in these, but in the geotropic labyrinth, in the skin, and in the muscles and joints of the limb itself and of the other limbs as well. Its motor nerve is a path common to all these.

Reflex arcs show therefore the general feature that the initial neurone is a private path exclusive for a single receptive point; and that finally the arcs embouch into a path leading to an effector organ, and that this final path is common to all receptive points wheresoever they may lie in the body, so long as they have any connection at all with the effector organ in question. Before finally converging upon the motor neurone arcs usually converge to some degree by their private paths embouching upon internuncial paths common in various degree to groups of private paths. The terminal path may, to distinguish it from internuncial common paths, be called the *final common path*. The motor nerve to a muscle is a collection of such final common paths.

Certain results flow from this arrangement. One seems the preclusion of qualitative differences between nerve-impulses arising in different afferent nerves. If two conductors have a tract in common, there can hardly be qualitative difference between their modes of conduction.

A second result is that each receptor being dependent for communication with its effector organ upon a path not exclusively its own but common to it with certain other receptors, that nexus necessitates successive and not simul-

taneous use of the common path by various receptors using it to different effect.

Let us consider this for a moment. Take the primary retinal reflex, which moves the eye so as to bring the fovea to the situation of the stimulating image. From all the receptors in each lateral retinal half rise reflex arcs with a final common path in the nerve of the opposite *rectus lateralis*. Suppose simultaneous stimulation of two of these retinal points, one nearer to, one farther from, the fovea. If the arcs of both points pour their impulses into the final common path together, the effect must be a resultant of the two discharges. If these sum, the shortening of the muscle will be too great and the fovea swing too far for either point. If the resultant be a compromise between the two individual effects, the fovea will come to lie between the two points of stimulation. In both cases the result obtained would be useless for the purposes of either. Were

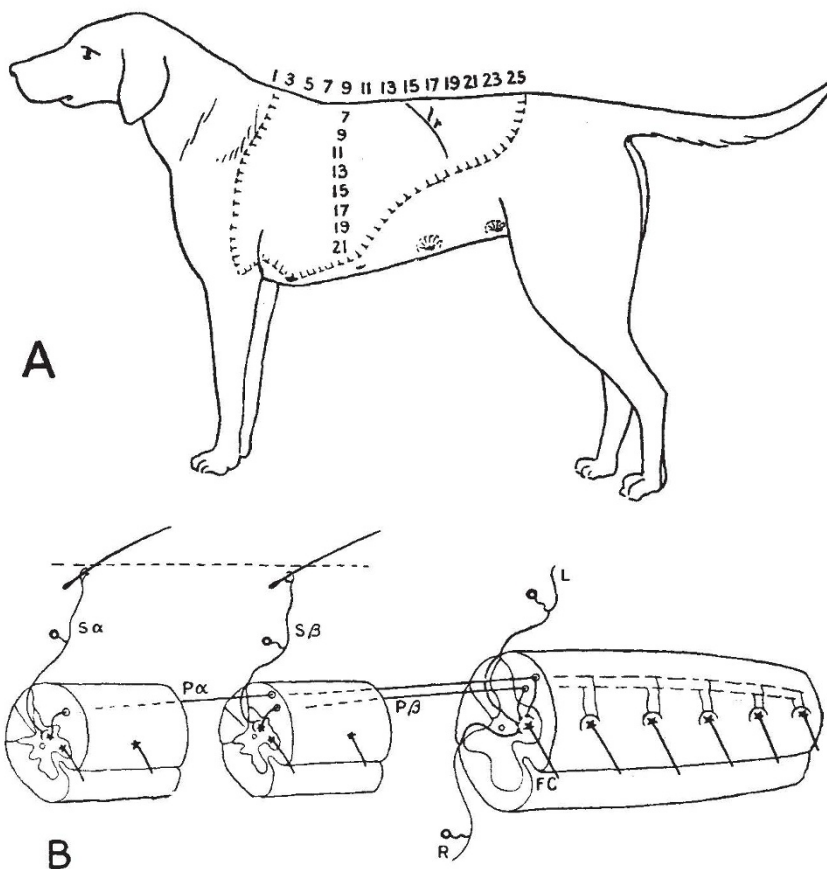


FIG. 1.—The Scratch Reflex. A.—The "receptive field," as revealed after low cervical transection, a saddle-shaped area of dorsal skin, whence the scratch reflex of the left hind limb can be evoked. *lr* marks the position of the last rib. B.—Diagram of the spinal arcs involved. *L*, receptive or afferent nerve-path from the left foot; *R*, receptive nerve-path from the opposite foot; *FC*, the final common path, in this case the motor neurone to a flexor muscle of the hip; *Pa*, *Pβ*, proprio-spinal neurones.

there to occur at the final common path summation of the impulses received from two unlike receptors, there would result in the effector organ an action useless for the purposes of either.

When two stimuli are applied simultaneously which would evoke reflex actions that employ the same final common path in different ways, in my experience one reflex appears without the other. The result is this reflex or that reflex, but not the two together. Excitation of the afferent root of the eighth or seventh cervical nerve of the monkey evokes reflexly in the same individual animal, sometimes flexion at elbow, sometimes extension. If the excitation be preceded by excitation of the first thoracic root, the result is almost always extension; if preceded by excitation of the

sixth cervical root, it is almost always flexion. Yet although the same root may thus be made to evoke reflex action of the flexors or of the extensors, I have never seen it evoke contrac-

Good opportunity for study of this correlation between reflexes is given in the "scratch reflex." When the spinal cord has been transected in the neck, this reflex in a few months becomes prominent. Stimuli applied within a large saddle-shaped field of skin (Fig. 1 A) excite a scratching movement of the leg. The movement is rhythmic flexion at hip, knee, and ankle. It has a frequency of about four per second. The stimuli provocative of it are mechanical, such as rubbing the skin, or pulling lightly on a hair. The nerve-endings which generate the reflex lie in the surface layer of the skin, about the roots of the hairs. A convenient way of exciting these is by feeble faradisation. A broad diffuse electrode is applied to some indifferent part of the surface elsewhere, and a stigmatic pole is brought to some point in the saddle-shaped area of dorsal skin. This pole is formed by a minute needle with fine wire attached; it is set lightly, so that its point just lies among the hair-bulbs.

Prominent among the muscles active in this reflex are the flexors of the hip. If we record their rhythmic contraction we obtain tracings as in Figs. 2, 3, 4. A series of brief contractions succeed one another at a certain rate, the frequency of which is independent of that of the stimulation. The contractions are presumably brief tetani. The stimulus to the hair-bulbs of the shoulder throws into action a lumbar spinal centre, innervating the hip-flexor much as the bulbar respiratory centre drives the spinal *phrenicus* centre. In the case of the respiratory muscle the frequency of the rhythm is, however, much less.

This reflex is unilateral: stimulation of the left shoulder evokes scratching by the left leg, not by the right. Search in the spinal cord for the path of the reflex demonstrates that a lesion breaking through one lateral half of the cord anywhere between shoulder and leg abolishes the ability of the skin of that shoulder to excite the scratch reflex, but leaves intact the reflex of the opposite shoulder.

In the lateral half of the spinal cord which the reflex path descends, severance of the dorsal column does not interfere with the reflex; nor does severance of the ventral and the dorsal columns together of that side; no more does severance of the grey matter in addition. But severance of the lateral part of the lateral column itself permanently abolishes the conduction of the reflex; and it does so even if all the other parts of the cord remain intact. The path of the reflex therefore descends the lateral part of the lateral column. I enter into these details because they help toward the construction of the reflex arc involved. For in the lateral part of the lateral column one has proved by "successive degeneration" that long fibres exist directly connecting the spinal segments of the shoulder

with the spinal segments containing the motor neurones for the flexor muscles of the hip, and knee, and ankle. The course of these long fibres can be traced and their number

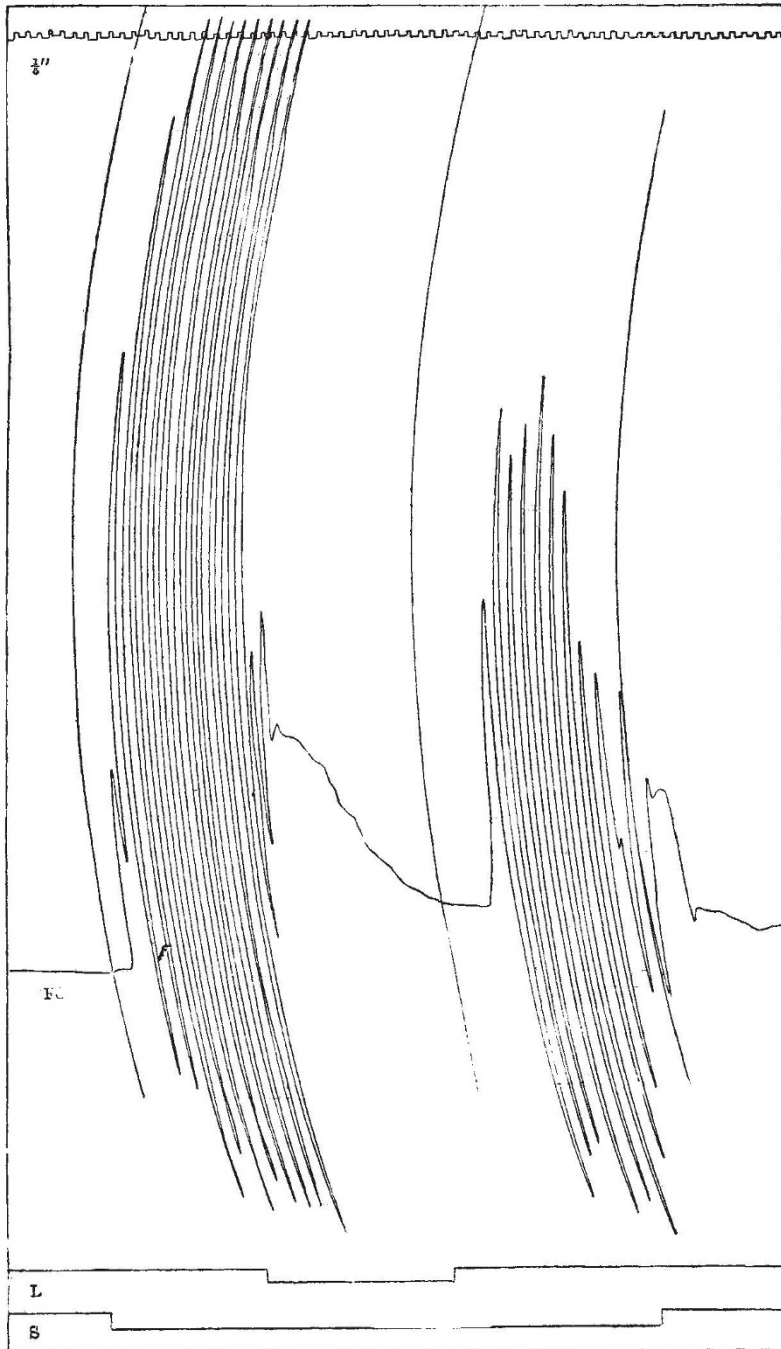


FIG. 2.—Interference between the reflex action of the left hip flexor, FC, caused by the nervous arc from the left foot (L, Fig. 1 B) and the scratch reflex. The stimulation of the dorsal skin (Fig. 1 A) inducing the scratch reflex began at the beginning of the notch in the signal line S, and continued throughout the period of that notch. Later, for the period marked by the notch in the signal line L the stimulation of the foot was made. This latter stimulation interrupts the clonic scratch reflex in the manner shown. The time is registered above in fifths of seconds. The tracing reads from left to right. It is noteworthy that the interruption of the scratch reflex by the foot reflex is not established directly the foot stimulus begins, and that it outlasts for a short time the application of the foot stimulus.

tion in both flexors and extensors in the same reflex response. Of the two reflexes on extensors and flexors respectively, either the one or the other results, but not the two together.

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counted. We thus arrive at the following reflex chain for the scratch reflex: (i.) The receptive neurone (Fig. 1 B, sa), from the skin to the spinal grey matter of the corresponding spinal segment in the shoulder. This is the exclusive or private path of the arc. (ii.) The long descending proprio-spinal neurone (Fig. 1 B, pa), from the shoulder segment to the grey matter of leg segments. (iii.) The motor neurone (Fig. 1 B, fc), from the spinal segment of the leg to the flexor muscles. This last is the *final common path*. The chain thus consists of three neurones. It enters the grey matter twice, that is, it has two neuronic junctions, two synapses. It is a *disynaptic* arc.

Now if, while stimulation of the skin of the shoulder is evoking the scratch reflex, the skin of the hind foot is stimulated (Fig. 2), the scratching is arrested. Stimulation of the skin of the hind foot by any of various stimuli that have the character of threatening the part with damage causes the leg to be flexed, drawing the foot up. This reflex response to noxious stimuli of the foot is one of great potency. The drawing up of the foot is effected by strong tonic contraction of the flexors of ankle, knee, and hip. In this reaction the reflex arc is (i.) the receptive neurone (Fig. 1 B, L) (nociceptive) from the foot to the spinal segment, (ii.) perhaps a short intraspinal neurone, and (iii.) the motor neurone (Fig. 1 B, fc) to the flexor muscle, e.g. of hip. Here, therefore, we have an arc which embouches into the same *final common path* as sa. The motor neurone fc is a path common to it and to the scratch reflex arcs; both arcs employ the same effector organ, a hip flexor. And, as you see, a condition for one reflex is the absence of the other.

The channels for both reflexes finally embouch upon the same common path. The flexor effect specific to each differs strikingly in the two cases. In the scratch reflex the flexor effect is an intermittent contraction of the muscle, in the nociceptive reflex it is steady and maintained. The accompanying tracing (Fig. 2) shows the result of conflict between the two reflexes. The one reflex displaces the other from the common path. There is no compromise. The scratch reflex is set aside by that of the nociceptive arc from the foot. The stimulation which previously sufficed to evoke the scratch reflex is no longer effective, though it is continued all the time. But when the stimulation of the foot is discontinued the scratch reflex returns. In that respect, although there is no enforced inactivity, there is inhibition. There is interference between the two reflexes, and the one is inhibited by the other. Though there is no cessation of activity in the motor neurone, one form of activity that was being impressed upon it is cut out and another takes its place. A stimulation of the foot too weak to cause more than a minimal reflex movement will often suffice to completely interrupt or cut short, or prevent onset of, the scratch reflex.

Suppose, again, during the scratch reflex, stimuli applied to the foot, not of the scratching but of the opposite side (Fig. 1 B, R). Stimulation (nociceptive) of the foot causes

flexion of its own leg and extension of the opposite. In numerous instances reflex contraction of one set of muscles is accompanied by reflex relaxation of their antagonists.

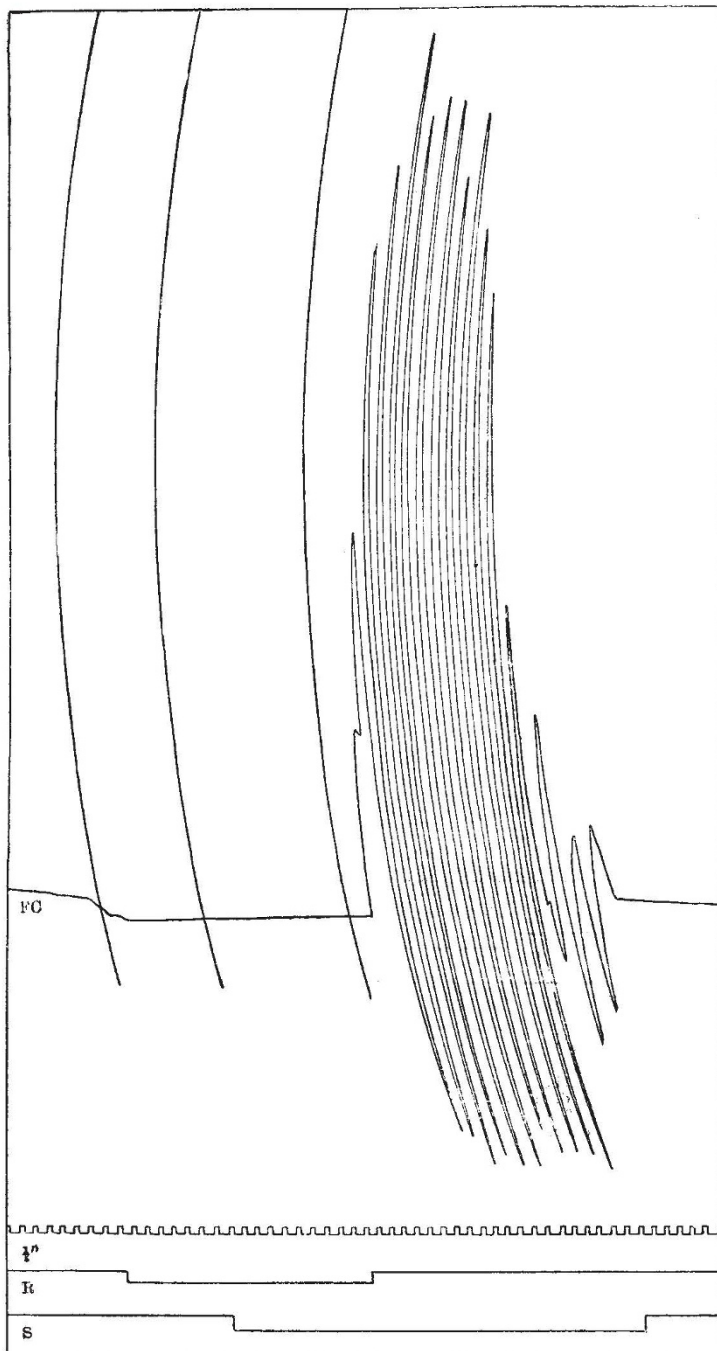


FIG. 3.—Interference of the reflex from the skin of the opposite foot with the scratch reflex, FC, the flexor muscle of the left hip (Fig. 1 B, FC) R, the signal line the notch in which marks the beginning, continuance, and conclusion of a skin stimulation of the right foot (Fig. 1 B, R). S, signal line similarly marking the period of stimulation of the skin of the left shoulder (Fig. 1 B, sa). The ability of stimulus S to produce the scratch reflex takes effect only on concluding stimulus R; that is, S obtains connection with the *final common path* (the motor neurone of the flexor muscle) only on R's relinquishing it. Stimulus R, while excluding S from FC, causes slight contraction of FC's antagonist, and coincident slight relaxation of FC itself. Time in fifths of seconds. Read from left to right.

The antagonistic muscle is thrown out of action. If, when the left leg is executing the scratch reflex, the right foot is stimulated, the scratching, involving as it does the left

leg's flexors, is cut short concomitantly with or preparatory to the entrance into contraction of their antagonists, the left extensors. Fig. 3 shows a record of this. This inhibition of the flexor scratching movement occurs sometimes when the contraction of the extensors is minimal or hardly perceptible (Fig. 3). As before, the inhibition may temporarily interrupt a reflex or may delay its onset, or simply cut it short, the result depending on the time relations of the applications of the stimuli to the conflicting arcs.

It is obvious from this that the final common path, FC, to the flexor muscle can be controlled by, in addition to the before-mentioned arcs, others that actuate the extensor muscles, for it can be thrown out of action by them. The final path, FC, is therefore common to the reflex arcs, not

is then examined it is found to present slight, steady extension with some abduction. This extension of the leg which accompanies the scratching movement of the opposite leg contributes to support the animal on three legs while it scratches with the fourth.

Suppose stimulation at the left shoulder evoking the scratching movement of the left leg, and the right shoulder then appropriately and strongly stimulated. This latter stimulus often inhibits the scratching movement in the opposite leg and starts it in its own. In other words, the stimulus at the right shoulder not only sets the flexor muscles of the leg of its own side into scratching action, but it inhibits the flexor muscles of the opposite leg. It throws into contraction the extensor muscles of that leg. In the previous example there was a similar co-ordination. The motor nerve to the flexor muscle is therefore under the control not only of the arcs of the scratch reflex from the homonymous shoulder, but of those from the crossed shoulder as well. But in regard to their influence upon this final common path, the arcs from the homonymous shoulder and the opposite shoulder are opposed. The influence of the latter depresses or suppresses activity in the common path.

Experiments by Verworn disallow any view that this kind of depression has its field in the motor nerve itself. Many circumstances connect it with the place where the converging neurones come together in the grey matter at commencement of the common path. The field of competition between the rival arcs seems to lie in the grey matter, where they impinge together upon the final or motor neurone. That is equivalent to saying that the essential seat of the phenomenon is the synapse between the motor neurone and the axone-terminals of the penultimate neurones that converge upon it. There some of these arcs drive the final path into one kind of action, others drive it into a different kind of action, and others again preclude it from being activated by the rest.

My diagram (Fig. 1 B) treats the final common path as if it consisted of a single individual neurone. It is, of course, not so. The single neurone of the diagram stands for several thousands. It may be objected that in the various given actions these motor neurones are implicated in particular sets—one set in one action, one set in another. That view seems unlikely. In the scratch reflex, I think we can exclude it. The rhythm of that reflex has the same frequency whether it be excited strongly or feebly: thus, whether the extent of the contractions be great or small they recur with practically the same frequency. That a muscle contracts feebly under feeble stimulation of its nerve may be due in some cases to a fraction only of the nerve-fibres and muscle-fibres of the preparation being then active. But in the scratch reflex the whole group of motor neurones seem to act, even when the grade of contraction exhibited is quite weak. Let the reflex be excited by stimulation of the skin-point *sa* (Fig. 1 B), and let the stimulus be weak, producing only a feeble reflex. Then let another skin-point, *sβ* (Fig. 1 B), be stimulated while *sa* is being stimulated, and let the stimuli at *sβ* be timed so as to fall alternately with those applied at *sa*. Then if the two paths impinge on two different sets of units in the compound group of

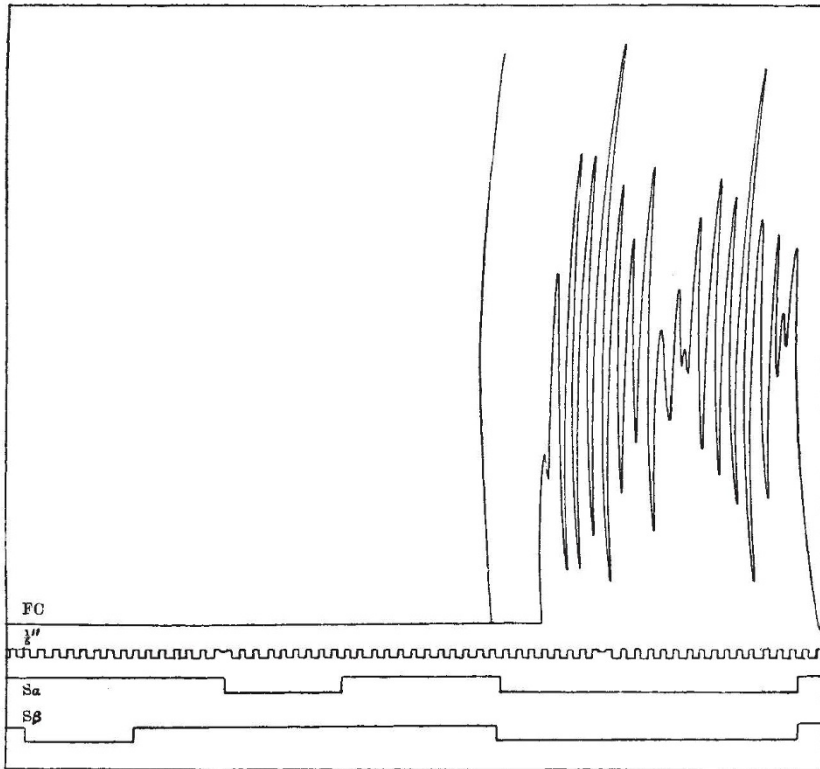


FIG. 4.—Summation effect between the arcs *sa* and *sβ* of Fig. 1 B. FC the flexor muscle of the hip. *sa* the signal line marking the period of stimulation of the skin belonging to arc *sa* (Fig. 1 B) of the shoulder skin. The strength of stimulus is arranged to be subminimal, so that a reflex response in FC is not obtained. *sβ*, the signal line marking the period of stimulation, also subminimal, of a point of shoulder skin 8 centimetres from *sa*. Though the two stimuli applied separately are each unable to evoke the reflex, when applied contemporaneously they quickly evoke the reflex. The two arcs *sa* and *sβ* therefore reinforce one another in their action on the final common path FC. Time in fifths of seconds. Read from left to right.

only from the same-side foot (Fig. 1 B, L) and shoulder skin (Fig. 1 B, *sa*, *sβ*), but also to arcs from the opposite foot (Fig. 1 B, R), in the sense that it is in the grasp of all of them. In this last case we have a conflict for the mastery of a common path, not, as in the previous instance, between two arcs both of which use the path in a pressor manner although differently, but between two arcs that, though both of them control the path, control it differently, one in a pressor manner heightening its activity, the other in a depressor manner lowering or suppressing its activity.

I said that the scratch reflex is unilateral. If the right shoulder be stimulated, the right hind-leg scratches; if the left shoulder be stimulated, the left hind-leg scratches. If both shoulders be stimulated at the same time, one or the other leg scratches, but not the two together. The one reflex that takes place prevents the occurrence of the other. The reason is, that although the scratch reflex appears unilateral it is not strictly so. Suppose the left shoulder stimulated. The left leg then scratches. If the right leg

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motor neurones, evidence of two rhythms should appear, for the muscle-fibres can respond to a much quicker rhythm than the four per second. But in result the rhythm remains unquicken and unaltered. Either  $s\alpha$  prevents the access of  $s\beta$  to the motor neurones of FC, or  $s\alpha$ 's reflex having impressed its own tempo on the neurones of FC, the stimuli from  $s\beta$  fall within a refractory period of the neuron apparatus. On either supposition,  $s\alpha$  and  $s\beta$  must play upon the same individual neurones of the final path. A like result is given by all other points I have tried in the receptive field of the scratch reflex. Again, in the inhibitions previously mentioned, when there occurs the tonic contraction or the relaxation of the flexor we find no intermittent contraction of the scratch reflex grafted on them, as would be the case were that intermittent contraction still involving some part of the whole muscle. These various reflexes seem to treat the final common path as a unit. The diagram therefore seems justified in representing the common path, FC, as a unit.

We have no time to multiply further now the categories of reflexes playing upon the final common path FC. I might cite the deep reflex arc which arises in the muscles themselves and is answerable for the mild reflex tonus that even in the spinal animal maintains the tonic posture of the limb. Or, instead of having taken arcs that arise in the skin of the foot, we might have taken others arising above the knee, and traced a reflex influence different from the arcs arising in the foot, but yet playing upon the same final common path; or we might have taken arcs from the skin of the tail, that inhibit the reflex; or from the fore feet, or the ears.

There is, however, one instance of action upon this final common path FC which I would quote. Suppose, while the scratch reflex is being elicited from a point at the shoulder, a second point, say 10 centimetres distant, but also in the dorsal field of skin, is stimulated. The stimulation at this second point favours the reaction from the first point. This is well seen when the stimulus at each point is of sub-minimal intensity. The two stimuli, though each unable separately to invoke the reflex, do so when applied both together (Fig. 4). This is not due to overlapping spread of the feeble currents about the stigmatic poles of the two circuits used. Mere cocainisation of either of the two skin-points annuls it. Moreover, it occurs when purely mechanical stimuli are used. It is evident that the arcs from the two points, e.g.  $s\alpha$  and  $s\beta$  (Fig. 1 B), have such a mutual relation that reaction of one reinforces reaction of the other, as judged by the effect upon the final common path FC. Such mutual reinforcement is usual between reflexes of identical species evoked from one and the same receptive field, e.g. the nociceptive of the foot.

Not for all the arcs arising in the receptive field of the scratch reflex can, in my experience, this mutual reinforcement be demonstrated. There seems a gradual fall in reinforcing power as the distance between the receptors of the arcs increases. In this connection the following point is noteworthy. The scratch reflex carries the foot broadly toward the place of stimulation. In the spinal dog the reflex does not succeed in bringing the foot actually to the irritated point, yet when the irritation is far forward the foot is carried further forward, and when the irritation is far back the foot is carried further back. A scratch reflex evoked by a stimulus applied far back and high up in the dorsal skin is therefore not wholly like a scratch reflex evoked from far forward and low down. Now, the mutual reinforcement between the scratch reflex arcs in their action on the final common path FC seems greater the greater the likeness between the reflex actions they initiate. The coalition between the reflexes gradually decreases as the interval between their receptive points at the skin surface becomes wider. Whether coalition fades into mere indifference, or passes over into antagonism, my observations as yet do not say. But there are various receptive regions of the body surface that do, in the spinal dog, appear indifferent for the scratch reflex. Were it not that the nervous system is perforce mutilated in the "spinal" animal, the number of these indifferent arcs might be fewer. In presence of the arcs of the great projectile receptors and the brain there can be few receptive points in the body the activities of which are totally indifferent one to another. Correlation of the activities of arcs from receptive points widely apart

is the crowning contribution of the brain toward the nervous integration of the individual.

In the case before us, then, the final common path—the motor neurone—to the hip flexor muscle is played upon by various categories of reflex spinal arcs. Of those mentioned, one category (i.), the nociceptive from the leg itself, induces strong, steady contraction in the muscle. A second (ii.), the scalptor or scratching from the dorsal skin, induces rhythmic contraction in the muscle. A third (iii.), from the deep structures of the limb itself, induces the mild enduring contraction known as spinal tonus. A fourth (iv.), e.g. the nociceptive from the opposite foot, depresses the activity of the muscle probably by excluding from it the activity of the other arcs which would excite the final path, the motor neurone. And there are many more we could trace from various regions of the body; also, pyramidal and other influences from brain for which our final path is likewise common. The arcs *within* one category may reinforce each other's action on the common path, but those in separate categories are generally correlated in their action on their final common path in such a way as to antagonise one another. They are rivals for possession of their final common path, rivals as retinal points may be rivals for possession of the visual sensorium.

The extent to which in the nervous system this competition for possession of the common path obtains is very great. The multiplicity of the conflict seems extreme. The afferent fibres—that is, private paths—entering the central organ are much more numerous than are the final common paths. We owe to Donaldson and his pupils enumerations which show that the afferent fibres entering the human spinal cord three times outnumber the efferent which leave it. Add the cranial nerves and the so-called optic nerves, and we may take the afferent fibres to be five times the greater. The receptor system bears therefore to the efferent paths a relation like the wide ingress of a funnel to its narrow egress. The simile is bettered by supposing that within the general systemic funnel the conducting paths of each receptor may be represented as a funnel inverted, so that its wider end is more or less co-extensive with the whole plane of emergence of the final common paths. All these private paths converge in the nervous system to the great central organ, the spinal cord and brain, whence on the other hand all the final common paths irradiate. This central organ is, to return to our earlier metaphor, a vast network the lines of which follow a certain pattern. But, as we see from the instances cited—more could be given abundantly, had we time—the pattern is unstable, the details of connection shift from moment to moment. We might compare the central organ with a telephone exchange, where from moment to moment the connections between starting and end points are changed to suit passing requirements. In order to realise the exchange at work, one has to add to its purely spatial plan the temporal datum that within certain limits the connections of the lines shift to and fro. The connections of any entrant path not only offer different degrees of resistance, but their resistances, both absolutely and relatively, vary from occasion to occasion. It is not merely that general conditions of nutrition, of blood-supply, &c., affect these resistances. The functional conductive activity of the nervous organ itself produces from moment to moment the temporary opening of some connections and the temporary closing of others. A good example is the "reciprocal innervation" of antagonistic muscles—when one muscle of the antagonistic couple is thrown into action the other is thrown out of action. This is only a widely spread special case of a general principle. The general principle is the mutual interaction of arcs which embouch upon one and the same common path. Unlike arcs have successive use, but not simultaneous use of the common path. Like arcs mutually reinforce each other in their action on the common path. Expressed teleologically, the common path, although economically subservient for various purposes, is yet used only for one purpose at a time.

Thus the reaction initiated by one receptor while in progress excludes in various directions the reactions of other receptors. In this way the motor paths at any moment accord in a united pattern for harmonious synergy, co-operating for one effect. In the case of simple antagonistic muscles, and in the instances of simple spinal reflex arcs, the shifts of pattern of the conductive network from occasion

to occasion are but of small extent. The co-ordination covers one limb or a pair of limbs. But the same principle extended to the reactions of the great arcs arising in the projectant receptor organs of the head, e.g. the eye, that deal with wide tracts of musculature as a whole, involves much further-reaching shift of the conductive pattern. The singleness of action from moment to moment thus assured is a keystone in the construction of the individual whose unity it is the specific office of the nervous system to perfect. Releasing forces acting on the brain from moment to moment shut out from activity whole regions of the nervous system, as they conversely call vast other regions into play. The interference of unlike arcs and the reinforcement of like arcs seem to lie at the very root of the great psychological process of "attention." I will not trench on psychological aspects of the problem.

I have urged that the struggle between dissimilar arcs for mastery over their final common path takes place in the *synaptic field* at origin of the final neurones. Mutual reinforcement by similar arcs seems also referable to the same synaptic field. As to the nature of the physiological processes involved, little, it appears to me, can be said. The final common path seems an instrument more or less passive in the hands of the various arcs that use it. Thus in the scratch reflex one arc can impress one rhythm on it, another another. And in "fatigue" *rc* reveals, though it does not share, the failure of force of the tired arc playing on it. In regard to the reciprocal innervation of antagonistic muscles W. MacDougall has offered a suggestion of great interest, for which he obtains support from various sensual reactions. He suggests that the neurones of an antagonistic pair are so coupled that when one becomes active it drains energy from its fellow. This takes cognisance of the significant fact that central inhibition seems always accompanied by heightened activity at some related spot. Yet at certain times both the antagonists can show high contemporaneous activity (strychnia, some forms of "willed" action). I think, rather, that in some way the terminal of that arc which for the moment dominates the final common path, disconnects that path from all terminals dissimilar from itself.

Whatever be the nature of the physiological process in the conflict between the competing reflexes, the issue of that conflict—namely, the determination of which competing arc shall for the time being reign over the final common path—is largely conditioned by three factors. One of these is the relative intensity of the stimulation of the rival reflexes. An arc strongly stimulated is *caeteris paribus* more likely to capture the common path than one which is excited feebly. In the spinal dog, retraction equally induced in both legs mutually excludes the crossed extension of either side, but if unequally induced allows the crossed extension of the stronger reflex to exclude the weaker reflex altogether. The common path is probably never out of the grasp of some one or other reflex. Thus, in the spinal dog even, with its limb apparently at rest, this is true. The final common path of the extensor of the knee lies, then, in the hands of a tonic reflex arising in the muscle itself. Given a strong skin stimulus, and it passes under the mastery of the reflex arising in the stimulated skin; but when that is over, the tonus arc immediately repossesses it, and for a short time, as shown by the knee-jerk, more strongly than before.

A second main determinant for the issue of the conflict between the rival reflexes is the functional species of those reflexes. Arcs belonging to species of receptors which, considered as sense-organs, provoke strongly affective sensation—e.g. pain, sexual feeling &c.—win the final common path with remarkable facility. Such reflexes override and set aside with peculiar potency reflexes belonging to touch organs, muscular sense-organs, &c. As the sensations evoked by these arcs, e.g. pains, exclude and dominate concurrent sensations in consciousness, so do the reflexes of these arcs prevail in the competition for possession of the common paths. They seem capable of pre-eminent intensity of action.

A third main factor deciding the conflict between the competing reflexes is "fatigue." An arc under long continuous stimulation of its receptor tends, even when it holds the common path, to retain its hold less well. Other arcs can then more readily dispossess it. A stimulus to a fresh arc has, in virtue of its mere freshness, a better chance of

capturing the common path. The common path does not tire. In the scratch reflex under stimulation of *sa* when the motor discharge becomes slow and irregular from fatigue, it is still perfect for *sβ*, or *L*, &c. (Fig. 1 B). This waning of a reflex under long-maintained excitation is one of the many phenomena that pass in physiology under the name "fatigue." Its place of incidence lies at the synapse. It seems a process elaborated and preserved in the selective evolution of the neural machinery. It prevents long continuous possession of a common path by any one reflex of considerable intensity. It favours the receptors taking turn about. It helps to ensure serial variety of reaction. The organism, to be successful in a million-sided environment, must in its reactions be many-sided. Were it not for such so-called "fatigue," an organism might, in regard to its receptivity, develop an eye, or an ear, or a mouth, or a hand or leg, but it would hardly develop the marvellous congeries of all those various sense-organs which it actually does.

But while talking of fatigue in general I forget the fatigue in particular of listeners. The principle I have tried to outline to you has many and wide applications; it seems fruitful for problems of Pathology and Psychology, as well as for those of Physiology. But I keep you too long. Let me sum up. The reflex arcs (of the synaptic system) converge in their course so as to impinge upon links possessed by whole varied groups in common—*common paths*. This arrangement culminates in the convergence of many separately arising arcs upon the efferent-root neurone. This neurone thus forms a final common path for many different reflex arcs and acts. It is responsive in various rhythm and intensity, and is relatively unfatigable. Of the different arcs which use it in common, each can do so exclusively in due succession, but *different* arcs cannot use it simultaneously. There is, therefore, interference between the actions of the arcs possessing the common path, some reflexes excluding others and producing inhibitory phenomena, some reflexes reinforcing others and producing phenomena of "bahnung." Intensity of stimulation, species of reflex, fatigue, and freshness, all these are physiological factors influencing this interaction of the arcs—and under pathological conditions there are many others, e.g. "shock," toxins, &c. Hence follows successive interchange of the arcs that dominate one and the same final common path. We commonly hear a muscle—or other effector organ—spoken of as innervated by a certain nerve; it would be more correct as well as more luminous to speak of it as innervated by certain receptors; thus, the hip flexor, now by this piece of skin, now by that, by its own foot, by the opposite fore-foot, by the labyrinth, by its own muscle-spindles, by the eye, by the "motor" cortex, &c. This temporal variability, wanting to the nerve-net system of medusoid and lower visceral life, in the *synaptic* system provides the organism with a mechanism for higher integration. It fits that system to synthesise from a mere collection of tissues and organs an individual animal. The animal mechanism is thus given solidarity by this principle which for each effector organ allows and regulates interchange of the arcs playing upon it, a principle which I would briefly term that of "the interaction of reflexes about their common path."

## SECTION K.

### BOTANY.

OPENING ADDRESS BY FRANCIS DARWIN, F.R.S., FELLOW OF CHRIST'S COLLEGE, PRESIDENT OF THE SECTION.

#### *On the Perception of the Force of Gravity by Plants.*

WHEN I had the honour of addressing this Association at Cardiff as President of the mother-section from which ours has sprung by fission, I spoke of the mechanism of the curvatures commonly known as tropisms. To-day I propose to summarise the evidence—still far from complete—which may help us to form a conception of the mechanism of the stimulus which calls forth one of these movements—namely, geotropism. I have said that the evidence is incomplete, and perhaps I owe you an apology for devoting the time of this Section to an unsolved problem. But the making of theories is the romance of research; and I may say, in the words of Diana of the Crossways, who indeed spoke of romance, "The young who avoid that region escape the title of fool at the cost of a celestial crown." I am prepared for the risk in the hope that in not avoiding

the region of hypothesis I shall at least be able to interest my hearers.

The modern idea of the behaviour of plants to their environment has been the growth of the last twenty-five years, though, as Pfeffer has shown, it was clearly stated in 1824 by Dutrochet, who conceived the movements of plants to be "spontaneous"—i.e., to be executed at the suggestion of changes in the environment, not as the direct and necessary result of such changes. I have been in the habit of expressing the same thought in other words, using the idea of a guide or signal, by the interpretation of which plants are able to make their way successfully through the difficulties of their surroundings. In the existence of the force of gravity we have one of the most striking features of the environment, and in the sensitiveness to gravity which exists in plants we have one of the most widespread cases of a plant reading a signal and directing its growth in relation to its perception. I use the word perception not of course to imply consciousness, but as a convenient form of expression for a form of irritability. It is as though the plant discovered from its sensitiveness to gravity the line of the earth's radius, and then chose a line of growth bearing a certain relation to the vertical line so discovered, either parallel to it or across it at various angles. This, the reaction or reply to the stimulus, is, in my judgment, an adaptive act forced on the species by the struggle for life. This point of view, which, as I regret to think, is not very fashionable, need not trouble us. We are not concerned with why the plant grows up into the air or down into the ground; we are only concerned with the question of how the plant perceives the existence of gravitation. Or, in other words, taking the reaction for granted, what is the nature of the stimulus? If a plant is beaten down by wind or by other causes into a horizontal position, what stimulative change is wrought in the body of the plant by this new posture?

It is conceivable in the case of a stem supported by one end and projecting freely in the air that the unaccustomed state of strain might act as a signal. The tissues on one side (the upper) are stretched, and they are compressed below: this might guide the plant; it might, in fact, have evolved the habit of rapid growth in the compressed side. This is only given as an illustration, for we know that the stimulus does not arise in this way, since such a plant, supported throughout its length, and, therefore, suffering no strain, is geotropically stimulated. The illustration is so far valuable, as it postulates a stimulus produced by weight, and we know from Knight's centrifugal experiment that weight is the governing factor in the conditions. Since we cannot believe that the stimulus arises from the strain as affecting the geotropic organ as a whole, we must seek for weight-effects in the individual cells of which the plant is built. We must, in fact, seek for weight-effects on the ectoplasm<sup>1</sup> of those cells which are sensitive to the stimulus of gravity.

If we imagine a plant consisting of a single apogeotropic cell we shall see that the hydrostatic pressure of the cell-contents might serve as a signal.

As long as the cell is vertical the hydrostatic pressure of the cell-sap upon the ectoplasm at C (Fig. 1) is equal to that at D. But the pressure on the basal wall, B, differs from that at A (the apical wall) by the weight of the column AB. If the plant be forced into the horizontal, the pressure at A and B becomes the same, while the pressure at C no longer equals that at D, but differs by the weight of the column CD. Here undoubtedly is a possible means by which the plant could perceive that it was no longer vertical, and would have the means of distinguishing up from down. So that if it were an apogeotropic plant it would need to develop the instinct of relatively accelerated growth on the side D, on which the pressure is greatest.

What is here roughly sketched is the groundwork of the theory of *graviperception*<sup>2</sup> suggested by Pfeffer<sup>3</sup> and supported by Czapek,<sup>4</sup> which I shall speak of as the radial pressure theory, and to which I shall return later.

<sup>1</sup> See Noll's ingenious reasoning by which he makes it clear that the stationary ectoplasm, not the flowing endoplasm, is the seat of stimulation. Noll (88).

<sup>2</sup> I propose this term in place of *geoaesthesia*, which does not lend itself to the formation of adjectives, or the hybrid word *geoperception*. By not using the form "geo" we avoid any necessary connection with geotropism, and may thus use terms compounded of *gravi* for phenomena other than those of curvature.

<sup>3</sup> Pfeffer (87).

<sup>4</sup> Czapek (98), (101).

It is obvious that there is another consideration to be taken into account, namely, that cells do not contain cell-sap only, but various bodies—nucleus, chloroplasts, crystals, &c.—and that these bodies, differing in specific gravity from the cell-sap, will exert pressure on the physically lower or physically higher cell-walls according as they are heavier or lighter than the cell-sap. Here we have the possibility of a sense-organ for verticality. As long as the stem is vertical and the apex upwards the heavy bodies rest on the basal wall, and the plant is not stimulated to curvature; but if placed horizontally, so that the heavy bodies rest on the lateral cell-walls, which are now horizontal, the plant is stimulated to curve. This is known as the *statolith* theory.

It seems to me quite certain that the stimulus must originate either in the weight of solid particles or in the weight of the fluid in the cells, or by both these means together. And for this reason. Take the statolith theory first. There undoubtedly are heavy bodies in cells; for instance, certain loose, movable starch-grains. Now, either these starch-grains are specialised to serve the purpose of graviperception or they are not. If they are so specialised, *cadit quaestio*; if they are not, there still remains this interesting point of view: the starch-grains fall to the lower end of the cells in which they occur; therefore, shortly before every geotropic curvature which has taken place since movable starch-grains came into existence, there has been a striking change in the position of these heavy cell-contents. Now, if we think of the evolution of geotropism as an adaptive manner of growth we must conceive plants growing vertically upwards and succeeding in life, others not so behaving, and consequently failing.

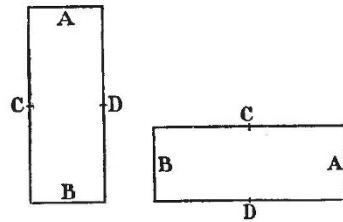


FIG. 1.

There will be a severe struggle tending to pick out those plants which associated certain curvatures with certain preceding changes, and therefore it seems to me that, if movable starch-grains were originally in no way specialised as part of the machinery of graviperception, they would necessarily become an integral part of that machinery, since the act of geotropism would become adherent to or associated with the falling of the starch-grains.

This argument must in fairness be applied to any other physical conditions which constantly precede geotropic curvature; it is therefore not an argument in favour of the statolith theory alone, but equally for the pressure theory, and cannot help us to decide between the two points of view.

Are there any general considerations which can help us to decide for or against the statolith theory? I think there are—namely, (1) analogy with the graviperceptive organs of animals; (2) the specialisation and distribution of the falling bodies in plants.

(1) Berthold<sup>1</sup> (to whom the credit is due<sup>2</sup> of having first suggested that Dehnecke's falling starch-grains might function as originators of geotropic reaction) is perhaps somewhat bold in saying that "the primary effect of gravity" as regards stimulation must depend on the passive sinking of the heavier parts. Noll, too,<sup>3</sup> says that Knight's experiment depends on weight, and not the weight of complete parts of the plant-body, but of weight within the irritable structure. I cannot see that these downright statements are justified on direct evidence, and I accordingly lay some stress on the support of zoological evidence. It

<sup>1</sup> "Protoplasmamechanik," 1886, p. 73. I was directed to this passage by Pfeffer's discussion ("Pflanzenphysiologie," ed. 2, ii., p. 641).

<sup>2</sup> Berthold's remarks seem not to have received much notice, and it was not till the publication of Noll's "Heterogene Induction," 1892, that a form of the statolith theory was at all widely recognised as a possible explanation.

<sup>3</sup> "Heterogene Induction," p. 41.



has been conclusively proved by Kreidl's<sup>1</sup> beautiful experiment that in the Crustacean Palæmon the sense of verticality depends on the pressure of heavy bodies on the inside of cavities now known as statocysts, and formerly believed to be organs of hearing. The point of the experiment is that when the normal particles are replaced by fragments of iron the Palæmon reacts towards the attraction of a magnet precisely as it formerly reached towards gravity.

It is unfortunate that Noll's arguments in favour of the existence of a similar mechanism in plants were not at once followed by the demonstration of those easily visible falling bodies, which, in imitation more flattering than accurate, are called *statoliths*, after the bodies in the statocysts of animals. Personally I was convinced by Kreidl, as quoted by Noll, that here was the key to graviperception in plants. But it was not until the simultaneous appearance of Haberlandt's<sup>2</sup> and Němec's<sup>3</sup> papers that my belief became active, and this, I think, was the case with others. The whole incident is an instance of what my father says somewhere about the difficulty of analysing the act of belief. I find it impossible to help believing in the statolith theory, though I own to not being able to give a good account of the faith that is in me. It is a fair question whether the analogy drawn from animals gives any support to the theory for plants. The study of sense-organs in plants dates, I think, in its modern development, at least, from my father's work on root-tips, and on the light-perceiving apices of certain seedlings. And the work on the subject is all part of the wave of investigation into adaptations which followed the publication of the "Origin of Species." It is very appropriate that one of the two authors to whom we owe the practical working out of the statolith theory should also be one of the greatest living authorities on adaptation in plants. Haberlandt's work on sense-organs,<sup>4</sup> especially on the apparatus for the reception of contact stimuli, is applicable to our present case, since he has shown that the organs for intensifying the effect of contact are similar in the two kingdoms. No one supposes that the whisker of a cat and the sensitive papilla of a plant are phylogenetically connected. It is a case of what Ray Lankester called homoplastic resemblance. Necessity is the mother of invention, but invention is not infinitely varied, and the same need has led to similar apparatus in beings which have little more in common than that both are living organisms.

But, whether we are or are not affected in our belief by the general argument from analogy, we cannot neglect the important fact that Kreidl proves the possibility of gravisensitiveness depending on the possession of statoliths. We must add to this a very important consideration—namely, that we know from Němec's work<sup>5</sup> that an alteration in the position of the statoliths does stimulate the *statocyte*.<sup>6</sup> Such, at least, is, to my mind, the only conclusion to be drawn from the remarkable accumulation of protoplasm which occurs, for instance, on the basal wall of a normally vertical cell when that wall is cleared of statoliths by temporary horizontality. The fact that a visible disturbance in the plasmic contents of the statocyte follows the disturbance of the starch-grains seems to me a valuable contribution to the evidence.

There is one other set of facts of sufficiently general interest to find a place in this section. I mean Haberlandt's result,<sup>7</sup> also independently arrived at by myself, that when a plant is placed horizontally and rapidly shaken up and down in a vertical plane the gravistimulus is increased. This is readily comprehensible on the statolith theory, since we can imagine the starch-grains would give a greater stimulus if made to vibrate on one of the lateral walls, or if forced into the protoplasm, as Haberlandt supposes. I do not see that the difference in the pressure of the cell-sap on the upper and lower walls (*i.e.*, the lateral walls morphologically considered) would be increased. It would, I imagine, be rendered uneven; but the average difference would remain the same. But in the case of the starch-grains an obvious new feature is introduced by exchanging a stationary condition for one of movement. And though I speak with hesitation on such a point, I am inclined to see in Haberlandt's and my own experiments a means of

distinguishing between the pressure and statolith theories. Noll,<sup>8</sup> however, considers that the shaking method is not essentially different from that of Knight's experiment, and adds that the result might have been foreseen.

#### Distribution.

As far as I know, the development of *statoplasts*<sup>2</sup> has not been made out. Are they at first like ordinary immovable amyloplasts; and, if so, by what precise process do they become movable? Where the two forms of starch are seen in close juxtaposition the difference between them is striking, and it is hardly possible to doubt that these differently situated bodies have different functions. In a seedling *Phalaris canariensis* the apical part has only falling starch-grains, while lower down both forms occur. It suggests a corresponding distribution of graviperception; and, as a fact, the seedling is gravisensitive throughout, but is especially so at the apex. If this is not the meaning of the statoplasts we must find some other. For instance, are the loose starch-grains connected in an unknown way with heliotropic sensitiveness, which often has the same distribution as that of graviperception? Or is the looseness of starch connected in some way with food storage? Is it to allow of starch being closely packed in part of the cell, leaving the rest of the space free?

Again, the most striking general fact about the distribution of falling starch is its presence in the endodermis.<sup>9</sup> If we believe that the endodermis is essentially a tissue of gravisensitive cells we can understand the striking fact that it contains loose starch only as long as the stem is capable of growth curvature.<sup>4</sup> Otherwise the theories of the function of the endoderm, which have never been very satisfactory, have the additional burthen of explaining this last-named fact.

According to Haberlandt (oo), some monocotyledons the leaves of which contain no starch have falling grains in the endodermis. Němec (01, p. 24) quotes from Sachs the case of *Allium cepa*, where statoplasts occur in the root-cap, the endoderm, and punctum of the seedling, and not elsewhere. Then we have occurrence of starch in the pulvinus of grasses and not in the rest of the haulm. *Viscum* is not geotropic, and has no statoplasts. In the holdfast roots of *Hedera* and *Marcgravia* there is no starch, and in *Hoya*, *Pothos*, and *Ficus* the starch is not movable, and these roots are not geotropic.<sup>5</sup>

Just (02) brought forward, as a serious objection to the statolith theory, the fact that tertiary roots possess statoliths, but are not sensitive to gravitation. This objection has been overcome by the discovery<sup>6</sup> that when the primary root is cut off and a secondary assumes its place and manner of growth, the tertiaries springing from it are diageotropic, and thus have at least an occasional use for their statoplasts.

I have shown<sup>7</sup> that the cotyledon of *Setaria* and *Sorghum* is the seat of gravi-perception, and it is there that the statoplasts are found.<sup>8</sup> Wiesner (02) was unable to find statoliths in the perianth-segments of *Clivia nobilis*, which are geotropic, nor in those of *Clivia miniata*, which are not geotropic. Here would seem to be a serious objection to the statolith theory, but Němec (04, p. 58), on repeating Wiesner's observations, finds, on the contrary, a confirmation of his own views. For movable starch-grains occur in the perianth of *C. nobilis*, but not in those of *C. miniata*. In the case of roots the distribution of the statoplasts is especially worthy of note. Physiologists have gradually come to believe that my father<sup>9</sup> was right in his view that

<sup>1</sup> Noll (03, p. 131).

<sup>2</sup> I would suggest the word *statoplast* in place of the cumbersome expression *movable starch-grains*.

<sup>3</sup> See Haberlandt (03) for a description of certain special cases of statocytetissue, apparently replacing the endodermis.

<sup>4</sup> According to Haberlandt (03, p. 451), it is easy to be deceived in asserting that the endoderm contains no starch. Thus Fischer failed to find it in outgrown stems of some plants which possess it when young. Tondera (03) asserts that in certain Cucurbits the falling starch is only present in the older parts no longer capable of geotropism. But Miss Pertz, who has examined most of the species investigated by Tondera, finds statoplasts in the young parts where he failed to find these. Tondera makes some interesting remarks on the distribution of starch in the Cucurbits harmonising with Heine's storehouse theory. It is obviously difficult in the case of the endoderm to distinguish between starch serving as a reserve and starch serving as part of the mechanism of perception. I see no reason why the second function should not be evolved from the first.

<sup>5</sup> Haberlandt (03, p. 461). <sup>6</sup> Darwin and Pertz (04). <sup>7</sup> F. Darwin (99).

<sup>8</sup> According to Němec they occur to some extent in the hypocotyl of *Panicum*. <sup>9</sup> C. Darwin ("Power of Movement").

<sup>1</sup> Kreidl (93).

<sup>2</sup> Haberlandt (00).

<sup>3</sup> Němec (00).

<sup>4</sup> Haberlandt (01).

<sup>5</sup> *Id est*, the cells containing statoliths.

<sup>6</sup> Němec (01, p. 153).

<sup>7</sup> Haberlandt (03) and F. Darwin (03).

the organ of graviperception is in the tip of the root; and it is there—generally in the root-cap—and there only, that statoplasts are found. But these facts do not entirely harmonise with the statolith theory, as I shall show later on in the section devoted to experimental evidence. Here I will only add that the group of statocytes in the root are strongly suggestive of some special function, and those who deny that they form an organ of graviperception must find some other use for them; and this will be no easy task. I must not omit to mention the ingenious experiments of Piccard (04), which prove (if they prove anything) that the root-tip is not the seat of the graviperception, but that this quality is found in even greater perfection in the growing region of the root. But until the whole of the other experimental evidence is proved to be illusory, I must suspend judgment on Piccard's results and treat the question provisionally from our previous standpoint.

The existence of statoliths in regions which have ceased to be capable of ordinary geotropic curvature is at first sight a difficulty. Thus Miss Pertz has found in the pith of the watercress (*Nasturtium officinale*) the most perfect statoplasts, and this in winter, when the capacity for geotropic curvature was probably absent. Again, she has found movable starch in the xylem elements and in the cortex of a number of trees. In this case we must remember that, according to Meischke (99), Jost (01), and Baranetzky (01), woody branches of several years' growth are capable of geotropic curvature. If so, graviperceptive organs must exist. We must remember, too, that in the regeneration of cuttings, Vöchting (78) has shown that gravitation has an influence in certain cases; such cuttings must therefore have organs of graviperception. Or, if this is not granted as necessary, it seems to me conceivable that falling starch-grains, though made use of, and in a certain sense specialised, for graviperception, should nevertheless exist and serve other purposes in the economy of the plant. But this question needs further detailed work.

Lastly, as part of the general question of distribution, it must be clearly pointed out that in a large number of plants, such as Algae and Fungi, no statoliths are known to exist, though their complete absence has not been proved.<sup>1</sup> Here we must either believe in Noll's minute and hitherto unseen statoliths or in a different mechanism, such as hydrostatic pressure. There is no more impossibility in this state of things than in the presence of statoliths in Palæmon and their absence in higher animals. And I am glad to note that both Pfeffer and Czapek are not disinclined to believe in the possibility of various forms of graviperception.

#### Experimental Evidence.

A flaw runs through a great part of the experimental evidence, which may be illustrated by an experience of my own. I found<sup>2</sup> that seedlings of *Setaria* and *Sorghum* could be nearly deprived of statoplasts by means of a high temperature, and, further, that such destarched plants were markedly less geotropic than normal specimens. Here seemed a proof of the theory; unfortunately, however, it turned out that the plants in question were also rendered less heliotropic. These facts make it impossible to allow Némec's gypsum experiment to be convincing. He caused a loss of starch by enclosing roots in plaster of Paris, and found that they had in great part lost their geotropic power. But he did not discover whether this loss depended on disappearance of part of the sense-organ or on general loss of curving power, though he has since (02) made the interesting observation that roots so treated are capable of hydrotropism. Again, Némec found in resting seeds of *Vicia Faba* that the statoliths are undeveloped, and that they appear synchronously with the power of geotroping. Would not a similar thing be true of the apheliotropism of *Sinapis* roots—i.e., might it not be found that they were not heliotropic until the starch appeared?

The same objection must be brought against Haberlandt's otherwise convincing observation<sup>3</sup> that *Linum* growing out

<sup>1</sup> See Némec (*Beihfte Bot. Central.*, B. xvii. 1904, p. 59), where he describes the cases and the occurrence of statoliths in the mosses and liverworts. Giesenhagen (01) has described heavy bodies at the tips of the rhizoids of *Chara* which fall to the physically lower side.

<sup>2</sup> F. Darwin (03).

<sup>3</sup> Haberlandt (03). It seems, however, that the starchless plants had some heliopic capacity.

of doors in late autumn or winter is both devoid of statoplasts and incapable of geotropism, and that the power of curvature returns on bringing the plants indoors, when the starch reappears. The full value of these experiments cannot be made clear without going into more detail than is here admissible. They are particularly interesting because, as Haberlandt remarks, so far as they prove the truth of the statolith theory, they also disprove the pressure theory. This may also be said of other experiments mentioned in the present section.

We must, I think, object on similar grounds to Némec's observations, suggestive though they are, on the absence of geotropism in certain individual leaves and roots which, through unknown causes, had no statoliths.<sup>1</sup>

The same must be said of the above-mentioned experiments of Haberlandt, in which geotropism is increased by rapid shaking in a vertical plane. I attempted<sup>2</sup> to avoid this fault in the similar experiments with a tuning-fork made independently, which showed that the effect of vibration in increasing reaction is far greater in the case of geotropism than in heliotropism.

Haberlandt (00) made the interesting observation that plants deprived of their endodermis by means of an operation lose the capacity of geotropism. Here, again, we ought to know how the operation affects sensitiveness other than geotropic; and, as Haberlandt grants, it may perhaps be said that the operation is too serious to allow of the foundation on it of a very convincing argument.

The question how far the statolith theory is applicable to the root is a difficult one. It involves the old and apparently insoluble difficulty of distinguishing between the removal of the tip of the root, considered as a perceptive organ, and the effect of the shock of the operation. The question is, moreover, complicated by contradictory evidence. According to Czapek, cutting off a small part of the root-tip, an operation which does not remove the whole of the statoliths, interferes with geotropism in the same way as does actual amputation.<sup>3</sup>

Némec, on the other hand, finds evidence for the operation depending on the removal of the sense-organ; for according to him the power of geotroping does not return with the appearance of general symptoms of recovery, such as cell division and the growth of a callus, but only with the actual reappearance of statocytes.

Némec's most recent experiments<sup>4</sup> are confirmatory of this result. He finds that *Lupin* roots, from which  $\frac{1}{2}$  mm., 1 mm., and  $1\frac{1}{2}$  mm. respectively are cut off, behave differently. The  $\frac{1}{2}$  mm. lot were clearly geotropic in seven hours, while no curvature occurred in the others. After a further interval of thirteen hours the 1 mm. lot had curved. Microscopic examination showed that statoplasts had appeared in these roots, but not in the  $1\frac{1}{2}$  mm. lot, which showed no geotropism. It is particularly interesting that according to Némec the statoplasts appeared in a new growth which was visible as a slight convexity of the cut surface.<sup>5</sup>

An experiment by Némec with the roots of *V. Faba* must also be mentioned. One millimetre was cut from the tips of each of a number of roots, and they were all placed horizontally. They were examined after fifteen hours, when considerable variety in the result of the operation was evident; some of the roots had bent geotropically, while others were still horizontal. On cutting sections it was found that the geotropic roots had statoplasts, the horizontal ones none. It may of course be said that the result depends on the effect of shock lasting longer in some individual roots, since, as Czapek has well said, the only proof of the disappearance of shock effect is the act of curving. But since the operation was approximately the same in all the roots, it is hard to believe in such a malicious coincidence as that the shock was smaller in all those roots which produced statoplasts. But it may be said that shock prevented both geotropism and statoplast-formation in certain roots.

<sup>1</sup> Némec (01).

<sup>2</sup> F. Darwin (03).

<sup>3</sup> Czapek (02, p. 118).

<sup>4</sup> Némec (04, pp. 46, 52).

<sup>5</sup> This agrees, as Némec says, with Wachtel's (99 resu who found geotropism returning before the whole tip was regenerated.

Czapek (02) quotes the experiment of Brunchorst, who found that a circular cut round the tip, not deep enough to free the terminal part, has the same effect as amputation. On the other hand, Némec<sup>1</sup> states that geotropism persists, if the root-tip is cut half through by two opposite incisions in different planes, so that the whole of the tissues are divided, and yet the tip is not amputated. Thus four out of five bean-roots treated in this way showed distinct geotropism in 5½ hours. This seems to me a striking result, as showing that the shock of the operation is not exclusively the decisive element. Némec has, moreover, shown that if geotropic curvature has begun on a normal root, a wound interferes with the amount of after-effect, and that the precise nature of the wound is not decisive, and this, as far as it goes, confirms the assumption that two half-cuts would produce as much shock as actual amputation.

Czapek<sup>2</sup> finds that splitting a bean-root longitudinally has the same effect as decapitation. This would mean that decapitation produces its results by shock only, since in a split root there is no removal of the tip. I think I was the first to make use of the splitting of roots in this connection. I wished to show<sup>3</sup> the incorrectness of Wiesner's view—viz., that amputation prevents geotropism by checking growth. In my experiments the split roots were greatly checked in growth, but curved geotropically, behaving in this respect quite differently from amputated specimens.

Another striking bit of evidence on Czapek's side of the question<sup>4</sup> is the fact that Lupin roots from which "½ mm. of the tip has been removed, and which, therefore, contain no statoliths," show the remarkable homogentisin reaction which he has convincingly proved to be a symptom of gravi-perception. Czapek adds that the same is true of roots from which 1 mm. has been removed. It seems to me that Némec's reply to this<sup>5</sup> is of value. He finds that the root-cap in Lupin is variable in length, but always longer than ½ mm.; therefore, in the roots from which ½ mm. only was removed there should have been some statocyte tissue remaining. Even after the removal of 1 mm. the root can, according to Némec, rapidly form statocytes, since the section is in the neighbourhood of the calyptrogen.<sup>6</sup>

Némec suggests it to be conceivable that differences of pressure in Czapek's sense may give rise to the homogentisin reaction, while the true act of gravi-perception is confined to the statoplasts. This is no doubt possible, but I confess that, if the homogentisin reaction can occur in root-tips which have no statoliths I should consider it a strong argument in favour of the view that pressure-difference in Czapek's sense supplies the machinery of perception in roots. Czapek also claims that his experiments with bent-glass tubes (Czapek, 95) prove the gravi-perceptive region of the root not to be confined to the region of statoplasts, since if the root-cap alone is in the vertical branch of the tube, geotropic curvature is not excluded. Némec (04) has attempted a rejoinder to this objection; with what success readers must judge for themselves.

It will be seen that, in my opinion, the balance of evidence is not fatal to the statolith theory. Czapek, who treats the question in a broad and liberal spirit, is by no means inclined to deny that statoliths have a share in gravi-perception; all he claims to prove is that the statoplasts do not supply the whole of the mechanism. It is not easy for an upholder of the theory to allow this much in the present stage of the controversy. The best way of testing the theory is by comparing the distribution of geotropism with that of statoliths; and if we are to allow, in all cases which are opposed to the statolith theory, that the stimulus depends on pressure differences in Czapek's sense, we deprive ourselves of the best means of proving the truth or falsehood of our theory. Those who uphold the theory must have the courage of their opinions and finally trust to the facts of distribution. But further knowledge is necessary before such a judgment can fairly be made.

<sup>1</sup> Némec (01, p. 19).

<sup>2</sup> Czapek, (98, p. 202) and (02, p. 118).

<sup>3</sup> F. Darwin (82).

<sup>4</sup> Czapek (02, p. 463).

<sup>5</sup> Némec (04, p. 53).

<sup>6</sup> He adds that the calyptrogen may in this way have an indirect importance, and Fritsch's belief that this tissue was the essential seat of gravi-perception may be accounted for.

### Centrifugal Force.

Jost<sup>1</sup> objects that plants on a centrifugal machine do not behave as the theory would lead us to expect. Thus he found that certain roots and seedlings showed geotropic curvature, although the statoplasts were scattered through the cell, not spread out on the cell-walls furthest from the axis of rotation. Miss Pertz<sup>2</sup> and I have repeated some of Jost's experiments, and have come to an opposite conclusion. We find that *Setaria* does not curve with a centrifugal force of less than 0.02 g., and this is about the limit for visible displacement of the starch-grains. As the centrifugal force increases up to 0.04 g. we get slight amounts of curvature and slight amounts of starch displacement. The two phenomena cannot be accurately compared, but so much is clear: that the result of Knight's experiment is not destructive of the statolith theory, but, on the contrary, is roughly in harmony with it.

The result of an intermittent stimulus may seem to some a difficulty. Jost<sup>3</sup> produced geotropic curvature by placing seedlings in the horizontal and vertical positions for alternate periods of 3½ minutes. With alternate periods of 50" horizontal and 2' 30" vertical he sometimes failed to get a geotropic curve, and exposures if less than 50" always failed. It is commonly said that 15–25 minutes are needed for the starch to fall on to horizontal cell-walls, and it may seem, therefore, that in these experiments neither 3½ minutes nor, *a fortiori*, 50" could produce a change of position in the statoliths, and that therefore the experiment is destructive to the theory. But this would be a wrong conclusion, for, according to my experience, the falling time of starch is often less than 15 minutes; and even if this were not so there would be no difficulty in understanding the above experiments, for, as Jost allows (*loc. cit.*), and as Némec (02) has also pointed out, the statoplasts may stimulate the cell without the occurrence of any visible displacement; for if the statoplasts do not fall over and spread out on the horizontal walls there must be a column or heap of starch-grains, the height of which equals the width of the cell, resting on the lateral wall of the cell instead of, as in the normal position, a shallower layer pressing on the basal wall. Here we have plain conditions of differentiation between the vertical and horizontal positions.

The same considerations apply to the whole question of what is known as the geotropic presentation time<sup>4</sup>—i.e., the minimal period of horizontality needed to induce a geotropic curvature. It has been said that the presentation time corresponds with the time needed for the statoliths to fall on to the horizontal walls of the sensitive cells. It seems to me that we hardly have knowledge enough to be certain of this coincidence, and since, as above pointed out, the statoliths may begin to stimulate before they are visibly displaced, the question is not one of much interest or deserving of special inquiry.

### Theoretical.

Elfvig's<sup>5</sup> well-known experiment with grass haulms shows that (in this instance) the action of the klinostat depends, not on the prevention of all gravi-perception, but on the equal distribution of stimulus.<sup>6</sup> But other plants react differently—that is to say, they do not exhibit increased rectilinear growth on the klinostat. This can best be accounted for, as Noll<sup>7</sup> suggests, by the supposition that the equally distributed stimulus tends to produce a simultaneous increase and decrease of growth-rate on opposite sides of the rotating plant.<sup>8</sup> We, therefore, get in an indirect way evidence in favour of what has not been directly proved—namely, that in geotropic curvature the diminution of growth

<sup>1</sup> Jost (02).

<sup>2</sup> Darwin and Pertz (04). By an oversight we omitted to give a reference to Némec's (02, p. 347) interesting reply to Jost's criticism.

<sup>3</sup> Jost (02), p. 175. See also Czapek (98), p. 206; and Noll (00), p. 462.

<sup>4</sup> Czapek (98), p. 183.

<sup>5</sup> Elfvig (84) proved that the pulvini of grass haulms increase in length when kept in slow rotation on a klinostat.

<sup>6</sup> My experiments on the germination of *Cucurbita* demonstrate the same point (Darwin and Acton, 94). Czapek (02, p. 469) shows that the homogentisin reaction occurs on the klinostat.

<sup>7</sup> Noll (92, p. 35).

<sup>8</sup> We have shown (Darwin and Pertz, 04) that in *Setaria* the statoliths undergo changes of position on the klinostat, indicating a succession of stimuli. See Heine (85), who briefly describes similar changes.

on the concave side is not the result of compression produced by increased growth on the convex side, but rather an independent reaction. It is necessary, therefore, to inquire what theoretical conclusions may be fairly made as to the stimulation correlated with such a mechanism of curvature. Noll<sup>1</sup> uses the term "Reizfeld," or "stimulation-area," to express the regions in which graviperception occurs. The distribution of these areas is expressed in diagrams which serve as shorthand methods of recording the geotropic reactions of various organs. All such ways of clarifying and expressing our ideas of the laws of perception are useful. I must confess that I do not find Noll's terminology easy to use, and I prefer to express the same ideas in terms of the distribution of the pressure of statoliths on the different parts of the ectoplasm of the gravi-sensitive cells.

Imagine an apogeotropic shoot placed in the horizontal position as shown in longitudinal radial section in Fig. 2, where C and C' are the cortical tissues and the seat of motile power; E and E' the endodermis, the supposed region of graviperception; M, the central tissues, which do not concern us.

The fact that the statoliths now rest on the horizontal (tangential) walls differentiates the horizontal from the vertical position of stable equilibrium. But what circumstance is there that can be conceived to originate curvature in one direction more than another? It can only be that in the endodermis E on the physically upper side the statoliths rest on the inner tangential wall, whereas in E' they

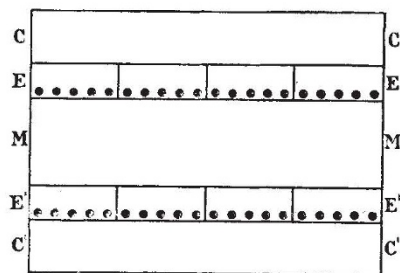


FIG. 2.

rest on the outer wall. This view agrees with Noll's hypothesis of the arrangement of stimulation-areas. There is no difficulty in believing that the inner and outer tangential walls have different individualities; Vöchting's work<sup>2</sup> on transplantation seems to indicate that this is the case. And if this analogy with formative polarity is not allowable, we must still insist that the presumption is in favour of E and E' in Fig. 2 being in different conditions, since we have certainly no right to assume that the outer and inner walls are identical in what we have called their individuality.

It is not here necessary to go into the question whether the radial walls of the endodermis are or are not sensitive, since the problem of geotropism in its broad outlines is not concerned with it.<sup>3</sup>

*The Position of Maximum Stimulation.*

This problem involves the question whether an orthotropic organ in the vertical position is or is not freed from stimulus. We will first take the question as to the existence of a stimulus in the normal (*i.e.*, not the inverted) position. One of Pfeffer's<sup>4</sup> arguments for the existence of a stimulus is as follows. A root having been allowed to curve from the horizontal to the vertical position is placed on a klinostat, and after a time the curve disappears. It is therefore assumed that there existed a geotropic stimulus keeping the root curved until the stimulus in question was rendered inoperative by the klinostat, when the rectipetality of the root could have free play. But it is not a necessary conclusion that while the root is strictly vertical any stimulus is acting. If from some internal cause the root leaves the vertical, the ordinary geotropic curvature depending on the

stimulation of the tangential walls will come into action and bring the root back to the vertical. To translate into the language of the statolith theory, it is not necessary to assume that the lower walls of the graviperceptive cells are sensitive to the pressure of the statoliths—the sensitiveness of the tangential walls will suffice. The experiment above mentioned does not therefore seem to prove that an orthotropic organ in stable equilibrium is stimulated. But it is quite conceivable that a stimulus might be originated by the loss of pressure on the lower wall, for this would be a well-marked change in the internal condition of the cell, and therefore might become associated with a reflex. Thus, when an organ is placed horizontal the stimulus from the pressure of statoliths on the lateral walls (now horizontal) may be combined with, or in some way influenced by, the loss of pressure on the terminal wall of the cell which was formerly horizontal. But if the absence of pressure on a cell-wall acts in this way are we not bound to consider the pressure (when present) as a stimulus? I think we are, and therefore, though I do not think that the particular experiment referred to supplies the necessary evidence, I hold the lower wall of an orthotropic cell to be sensitive to the stimulus of statoliths, though such stimulus cannot be of a *directive* nature.

Since an organ when accurately inverted<sup>1</sup> and prevented from circumnutating receives no impulse to curve, it is assumed that the normally upper cell-wall (which is now below) is not stimulated. According to the statolith theory it is inconceivable that the organ should curve, since uniform pressure on the horizontal terminal wall cannot determine the *direction* in which such curve shall begin.

But though no directive stimulus seems to be a possible result of uniform pressure on the end-walls, it does not follow that such pressure has no effect. It seems to me that such a striking change as pressure on a wall which in normal circumstances does not receive pressure may very well modify the result of the normal stimulation of the lateral walls of the cell.

Czapek<sup>2</sup> has shown that with both stems and roots the gravistimulus is greater when the organ is removed from the normal vertical position by 135° than when it deviates from the normal by 45°. In the case of an apogeotropic shoot the position of the starch in the endoderm is given in Fig. 3. The pressure of the starch on the lateral walls is the same in the two cases. In *i.*, however, the starch rests partly on the basal wall (B), while in *ii.* it rests, to the same degree, on the apical wall (A). On the usual assumption that the basal and apical walls are insensitive, there is nothing to differentiate *i.* from *ii.* I cannot help suspecting that the pressure on the apical wall does in some way affect the sensitiveness of the tangential walls. If the pressure on the wall (A) was in itself the decisive element we should expect the stimulus to increase as the angle increased—from 135° to nearly 180°—which is not the case. From my point of view we can dimly understand why 135° should be the position of maximum stimulation. It would be the result of a compromise, being a position in which the combined pressure on both lateral and apical walls was as high as possible<sup>3</sup>—a mean, in fact, between full pressure on the lateral walls (as in the horizontal position) and full pressure on the apical walls (as in the vertical position).

If some such theory is not adopted we must imagine with Haberlandt that the difference between positions *i.* and *ii.* depends on the weight of the statoliths in *i.* being on the *basal half* of the lateral wall, and on the *apical half* in *ii.* It seems to me that the difference of sensitiveness in the two regions would have to be very great, considering that in the horizontal position, in which the gravistimulus is less than in position *ii.*, the full pressure of a considerable fraction of the total starch acts on the supposed extra-sensitive region of the cell-wall.

But when all has been said there remains a difficulty with which I do not know how to deal. It is clear that, according to either theory, the critical position should be the hori-

<sup>1</sup> In the whole of this discussion the organs are supposed to be supported by the morphological base.

<sup>2</sup> Czapek (95, 1). As doubt has been expressed as to the actual facts, it is worth while mentioning that Miss Pertz (99) has confirmed his results for the haulms of grasses.

<sup>3</sup> The fact that at angles above 135° the stimulus remains greater than when the organ is horizontal seems to point to the conclusion that the share of the end wall in graviperception is relatively great.

<sup>1</sup> Noll (92, p. 19).

<sup>2</sup> Vöchting (92, p. 157).

<sup>3</sup> See the discussion in Haberlandt (93, p. 467).

<sup>4</sup> Pfeffer (93, p. 19). I am only concerned with this special point, not with Pfeffer's general argument.

zontal, and that as the organ is moved further and further from the normal (in successive experiments) the geotropic reaction ought to increase decidedly as the horizontal is passed; and this is not the case.

#### Diageotropism.

The diagram, Fig. 2, will serve to represent a diageotropic organ in stable equilibrium. In spite of the fact that it is at rest in the horizontal position, we must assume that the tangential (horizontal) walls of the endodermis are sensitive to the pressure of the statoplasts. For when the organ is placed obliquely it has the power of returning, by curvature, to the horizontal; and this requires that the plant shall distinguish up from down. If its apex is above the horizon it must curve downwards, *i.e.*, towards that side on which the statoplasts rest on the *external* walls of the endoderm cells, and *vice versa* if the apex is below the horizon. But what signal tells the plant that it is not horizontal? This can only be effected by the statoplasts pressing on the basal or apical walls, as in Fig. 3.

The difficulty is increased by the fact that when a diageotropic organ is fixed vertically, the apex being up or down,<sup>1</sup> no curvature follows. This, according to the usual idea, would mean that the terminal walls are not sensitive. But the walls must be sensitive in some way, or the plant would not react to the gravistimulus, as it undoubtedly does. The only conclusion I can come to is that the position of the statoliths shown in Fig. 3, in which they rest partly on the terminal wall and partly on the lateral (tangential) wall,

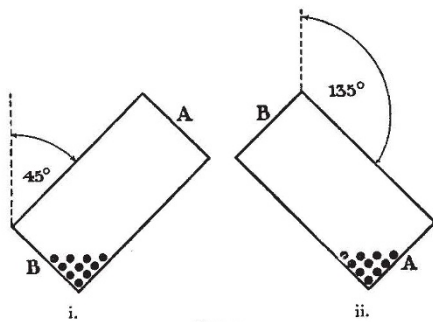


FIG. 3.

must be capable of giving the combined stimulus,<sup>2</sup> as above suggested.

Personally I do not attach great importance to the details of how the statoliths act on the different walls of the cells, although as part of the history of the inquiry I feel bound to discuss it. The broad fact that the statoliths rest on different parts of the cell-walls when the geotropic organ is placed at different angles with the vertical seems to me sufficient. The precise manner in which various reactions are associated with the position of the statoliths may be confessed to be for the present beyond our knowledge or powers of imagination, and such confession need not weaken the position of our theory.

Finally, I desire to say a word on a subject having but a remote connection with my theme. There is at the present time a tendency to pay an increasing attention to what is known as rectipetality or autotropism—*viz.*, the inherent capacity of rectilinear growth. In my Cardiff Address<sup>3</sup> to Section D I showed that rectipetality is really part of the phenomena of circumnutation. We must believe that rectipetality does not merely come into play in those comparatively crude experimental instances in which a geotropic curvature is flattened out by means of growth on the klinostat. We must believe that it also corrects curvatures which arise from the slight irregularity of normal everyday growth. This will imply that normal growth is built

<sup>1</sup> Czapek (93, p. 243). Noll (92, p. 37) had foreseen on theoretical grounds that this would prove to be the case. See also Noll (90, p. 473).

<sup>2</sup> In Noll's diagram of the stimulation-areas in a diageotropic organ the obliquely placed areas seem to suggest a similarity to what is here given [see Noll (92, p. 29)]. But his stimulation areas in which only a single statolith occurs are not strictly comparable to cells containing numerous statoplasts.

<sup>3</sup> F. Darwin (91).

of a series of internal corrections; in other words, of circumnutation. The point I wish now to emphasise is that the stimuli, be they of geotropic or any other nature, should be conceived as acting not on a stationary but on a moving plant—acting, in fact, on the spontaneous correcting power, whether we call it rectipetality, autotropism, or circumnutation. It is impossible to say how this consideration might modify our speculations as to the manner of action of the gravistimulus. It is quite conceivable that it might not alter our theoretic views at all, but without more knowledge we cannot be certain. My only point at present is that if we are led into contradictions or confusion by attempts to analyse what goes on in the gravisensitive region according to the statolith theory, such a result must not be held to be fatal to the theory until we know more of the problem.

In conclusion—and to clear our minds of the doubtful speculations in which I have entangled myself—I should like to reiterate my belief in the general, though not the universal, applicability of the statolith theory. I find it impossible to doubt that, in the case of the higher plants, sensitiveness to the pressure of heavy bodies will be found to be by far the most important, if not the exclusive, means by which gravity is perceived. We have seen that the stimulus must depend on weight; and since neither the theory of radial pressure nor Noll's supposition of stimulation by small unknown bodies lends itself to experimental inquiry we are driven, as practical people, to test the views of Haberlandt and Némec.

I base my belief partly on what I have already said, namely, that geotropism, being an adaptive reflex action, must during its development have been correlated, by that mysterious bond which unites stimulus to reaction, with some change, by which in the natural course of events it is uniformly preceded. Now the most obvious change which precedes geotropism is the disturbance of the falling starch-grains. This fact, together with what we know of the distribution of statoplasts, would almost force conviction on me. But this is not the whole of the evidence. We know from Némec's researches that the protoplasm, in the cells assumed to be sense-organs, is sensitive to the pressure of the statoplasts; and we know from zoological evidence that heavy bodies resting on a sensitive surface can function as a sense-organ for gravitation. Finally, the experimental evidence, though not absolutely convincing, has not revealed any absolute bar to our belief in the statolith theory, and has brought to light a number of facts harmonising with it in a remarkable manner. It seems to me that the theory of Némec and Haberlandt may fairly hold the field until a better theory of graviperception and a better theory of the function of falling starch-grains are established.

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gentlemen, Profs. Studer, Minot, Grassi, and Perrier, were afterwards elected presidents for the general meetings, and Profs. Emery, Fujii, Spengel, Osborn, v. Graff, Pelseneer, Lönnberg, Blanchard, Chun, v. Wijhe, Lang, and Drs. Horvath, Stejneger, Stiles, and Miller as vice-presidents. The meeting also agreed to divide into seven sections, viz. :—General Zoology, president, Prof. Salensky; vice-president, Mr. Schlumberger; secretary, Dr. Gurwitsch. Vertebrata (systematic), president, Dr. Jentink; vice-president, Dr. Scharff; secretary, Dr. André. Vertebrata (anatomy, &c.), president, Prof. Monticelli; vice-president, Dr. Bashford Dean; secretary, Dr. Penard. Invertebrata (excluding Arthropoda), president, Prof. Ehlers; vice-president, Prof. Koehler; secretary, Dr. Fuhrmann. Arthropoda, president, Prof. Heymons; vice-president, Dr. Janet; secretary, Dr. Steck. Applied Zoology, president, Prof. Hoek; vice-president, Prof. Plate; secretary, Dr. Duerst. Zoogeography, president, Prof. Hérouard; vice-president, Prof. Blasius; secretary, Dr. Roux.

Two propositions had been received by the president, Prof. Studer, one from the Prince of Monaco, to hold the next congress at Monaco, and another from the zoologists of the United States of America. After due consideration of these proposals, it was decided by the permanent committee and by the delegates of the scientific societies to recommend that the latter invitation be accepted, which was unanimously adopted at the general meeting. It was therefore agreed that the next congress, in 1907, should be held at Boston, and that Prof. Agassiz be asked to preside. Prof. Minot expressed the hope that it might be possible to place at the disposal of the European zoologists a large steamer, which would call for them at Hamburg, Cherbourg, and Southampton.

Subsequently, Prof. Blanchard gave an interesting address on the production of disease in man by animal parasites, and also pointed out in how many ways zoological discoveries had aided not only the elucidation and diagnosis of disease, but also its cure; after which Prof. Lang made some remarks on the life of the Swiss naturalist, Alexander Morizi, born in 1806 at Chur, who, some years before the appearance of Darwin's "Origin of Species," had published a paper in which he promulgated the theory of evolution and supported the view that man had evolved from the higher animals.

At one of the later general meetings, Profs. Salensky, Osborn, Chun, Hoek, and Sarasin delivered addresses. Prof. Salensky referred to the results of the most recent investigations of the life-history and anatomy of the mammoth, and exhibited photographs of a specimen *in situ* (already noticed in NATURE), as well as preparations of the skin, muscles, hairs, &c. It seems now to be a well established fact that the mammoth was a northern species feeding especially on conifers, but also on cyperaceous, graminaceous, and leguminous plants. The recently discovered stages in the evolution of the horse and contemporary mammals in North America formed the subject of Prof. Osborn's lecture, while Prof. Chun dealt with the vertical distribution of the marine plankton.

Altogether more than four hundred zoologists, many of whom brought one or more members of their family, took part in the congress. The general meetings were held in the large hall of the Swiss House of Parliament, and the sections met in the lecture rooms of the splendid university buildings, of which the country is justly proud.

I.—GENERAL ZOOLOGY.

It has been assumed that the South American Stegomyia was the means of transferring a blood parasite to man, which gave rise to yellow fever; Prof. Goeldi, of Para, however, gave reasons for his belief that this disease is not due to any blood parasite, but to an organic toxin which he discovered in the saliva of Stegomyia.

The zoological aspect of De Vries's mutation theory was discussed by Prof. Plate, who recognised that the theory signified an important advance of knowledge in so far as it showed that sudden changes could arise in the organism which were highly transmissible, but he urged that a sharp morphological boundary could not be drawn between variations and mutations. The former must be considered as changes with a slight capacity of inheritance, the latter as such with a high capacity.

THE SIXTH INTERNATIONAL CONGRESS OF ZOOLOGY.

THE smoothness with which the complicated arrangements for the reception and housing of so many guests were carried out, and the kindness and hospitality of the welcome extended to them, formed a good augury for the success of the sixth International Congress of Zoology, which opened at Berne on Monday, August 15. On the previous day the members, gathered from many parts of the world, were received by the reception committee at the railway station, and invited afterwards by the Mayor of the city to a "symposium" in the "Kornhauskeller." The gaiety of the assembly, which did not break up until a late hour, formed an agreeable prelude to the work of the congress, which was throughout interspersed with pleasant entertainments.

At the general meeting the next morning Prof. Studer, the president, chose as the subject of his address the Swiss fauna, to the study of which he has devoted so much of his life. Prof. Perrier, of Paris, as president of the permanent committee, thereupon expressed his feelings of gratitude to the Swiss Government and to the authorities of the canton of Berne for the hospitality which had been extended to the members of the congress. The following