

The Integrative Action of the Nervous System

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WITH ILLUSTRATIONS



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LECTURE V

COMPOUND REFLEXES: SIMULTANEOUS COMBINATION

Argument: Combination of reflexes simultaneously proceeding. Spread of reflex-response about a focus. Gray matter and lines of reflex resistance. "Short" reflexes and "long" reflexes. Rules decipherable in the spread of reflex reaction. Pflüger's "laws" of spinal irradiation. The "reflex figure." Variability of reflex result. Irradiation of a reflex attaches itself to the problem of the simultaneous combination of reflexes. Co-ordination of reflex result obtains even when large mixed afferent nerve-trunks are stimulated. The movement excited by stimulation of the motor spinal nerve-root does not really resemble a movement evoked reflexly or by the will. Extent of simultaneous combinations of reflexes. Simultaneous stimuli arrange themselves naturally in constellations in which some component is usually of pre-eminent intensity. The resulting compound reaction has both positive and negative sides.

A LARGE part of co-ordination consists in the orderly combining of reflexes. In studying this co-ordination we have to deal with and discriminate between simultaneous combinations and successive combinations of reflexes. We may proceed to attempt the former problem.

Irradiation. If by appropriate stimulation of the skin of the foot, say by unipolar faradization of a spot of the plantar skin of a digit, the ordinary flexion-reflex of the hind limb of the dog be evoked, the extent of the reflex increases with increase in the intensity of the stimulus. The reflex-effect spreads over a larger and larger field, irradiating as it were in various directions from a focus of reflex-discharge which takes effect on the limb itself.

The centrifugal discharge elicited by any reflex seems as regards its spatial distribution to be focussed about a centre round which its irradiation varies according to circumstance. In the scratch-reflex the pretibial muscles that dorso-flex the ankle seem to lie at the focus of the motor discharge. In

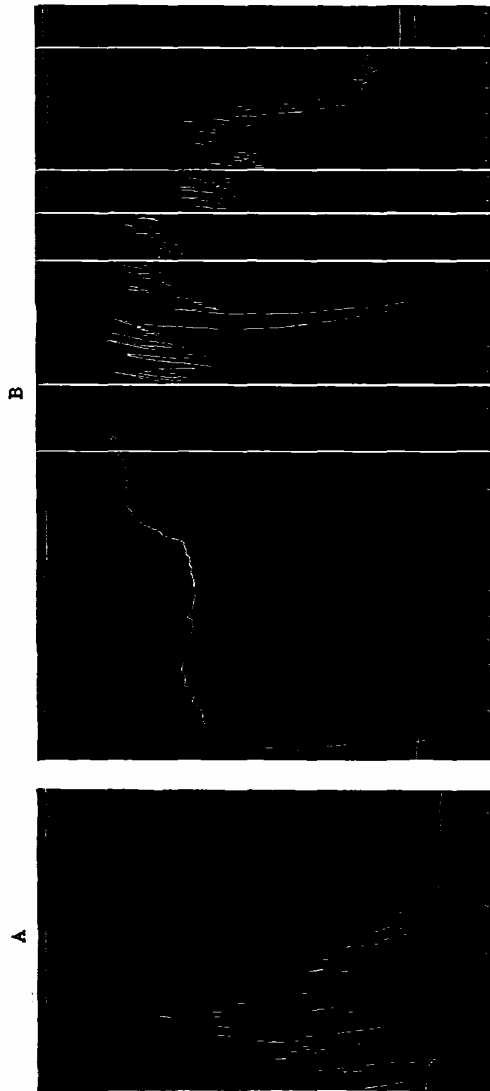
the "flexion-reflex," if the reaction evoked is very weak a band of the deep inner hamstring muscle has often in my experience seemed the only part of the musculature thrown into action. On the other hand, when the reflex is evoked with medium strength it can often be seen that after the reflex (the exciting stimulation being continued unaltered) has been in progress for a few seconds, flexion at hip adds itself to the flexion at the knee (see Fig. 45). And by strong stimulation, strong flexion at hip occurs together with that at knee and practically from the very outset. In my experience the condition of "spinal shock" is very favourable for noting the seat of the focus of the motor discharge in a reflex, because in that condition it happens often that the piece of musculature which is at focus of the discharge is the only one which can be got to give the reflex-response. It seems possible in this way to determine what reflex in, for instance, a "spinal" monkey corresponds with this or that reflex in a "spinal" dog. In the monkey the severity and long duration of spinal shock allows merely the focal reply in the musculature. Thus a feeble tightening of a part of a hamstring muscle in the "spinal" monkey affords fair evidence, in response to a stimulus of the foot, that the flexor-reflex—for the full extent of which one must turn to the "spinal dog"—is evoked. In man spinal shock seems still more severe and lasting than in the monkey. The situation of the weak brief contractions evoked can still reveal which they correspond with among reflexes better open to study in the lower mammals.

The more intense the spinal reflex—apart from strychnine and similar convulsant poisoning—the wider, as a general rule, the extent to which the motor discharge spreads around its focal area. Thus, as stimulation of the planta causing the flexion-reflex is increased there is added^{182, 275} to the flexion of the homonymous hind limb extension of the crossed hind limb, then in the homonymous fore limb extension at elbow and retraction at shoulder, then at the crossed fore limb flexion at elbow, extension at wrist, and some protraction at shoulder; also turning of the head toward the homonymous side, and often opening of the mouth, also lateral deviation of the tail.

According to circumstance, especially according to intensity of stimulation, the field of end-effect of the flexion-reflex may vary from a minute field occupying part of a flexor muscle of the knee to a field including musculature in all four limbs and neck and head and tail.

That the reaction should spread in its spatial extent is not surprising. The afferent neurone on entering the central organ, the spinal cord, enters a vast network of conduction of paths interlacing in all directions. A glance at any Weigert preparation of the spinal cord shows a tangle of branching nerve-fibres, the richness and intricacy of which seems practically infinite. Into this forest the receptive neurone conducts the impulses, and can itself be traced, breaking up into many divisions that pass in many directions and to various distances. And this web of conductive channels into which the centripetal impulses of the reflex are thus launched is known to be practically a continuum in the sense that no part of the nervous system is isolated from the rest. "A group of nerve-cells disconnected from the other nerve-tissues of the body, as the muscles or glands are disconnected from each other, would be without physiological significance. To understand the physiology of the nervous system it is important to keep in mind the fact that by histology it is found to be continuous throughout its entire extent."²⁰⁹ And there is the generally accredited statement that on exhibition of strychnine centripetal impulses poured in *via* any afferent nerve, excite reflex-discharge over the efferent channels of the whole nerve-system. This, even if not strictly true, is sufficiently approximate to the truth to show the enormous interconnections between any afferent channel and the congeries of arcs of the

FIGURE 45.— Maintenance of the scratch-reflex A and the flexion-reflex B respectively under unipolar faradic stimulation of comparable intensity. The diffuse electrode (anode) was on the fore limb in each case; the primary circuit and its rate of interruption was the same, and the secondary coil of the inductorium remained at the same distance from the primary. For the scratch-reflex the needle electrode was set in the skin of the loin, for the flexion-reflex in the plantar skin of the outermost digit. After giving 28 beats the scratch-reflex died out, having lasted about seven seconds. Further continuation of the stimulation was cut short as useless after four more seconds. The flexion-reflex, on the other hand, is in full intensity at the end of the 13th second of continued application of the stimulus, and its amplitude is perfectly maintained at the end of the 20th, although the reflex is rather tremulant. At the 44th second, when it has become more tremulant



still, it suddenly shows a brief, complete relaxation, lasting somewhat less than a second. This is accompanied by contraction of the extensor muscle of the knee (successive spinal induction, Lect. VI). After this the reflex is well maintained, although tremulant to the 54th second; thence onward it shows gradual decline, reducing it by about a third of its original amplitude, when the stimulus is stopped at the 95th second. Relaxation then sets in promptly and the tremor diminishes, but the original base line is hardly reached even fifteen seconds later. At the 10th second the flexion-reflex shows an increase due to sudden spread of the reflex to the flexors of the hip. The break shocks used in stimulation were at the rate of 33 per second. The signal line above marks the rate of repetition of double-induction shocks used in stimulation. Time below in seconds.

whole central nervous system. It is therefore not surprising that the reflex reaction should spread. On the other hand, the data leave unexplained certain features of the spread. How is it that the spread, as the reflex is intensified, does not extend everywhere, as it is said to do in strychnine poisoning? How is it that in the flexion-reflex, of the cat for instance, the spread does not extend to the muscles of the pinna of the ear? It is easy from certain parts to obtain the brisk reflex retraction of the pinna. Yet in my experience the stimulation of the foot that causes the flexion-reflex and all its various irradiations may be pushed without evoking retraction or other movement of the pinna. In other words, the irradiations of the reflex occur along certain lines only and not along others, and the line to the pinna is of these latter.

Evidently the irradiation from each entrant path tends to run in certain directions and not in all. This fact is sometimes stated in the form that gray matter offers to the entrant path lines of conduction possessing different degrees of resistance. To say this merely of course restates the fact in terms suggesting analogy between nerve-paths and electric circuits. Before the Golgi and methylene-blue methods had thrown doubt on the intricate forest of nerve-fibres in the gray matter being a network structurally continuous in all directions, as supposed from the Gerlach preparations and the universal irradiation under strychnine, the differences in conductive resistance were attributed mainly to differences in the length of the network to be traversed by some reflexes as compared with others. The longer that path in the gray matter the higher was thought to be the resistance. Evidence indicating slow travel of impulses in gray matter was taken as evidence of resistance in gray matter. In certain reactions the impulses were supposed to have very long paths of travel in gray matter. Thus, impulses of pain were supposed to ascend along the spinal gray matter to the brain. The path of impulses connected with pain does plunge into the gray matter very soon after entering the spinal cord; it then, probably after a short course, emerges into the lateral white columns, preponderantly of the side crossed from that on

which it entered. This short in-and-out traverse of the spinal gray matter seems typical of all paths in the gray matter; they are probably all quite short.²⁰⁵ If all synapses lie in the gray matter, each path where it involves a passage from one link to another of the neural chain must enter the gray matter to establish its linkage; it probably soon emerges thence again.

Neurone-threshold. But one finds still very generally expressed the view that the differences of resistance to irradiation in different directions are referable to different conductive resistance offered by different fibres in the gray matter. The different resistance seems more probably referable to differences in the facility of conduction at different synapses. At each synapse there is a neurone-threshold.¹⁸⁷ At each synapse a small quantity of energy, freed in transmission, acts as a releasing force to a fresh store of energy not along a homogeneous train of conducting material as in a nerve-fibre pure and simple, but across a barrier which whether lower or higher is always to some extent a barrier. There is abundant evidence that different synapses differ from one another. That neurones should differ in the threshold value of the stimulus necessary to excite them seems only natural. The arguments adduced by Goldscheider point in this same direction. Many of the phenomena considered in the first three lectures are easiest explicable by such differences. The distinctions between different synapses in regard to ease of alteration by strychnine and by tetanus toxin emphasize this probability further. On this view the fact that irradiation of a reflex reaction spreads along certain conductive arcs more readily than along others, can be schematically figured as in the diagram (Fig. 46). A receptive neurone A enters the cord and forms synaptic connections with three neurones, the neurone-threshold at the synapse with one of the neurones is higher than that at the synapses with the others. The threshold heights (resistances) are represented by whole numbers, two and one respectively. Each of the intraspinal neurones in its turn forms two synaptic connections with two neurones, and in these cases also the thresholds at the synapses are of different heights, numerically, two and one respectively. On the view that the

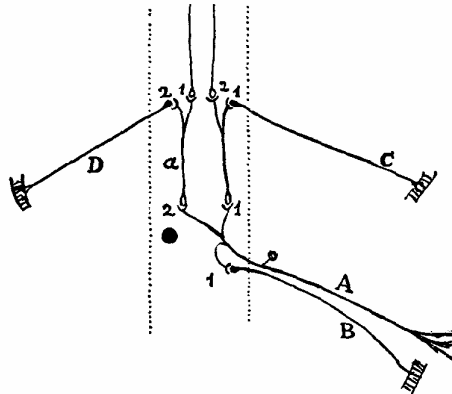


FIGURE 46. — Explanation in text.

action of one neurone upon the next is that of a releasing force liberating a potential system across a barrier whose resistance we do not exactly know, it is impossible to predict how the resistance will sum along the whole conductive chain. It is clear that although the total resistance of the reflex-arc A B may be numerically represented by 1, the resistance along A D need not, on the numerical values assigned to the synapses in the diagram (Fig. 46), sum to the value 4. Yet it is also clear that the threshold for any whole arc cannot be lower than the highest individual threshold in it. Further, the individual thresholds will tend to sum, for an excitation of neurone A just sufficient to excite neurone *a* is hardly likely to excite *a* sufficiently to overcome the threshold of synapse *a* D. Thus, with even small grades of difference of threshold at different synapses, large differences in the conductive facility of different reflex-arcs can be established.

Similarly, an additive influence of the threshold will make a reflex-chain consisting of several neurones offer *caeteris paribus* higher resistance than a chain of fewer neurones. The diagram is therefore in accord with the rule that the reflex-chains which conduct to parts segmentally distant require generally intenser stimulation to excite them than do merely local arcs.

Short and long reflexes. For many purposes of description it is convenient to divide reflexes into "short" and "long."²⁰⁵

The cord may, in its relation to the receptive surface and skeletal musculature, be considered divisible into right and left lateral halves, each subdivisible into regions of neck (cervical, including pinna), fore limb (brachial), trunk (thoracic), hind limb (crural), and tail (caudal). A reflex action in which the stimulus applied to a receptive area in one of the above regions evokes a reaction in the musculature of another of the regions is conveniently called a *long spinal* reflex. A reflex reaction in which the muscular reply occurs in the same region as the application of the stimulus is conveniently called a *short spinal* reflex. Short spinal reflexes are, as a rule, more easily and regularly elicitable than are long spinal reflexes. It might further be convenient to allocate hard-and-fast boundaries to these regions, but such limits would of necessity be artificial and arbitrary. The scope of the delimitation is indicated and its purpose better served by comparison with one retina, say of the bird, the one lateral half of the skin corresponding with one retina; one optic nerve would correspond with the lateral half of the spinal cord and bulb. Between these comparable surfaces a difference exists, in that the receptive field of the skin, unlike the retinal, has instead of one (or two, cf. Kalischer)³¹⁰ focal region of concentrated responsiveness, several such foci, *e. g.* the relatively highly responsive skin at the apex of each limb. As the retina has muscles at call, so also the skin. The closeness of nexus between a retinal point and the visual musculature is graduate in degree, *e. g.* most close for the muscles of its own bulbus, next for those of the contralateral, then for the neck muscles, etc. Similarly there are degrees of nexal closeness between a point of skin and the related musculature: its connection is most close with muscles of its own limb, next with those of another limb or other region. The main interest of direction of nervous irradiation *per se*—apart from light it may incidentally cast upon the integrative work of the nervous system—lies in its elucidation of the machinery for working sentient surfaces. That the skin is a region which morphologically

considered is composed of a segmental series seems to have been allowed greater weight in the estimation of its receptive functions than is fully justified, at least in the higher vertebrata. That its segmental innervation demonstrably limits existing reflex spinal functions in the mammal has not been shown.¹³⁶

Rules observed in the spread of impulses in spinal reflexes.

Regarding short spinal reflexes, and the directions taken by the examples of intraspinal irradiation which they furnish, it is possible to make certain general statements.¹³⁶

I. Broadly speaking, *the degree of reflex spinal intimacy between afferent and efferent spinal roots varies directly as their segmental proximity.* Thus excitation of the central side of a severed thoracic root, *e. g.* seventh, evokes with especial ease contraction of muscles or parts of muscles innervated by the corresponding motor roots, and next easily muscles innervated by the next adjacent motor roots. The spread of short spinal reflexes in many instances seems to be rather easier tailward than headward. This may be related with the oblique correlation that so largely holds between the distribution of the afferent root in the skin and the distribution of the efferent root in the underlying muscles.

II. Taken generally, *for each afferent root there exists in immediate proximity to its own place of entrance in the cord (e. g. in its own segment) a reflex motor path of as low a threshold and of as high potency as any open to it anywhere.* Further, in response to excitation even approximately minimal in intensity a single afferent root, or a single filament of a single root, evokes a spinal discharge of centrifugal impulses through more than one efferent root, *i. e.* the discharge is plurisegmental. And this holds especially in the limb regions. In the limb region the nerve root is therefore a morphological aggregate of nerve-fibres, rather than a functionally determined assortment of impulse-paths. The view that the efferent spinal root is a functional assemblage of nerve-fibres is certainly erroneous. The formation of functional collections of nerve paths (peripheral nerve-trunks) out of morphological collections (nerve roots) seems to be the meaning of the limb-plexuses.

III. Motor mechanisms for the skeletal musculature lying in the same region of the cord, and in the selfsame spinal segment, exhibit markedly *unequal accessibility to the local afferent channels as judged by pressor effects*. For example, if pressor effects only, and the primary phase only, of the reflex movement be considered, the flexors of the homonymous knee and the extensors of the contralateral are in many animals much more accessible than the extensors of the homonymous and the flexors of the contralateral. Inasmuch as at many joints the flexors and extensors are *both* innervated by motor-fibres contained in one and the same efferent root, it follows that the reflex movement obtained by excitation of an afferent root in many cases is quite dissimilar from the movement obtained by excitation of the corresponding efferent root, in spite of the rule of segmental proximity.

It is necessary to insert the qualification "pressor" before "effects" ("reciprocal innervation"). It is only in regard to pressor effect that the above statement holds for such contrasted neurones as those of "extensors" and "flexors." I have stated the rule in this way because more in conformity with the oft-quoted rule of spinal reflexes coming to us from Ludwig's laboratory, which insisted on the rarity or impossibility of obtaining hind-limb extension as a primary homonymous spinal reflex. But how easy and direct is really the reflex nexus between the receptive surface of the limb and its extensor muscles, *e. g.* at knee, is shown by nothing better than by giving a small dose of strychnine. That alkaloid has, as has been mentioned, the property of converting spinal reflex inhibition into excitation. The same stimulus which normally reflexly excites the knee-flexors to contraction is seen after the strychnine to excite the knee-extensors to contraction. The reflex inhibition of the extensors which was previously the reflex-effect is more difficult to observe, but by turning it into excitation the facility of the reflex nexus with the extensors is found to be as close as with the flexors. Therefore, in the rule before us, if inhibition and excitation are *both* — as they should be — counted as evidence of the reflex nexus, then the reflex nexus with the homony-

mous knee-extensors and with the crossed knee-flexors, is as close as with the homonymous knee-flexors and the crossed knee-extensors.

In the question, therefore, that was put above, How is it that the spread of a reflex reaction, when the reflex is intensified, does not extend to all parts, as it is said to do in strychnine poisoning? there are two different things involved. It does not spread to some parts because, as argued above, an additive synaptic resistance intervenes across the potentially conductive path. An instance of such a path was given. But the absence of apparent irradiation to certain others is for a different reason. Keeping to the flexion-reflex as elicited by unipolar faradization of the plantar skin of a digit as illustration, the instance of the knee-extensor may be taken. However intensely the stimulation may be pushed, although the reflex reaction is thereby more and more intensified, contraction of the knee-extensor does not result, — but for a wholly different reason than that suggested for the absence of spread of the reflex from the leg to the pinna. The muscles of the pinna, in my experience, do not at all easily become involved in the reaction; but the extensor muscle of the knee is really involved in the reaction from the beginning, only it is involved in a way that escapes observation unless special means be taken to reveal it. The reflex-effect upon it takes the form of an inhibition of the efferent path just central to its motor neurone, an inhibitory block, which in proportion as the intensity of the exciting stimulus of the reflex is increased simply becomes itself the more intense. There is no evidence that this can be broken down and converted into excitation by merely increasing the intensity of the stimulus that is evoking it. On the other hand, as shown above, strychnine and tetanus toxin convert it into excitation, and that is one reason why strychnine seems to increase the spread of reflexes so greatly; but in this case the increase of spread which that drug appears to cause is really merely apparent. The reflex-effect was there already, but had another form of expression.

IV. *The groups of motor nerve-cells contemporaneously discharged by spinal reflex action innervate synergic and not antergic*

muscles. This is the reverse of the view that since Winslow and Duchenne⁴⁹ has been common doctrine concerning muscular co-ordination. It controverts an argument adduced for the view that the limb movement evoked by excitation of an *efferent root* represents a highly co-ordinate functional synergism.^{96, 97} The spinal reflex in its intraspinal irradiation develops a combined movement and synthesizes a muscular harmony.

V. It follows almost as a corollary from this, and from the *rule of spatial proximity* (p. 158), that *the spinal reflex movement elicitable in and from any one spinal region will exhibit much uniformity despite considerable variety of the locus of incidence of the exciting stimulus.* Approximately the same movement, *e. g.* in the hind-limb flexion of the three great joints, will result, whatever piece of the limb surface be irritated. The locus of incidence of the stimulus will only influence the character of the general movement executed by the limb musculature, in so far that the flexion will tend to predominantly occur at that joint the flexor muscles of which are innervated by motor cells segmentally near to the entrance of the afferent fibres from the particular piece of skin the seat of application of the stimulus. Another way of expressing this rule is to say that the receptive field of a "type-reflex" is usually of plurisegmental cutaneous extent.

Part of the question of spatial distribution of the motor discharge of a spinal reflex has long been studied, and a fundamental contribution to knowledge of it was made by Pflüger.²⁴ His inductions were based chiefly upon observations on the frog and on the records of clinical cases of spinal lesion in man. They were drawn up in the form of four "laws."

It was regarding the course of irradiation in *long spinal reflexes*, namely *those spinal reflexes that initiated from one of the above mentioned spinal regions spread over into others* that Pflüger,²⁴ in 1853, formulated his four "laws." These "Laws" have for many years been widely accepted.¹³² They are stated as follows: —

1. The law of homonymous conduction for unilateral reflexes. If a stimulus applied to a sensory nerve provokes mus-

cular movements solely on one side of the body, that movement occurs under all circumstances and without exception on the same side of the body as the seat of application of the stimulus.

If, as is clear from the context in the original paper, by movement on the same side is meant contraction of muscles on the same side, this statement does not in reality very completely express the facts.¹⁸³ It is in part an outcome of the rule of spatial proximity, but certain cases which conform to the latter yet offer striking exception to the former; for instance, when the skin of the tail is stimulated on one side the organ is very frequently moved towards the opposite, and this in a great number of classes, from fish to mammal inclusive.

2. The law of bilateral symmetry of the reflex action. When the change produced in the central organ by excitation of a sensory nerve has already evoked unilateral reflex, it, if it spreads farther, excites in the contralateral half of the cord only those motor mechanisms which are symmetrical with those already excited in the homonymous half of the cord. This statement, although true of a number of instances, fails to conform with fact in many, even perhaps the majority.

The important cross-reflex from the hind limb of the bird and mammal does not conform to it; so similarly with the fore limb. The asymmetry of the crossed reflexes of the limbs is important because probably connected with the fundamental co-ordination of muscles for progression. Again, the wag-reflex of the tail, and a reflex I have called the "torticollis reflex"¹⁸³ (cervical region), afford important exceptions to the "law." And many other exceptions can be found. In the spinal rabbit, on the other hand, and less often in the dog, the crossed reflex from one hind limb to the other is sometimes not an asymmetrical movement, but a symmetrical one: this seems to stand in obvious relation to the hopping mode of progression of the animal.

3. The law of unequal intensity of bilateral reflexes. When the excitation of a sensory nerve elicits reflex action involving both halves of the body, and the action is unequal on the two

sides, the side of stronger contractions is always that homonymous with the seat of application of the stimulus.

This statement is in conformity with a number of instances. The following are examples. When bilateral retraction of the abdomen is excited from the skin of the chest, the contralateral retraction is much the less marked: in the bilateral protraction of the "whiskers" (cat, rabbit, dog) on the excitation of the skin of the face, the crossed movement is the less ample. An interesting illustration,^{183, 206} because it involves inhibitory as well as pressor influence, can be demonstrated in the spinal cat or dog thus:—The animal resting comfortably on its back, if one hind paw be pressed that leg will be flexed at hip, knee, and ankle, in accordance with the rules laid down on p. 158, and if the stimulus be strong, or the reflex excitability good, the fellow hind limb will be extended. If instead of one hind paw both hind paws be pressed, both hind limbs are simultaneously flexed, and there is no trace of extension (Fig. 66, Lect. VI. p. 225). The homonymous reflex is prepotent, therefore, and inhibits the crossed reflex.

But there are also a number of exceptions to this "law," among others, the abduction of the tail from the side stimulated already referred to.

4. The fourth of Pflüger's classical "laws" of spinal reflex action states that with associated spinal reflex centres the irradiation spreads more easily in the direction toward than in the direction away from the head.

My own experience in the mammal is far from completely accordant with this statement: in, I think, the majority of instances, irradiation has spread more easily down than up the cord.^{183, 206, 261} It is easy to obtain reflex movements of the limbs and tail by excitation of the skin of the pinna, whereas the reverse is rare. To elicit by excitation of the hind limb a movement of the fore limb, is more difficult than by excitation of the fore limb to elicit movement of the hind limb. To elicit movement of the tail by excitation of the fore limb is easier than to move the fore limb by excitation of the tail. The irradiation has in my experience been easier across the cord from hind

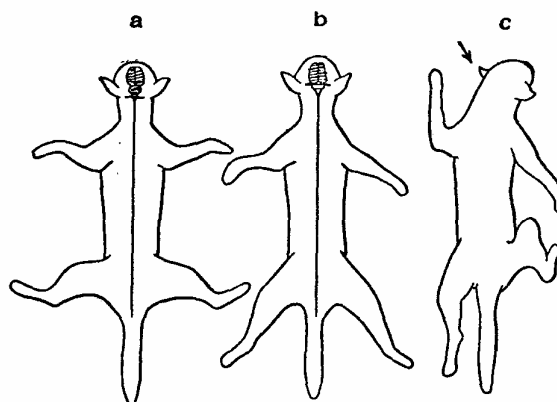


FIGURE 47.—*a*. Position of animal after transection at *calamus scriptorius*.
b. Position under decerebrate rigidity.
c. Change of attitude from *b* evoked by stimulation of left pinna.

limb to hind limb than from hind limb to fore limb; but it is often easier down the cord from fore limb to hind limb than across from fore limb to fore limb. In such reflexes also as the "shake" reflex (a reflex in which the trunk is shaken, as when a dog comes out of water), which implicate the trunk more than the limbs, the radiation is away from the head, for it is well obtained as a rump reflex when the skin of the shoulder is the part rubbed. In the "scratch-reflex," too, the skin stimulus is applied far headward of the region of the muscular contraction evoked.

These so-called "laws" of reflex irradiation were so generally accepted as to obtain a doctrinal eminence which they hardly merit. It seems here less profitable to attempt adapting them to better fit the observed facts than to briefly describe the salient features of the long spinal reflexes as exhibited in an ordinary experiment on the spinal mammal.

The reflex figure. When the animal is supported freely from above, with its spine horizontal and the limbs pendant, a point that early strikes the observer is that there are ten areas whence bulbo-spinal reflexes employing skeletal musculature can be provoked with pre-eminent facility. These areas

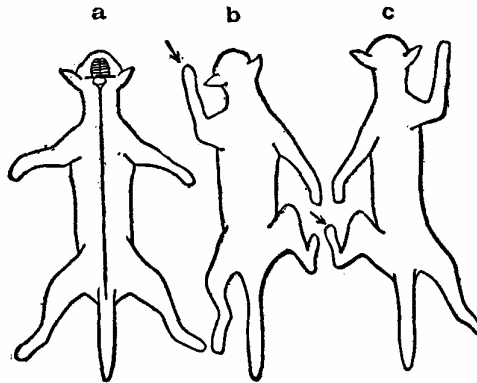


FIGURE 48.—*a*. Position under decerebrate rigidity.
b. Change of attitude from *a* evoked by stimulation of left fore foot.
c. Change of attitude from *a* evoked by stimulation of left hind foot.

are the soles, the palms, the pinnae, the mouth, the snout, and the tail and cloacal region. It is significant that nine of these areas are those which possess the greatest range of motility if the axis of the animal be considered fixed. Stimulation at any one of these areas causes a particular attitude — a *reflex figure* — to be struck. From the pinna is excited movement of each limb, the neck, the tail, and the trunk (Fig. 47). The irradiation from this reflexigenous area usually presents the following order: (1) Neck and homonymous fore limb, (2) homonymous hind limb, (3) tail and trunk on both sides, (4) contralateral hind limb, (5) contralateral fore limb. From the fore foot (Fig. 48) can be excited besides movements in the fore limb itself, movements in the other limbs and tail. The facility of radiation is usually in the following descending series: (1) homonymous hind limb and the tail, (2) crossed hind limb, (3) crossed fore limb. The relative facility of spread of the reaction to the crossed fore limb seems subject to much variation. In the frog the path between the two fore limbs is, especially in the breeding season, very open and facile. In the cat and monkey it seems to be much more open in the bulbo-spinal than in the spinal animal. From the hind foot (Fig. 48) the frequency

and ease of irradiation into other spinal regions usually appears to exist in the following order: (1) extension of crossed hind limb and tail, (2) extension of homonymous fore limb, (3) flexion of crossed fore limb. The facility of "spread" from one lateral half of the cord to the other is very dissimilar at different levels of the cord. It is particularly easy in certain parts of the tail region. Motor mechanisms which are yoked together are for the most part, as with the flexion-extension mechanisms of the hip and knee, of an asymmetrical kind. In the hind-limb region the crossed irradiation is also fairly free, and largely connects asymmetrical muscle-groups; but one of the most facile and persistent of all bilateral reflexes resulting from unilateral stimulation is the adduction of both thighs, a bilaterally symmetrical movement.

In the trunk the spread across the median plane is most free for skin reflexes excited from near the midline; this is seen in the venter of the frog; the yoking is of bilaterally symmetrical muscles. To excite movement of one fore limb from the other is less easy than to excite one hind limb from the other, at least in many animals. In the neck region irradiation across the median sagittal plane is fairly easy, and the yoking connects in large part asymmetrical muscles.

On the whole, the "long" spinal reflexes are more variable and less validly predictable than the short. They vary in a series of experiments, not only as to order of relative facility of direction of irradiation, but as to the sense of the movement elicited at the joint, whatever it may be, to which irradiation extends. Not unfrequently a region to which the reflex usually irradiates is altogether omitted, and omitted consistently throughout the whole of a lengthy experiment, although the spinal region in question has, so far as known, suffered no damage, nor indeed been directly implicated in any of the procedure. Thus, excitation of the skin of the neck or pinna will sometimes spread back along the cord and produce movement in the tail, or in the hind limbs, and in doing so pass by the fore limbs without evoking a twitch in either of them. The motor mechanisms of the fore limb thus skipped over may show

no sign when examined by the local reflexes of being less amenable than usual.

The inconstancy of the irradiation as to the kind of movement produced, *e. g.* whether it flex or extend a limb, is different in different reflexes. The irradiations from the "drawing-up reflex" of the hind foot (*i. e.* the flexion-reflex) have great constancy; the irradiation is shown in Fig. 48; to the figure the turning of the head to the homonymous side may be added; the irradiation from the fore-foot reflex is less regular; sometimes flexion at crossed knee, sometimes extension. The variation is from experiment to experiment, not during a single experiment.

There is some evidence that the influence exerted on a common path by one and the same afferent arc may not always be of the same kind. It is true that the regularity with which the same end-result appears and reappears in observations dealing with certain reflexes is very great, and inclines the observer to regard the reaction of the reflex-arc as perfectly constant. But that is not equally clear of all the reflexes. Instances of inconstancy seem to occur in some reflex-arcs, and these suggest the possibility that in some cases one and the same afferent arc may exert on a final common path even reverse effects at different times; in other words, under different conditions. The effect of stimuli to the pinna of the "bulbo-spinal" cat seems sometimes to be flexion of the hind limb, sometimes extension of that limb. Stimulation of the afferent nerve of a part of the vastocrureus muscle is often inhibition of the rest of that muscle, but sometimes not. In my experience these results, though variable from experiment to experiment, do not vary during the same experiment. Again, the afferent nerve, stimulation of which excites reflex rise of arterial pressure under curare, is known to yield reflex fall of pressure under chloral. It must be admitted that here other explanations are indeed possible, besides the supposition that the kind of influence excited by the afferent arc on the efferent path has changed.

Irradiation of a reflex attaches itself to the problem of the simultaneous combination of reflexes. It does so because it affords clear evidence that by irradiation a reflex assumes use

of a number of final common paths which do not in the first instance belong to it, but belong in the first instance rather to reflexes arising in their own immediate segmental locality. From them a "reflex figure" is formed. Thus, by irradiation, the flexion-reflex of the right *planta* causes reflex-discharge down the motor nerve of the cubital extensor (part of triceps) of the homonymous fore limb. But this reflex motor discharge to the cubital extensor is more easily excited by stimulation of the left fore-paw. Again the flexion-reflex of the right *planta*, if strong, will irradiate as motor discharge into the flexors of the left elbow, but the reflex motor discharge into the flexors of the left elbow is much more easily obtained by stimulation of the left fore paw; so that the irradiation welds into a single combined reflex effects belonging primarily, as it were, to several reflexes. But the reflexes whose effects are thus combined are always reflexes of what was termed above "allied" relation. Thus, if a stimulus exciting the flexion-reflex from the right *planta* be just subliminal for evoking the irradiation to the homonymous cubital extensor and a stimulus be applied to the left fore paw of an intensity by itself just subliminal for provoking crossed elbow-extension, the two stimuli applied simultaneously mutually facilitate and the reflex of the right fore limb results.

Moreover, it seems to me significant that the irradiation extends rather *per saltum* than *gradatim*. As the flexion-reflex is continued, flexion at hip (Fig. 45, p. 153) can be seen to add itself almost suddenly to flexion already in progress at knee.

Romanes⁷² writes of irradiation in *Medusa* as follows: "It is not difficult to obtain a series of lithocysts connected in such a manner that the resistance offered to the passage of the waves by a certain width of the junction-tissue is such as just to allow the residuum of the contraction wave which emanates from one lithocyst to reach the adjacent lithocyst, thus causing it to originate another wave, which in turn is just able to pass to the next lithocyst in the series, and so on, each lithocyst acting in turn like a reinforcing battery to the passage of the contraction wave. Now this, I think, sufficiently explains the mech-

anism of ganglionic action in those cases where one or more lithocysts are prepotent over the others; that is to say, the prepotent lithocyst first originates a contraction wave which is then successively reinforced by all the other lithocysts during its passage round the swimming-bell." If we read for "prepotent lithocyst" the "exciting external stimulus" of the arc primarily stimulated and for the other lithocysts the other arcs to which the excitement of the one primarily stimulated extends, it seems to me we have in the above description of *Aurelia aurita* a description that applies well to the process of reflex irradiation in the central nervous organ of vertebrates.

It may be objected that in the case of Medusa the wave of contraction is reinforced by, on reaching the lithocyst, initiating through that a new reflex which reinforces the one already in progress; whereas in the spread of the flexion-reflex to the reflex-arcs of the fore limb, the reaction does not initiate in these latter anything that can be called a new reflex because the reaction in them is not excited through their local receptors, the normal point of departure for their reflexes. That is a difference certainly, and a significant one. But it does not vitiate the analogy from the point of view under consideration now. In Medusa the irradiation of the reflex is in its propagation reinforced at the certain points mentioned by the reaction in its spread exciting a new neurone, attached to its path, across a definite threshold resistance. In Medusa the threshold lies in Romanes' view at the receptor organ. In the irradiation of the flexion-reflex the reaction also breaks at certain points into new arcs across a threshold resistance, and once over the threshold, propagates itself along those arcs, as evidenced by the movements produced. It is in accordance with that mode of propagation that the irradiation of the reflex appears to occur *per saltum* rather than *gradatim* (Fig. 45). Here again it is noteworthy that the places of reinforcement in the spread of the reaction which are peripheral in Medusa are central in the vertebrate; in other words, just as refractory state, inhibition, interference, etc., which are peripheral in Medusa are central in the vertebrate, so with this latter instance of "rein-

forcement." The reason which seemed obvious before, applies in the present instance also, and is the same as that which explains the centrality of the central nervous system itself (Lect. IX).

It is not only when the spot stimulated is a *receptor* that the reflex shows itself co-ordinate. The stimulation of the central end of any even large afferent nerve-trunk, or even the central end of a whole spinal afferent root, evokes reflexly a movement that is co-ordinate. This result is familiar and commonplace, but it is also remarkable.

For stimulation of the central ends of that vast medley of afferents, from different sources and of various species, collected together in one afferent spinal root (*e.g.* eighth cervical) to evoke no inharmonious confusion of various reflexes, such as the component fibres in it must, taken individually, represent, but one allied group of harmonious reflexes, is a result that, though regularly obtainable, is surely not what the observer might have expected would occur. Stimulation of the central end of the tibial nerve behind the ankle causes flexion at knee, hip, and ankle, in which the normal inhibitions of extensor muscles accompany the contractions of the flexor muscles. Yet in that nerve are included the afferent fibres from the *planta* which evolve the powerful extension-reflex, the extensor-thrust. How is it that this reflex does not appear conjoined with the flexion-reflex produced by the other afferent fibres in the posterior root or tibial nerve? The principle of interference of antagonistic reflexes central to the mouth of the common path on which both embouch precludes such confusion of reflexes. Such simultaneous combination of flexion and extension reflexes would be inco-ordination. The formation of a common path from tributary paths is a mechanism ensuring co-ordination against that. The stimulation of the nerve containing admixed receptive paths of different and antagonistic reflexes excites reflexly through the central organ an effect in the skeletal musculature which is co-ordinate and synergic. It is as though a solvent were simultaneously supersaturated with two crystalloids, and as though when a pair of these crystals were simultaneously dropped into the solution the crystallization out took place of one salt or of

the other, but not of both together. What happens resembles what occurs when there is presented to the eye one of the plane figures suggesting visual perspective, but equivocally in either of the two ways; the *whole* of the beaker or of the flight of steps appears set in one way or in the other, never partly in one way, partly in the other. And this is a really germane analogy.

The mode of preclusion of the antagonistic reflexes seems so closely akin to the process which occurs when one reflex in its supervention on another dispossesses an antagonistic reflex from the common path that its discussion may be deferred until treating of the co-ordination of successive reflexes. But it is obvious that in the irradiation of a reflex so as to produce a combined movement of remote parts we have really a synthesis of simultaneous reflexes. The parts of the reflex finding simultaneous expression in the efferent paths of other reflexes are combined by a process which tends to exclude the antagonistic reflex for each component part. It is obvious that while "allied" reflexes can be compounded together both in simultaneous and successive combination, antagonistic reflexes can be combined only in successive combination.

The collection of fibres in a motor spinal root does not represent a "reflex figure." The supporters of the view that the motor-fibres gathered together in a motor spinal root form a collection assorted so as to represent the fibres that normally are excited together in willed and other actions adduce the fact that antagonistic muscles are together thrown into contraction on exciting this or that spinal motor nerve root supplying a limb — *e. g.*, the arm. This fact, as I pointed out some years ¹³⁶ ago, is in reality one of the clearest evidences that their view is erroneous, because most commonly in normal movements the antagonistic muscles, far from being thrown into contraction together, are reciprocally innervated, one antagonist being made to contract and the other to relax. Further, far from a normal action ever throwing into activity all the motor-fibres of a single motor root, still less using that one root thus solely without other roots, in reality the evidence is that in all normal

actions, reflex or voluntary, especially in the limb regions, the centrifugal discharge to the muscles takes place through scattered motor-fibres contained in several roots, even when the action provoked and the movement effected are weak. Outside the limb region, those who argue that the aggregation of motor-fibres in each efferent spinal root represents some definite synergic contraction of muscles for a co-ordinate movement must disregard the observation of Newell Martin, and Hartwell⁷⁹ that in the normal breathing of the dog the action that goes forward in the internal and external intercostal muscles is alternating in them. One relaxes as the other contracts; yet both the external and the internal intercostal muscle of the space receive their motor supply from one and the same motor spinal root.

Those who hold the view that the assortment of the fibres of the motor root is functional, state that the movements which result from stimulation of these individual roots in the brachial region are not mere contractions more or less strong of various muscles, but are a highly co-ordinated functional synergy in each case. To this one may reply that the mere superficial resemblance of the position assumed by the limb, to one of the manifold positions assumed by it in the normal activity, is a slender analogy. The hind limbs of a frog, when it tries to climb the side of the bell-jar which confines it, assume an attitude of extreme extension, in outward semblance like that of a strychnine cramp, or that due to excitation of the eighth root; but is it permissible from that resemblance to argue that excitation of the eighth root produces a co-ordinate movement of the limb? The same analogy would argue that the strychnic cramp is also a co-ordinate movement of the limb, whereas it is definitely known to be inco-ordinate.

Myself I have not been struck by resemblance between the movement produced by excitation of the motor spinal root of a limb-plexus and the co-ordinate normal movements of the limb. It may be urged that in order to obtain the resemblance the excitation employed must be strong, so as to bring into full action every component of the complex entity of the root. When I have done this the resulting movement has seemed to

me, *e. g.* in the case of the sixth subthoracic root of the monkey, like a strychnine cramp rather than a movement of co-ordinate adjustment. If, on the other hand, it be urged that minimal excitation must be used, I have not been able to obtain in that way any more obvious relation to a co-ordinate movement. For instance, in the lumbo-spinal region of the monkey, excitation when just effective induces through the ninth subthoracic motor root abduction of the tail and flexion of the toes without any movement elsewhere. Similar excitation of the eighth motor root induces reflexion of minimus and hallux without the intervening digits, not infrequently accompanied by pursing of the anus. Such combinations strike the observer as bizarre and give little suggestion of the bringing into play of a highly co-ordinate functional synergy.

On the view that the compound muscular contraction obtained by excitation of one whole motor root is highly co-ordinated and due to a group of contractions combined in accordance with some plan for a functional result, it might be expected that the severance of one such motor root in a limb region would result in loss of some particular co-ordinate movement, and that the disappearance of that movement might be fairly clearly detectible. I was unable to detect such a result and saw no evidence in support of its existence. The severance of a single motor root seemed to produce not the complete loss of any one particular movement, but a weakened condition of many movements. Even when two of the motor spinal roots were cut the effect on the movements of the limb was rather weakness of movement than inco-ordination of movement. When the number of consecutive nerves cut was more than two there appeared limitation of the range of movement by loss in some particular direction. I inferred from my experiments that the mechanism for specific movement of each part of a limb (*e. g.* a digit) is so placed in the cord that the efferent fibres debouching from it into the motor roots pass via many root filaments and via at least two, usually more, spinal roots. Thus there is not in any one motor root filament, nor even in any one motor root, a perfect representation of any one movement, but only an

imperfect representation of several adjacent local movements, though not for each equally imperfect.

Against the view that the aggregation of efferent fibres in a motor spinal root represents a functionally co-operative collection is the fact that between them there may intervene a high resistance; that is to say, afferent impulses that easily throw some of them into action have great difficulty in throwing others of them into action. Thus, the ninth subthoracic motor root of the monkey sometimes contains efferent fibres to the urinary bladder and to the muscles of the leg. It is easy to obtain a reflex on the latter through the afferent root of the ninth, but relatively difficult to obtain a reflex upon the bladder. The synergetic view of the character of the collection of fibres in the spinal motor root presupposes or infers that mere spatial juxtaposition possesses curiously high value for spinal co-ordination; but are the separate spinal and bulbar elements of the respiratory centre less perfectly associated in function because in the neural axis they are placed apart? Likeness of quality rather than proximity in space insures the harmony of their reactions. I conclude, therefore, that the collection of fibres in a spinal motor root is not a functional collection in the sense that it is representative of any co-ordination.¹³⁸

The receptive field of a reflex does not conform with the field of distribution of an afferent spinal root. Similarly with the afferent root. The distribution in the skin of any afferent root does not correspond with the receptive field of any cutaneous reflex. The skin-field of the scratch-reflex is made up of parts of the skin-fields of many adjacent spinal roots (compare Fig. 49 with Fig. 39, p. 121). The skin-field of the flexion-reflex of the hind limb similarly; that of the fore limb similarly. Even the relatively limited receptive field²⁵¹ of the extensor-thrust is a patch into which parts of the fields of at least two spinal roots enter. Nor do the *limits* of the receptive fields of cutaneous reflexes respect the limits of spinal root skin-fields. Again, the afferent nerve of the extensor cruris muscle evokes the same reflex as does that of the flexor muscle, yet the two belong to wholly different spinal nerves.

Reinforcement. The overflow of reflex action into channels belonging primarily to other reflex-arcs than that under stimulation leads to the production by the single stimulus of a wide, compound reflex which is tantamount in effect to a simultaneous combination of several allied reflexes.

When in the spinal animal the one fore foot is stimulated, flexion of the hind leg of the crossed side is often obtained. Stimulation of that hind foot itself also causes a like reflex of that limb. When these two are concurrently stimulated, the flexion movement is obtained more easily than from either singly. These widely separate reflex-arcs therefore reinforce one another in their action on the final common paths they possess in common. Similarly with certain reflex-arcs arising from the skin of the pinna of the crossed ear. In them excitation reinforces that of the just mentioned arcs from the fore foot and opposite hind foot.

This reinforcement is significant of the solidarity of the whole spinal mechanism; but significant of more extensive solidarity still are results observed by Exner.^{99, 149} A sound conveyed to the ear of a chloralized rabbit, he found, increased the amplitude of a reflex movement of the foot, induced by the stimulus applied to the foot a moment later. Sternberg has studied similar summation of reflexes.¹⁸⁰ The same significance probably attaches to the influence of various precurrent stimuli on the knee-jerk in man, studied by Jendrassik,¹⁰⁵ Mitchell and Lewis,¹⁰⁷ Lombard,¹²⁰ and by Bowditch and Warren.¹²³ In these cases of course cerebral as well as subcerebral arcs were in action. And in regard to these, we have the observations by Bubnoff and Heidenhain,⁹² and by Exner,⁹⁹ in the narcotized dog and rabbit. In their experiments gentle stimuli to the skin of a limb exerted a reinforcing influence on closely following stimuli applied to the limb region of the cortex of the brain. Exner's observations proved that minimal electrical stimuli applied near together in point of time to the fore-limb region of the rabbit's cortex and to the skin of the crossed foot, exerted a facilitating influence, "bahnung," on each other. He points out that this reinforcement occurs when the cortex itself

has been removed, and the stimulation of the brain is applied direct to the underlying white matter. He argues, therefore, that the seat of production of the facilitation lies in the spinal centres. With that view, the argument followed here is in complete accord.

The co-ordination, in some of the instances taken, has covered but one limb or a pair of limbs. But the same principle extended to the reactions of the great arcs arising in the projicient receptor organs of the head, *e. g.* the eye, that deal with wide tracts of musculature as a whole, involves further-reaching co-ordination. 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. And in the instance taken, namely, concurrent stimulation of the one fore foot and the crossed hind foot, the co-ordination can be easily traced further; the crossed fore foot is extended at elbow and retracted at shoulder under the combination of the two stimuli, and the homonymous hind limb is extended at knee and hip. We might also add to these movements others, also caused by the same stimulus, of the eyeballs, the lips, the larynx, and the arterial wall of the splanchnic area. But these would not for the present purpose emphasize the main point further.

As remarked above, it is not usual for the organism to be exposed to the action of only one stimulus at a time. It is more usual for the organism to be acted on by many stimuli

FIGURE 49 (opposite). — The skin-fields of the afferent spinal roots of the monkey (*Macacus rhesus*), showing their general arrangement in the trunk and hind limb. On the right side only the posterior limit of each field is shown, on the left side only the anterior limit. The fields were observed by the method of "remaining aesthesia." After determination of the limits of the field for a spinal root in a number of individuals the mean of the observations for that root was transferred to a plaster cast of *Macacus rhesus*, and the lines thus gradually built up on the model. The dotted line extending from the mid-dorsum outward along the dorsal aspect of the thigh is the "dorsal line" of the hind limb, and to it the fields of the sensory roots distributed to the skin of the limb behave as do those of the skin-fields of the trunk to the mid-dorsal line of the body. It will be noticed that the boundaries of the spinal root-fields neither in the limb nor in the trunk conform with the limits of the "receptive-fields" of cutaneous reflexes. The cutaneous fields of the "scratch-reflex," the "flexion-reflex," the "extensor-thrust," are areas which in nowise fit in with the pattern of the cutaneous fields of the afferent spinal roots. Compare this figure with Figure 13 A, Lecture II, p. 46.



concurrently, and to be driven reflexly by some group of stimuli which is at any particular moment prepotent in action on it. Such a group often consists of some one pre-eminent stimulus with others of harmonious relation reinforcing it, forming with it a constellation of stimuli, that, in succession of time, will give way to another constellation which will in its turn become prepotent.

The concurrent stimuli keep a number of arcs in active touch with their final paths, and a number of other arcs out of active touch with the final paths belonging to them. In the particular instance taken, they keep arcs of one fore limb and one hind limb in action upon final common paths of flexion of those limbs, upon final common paths of extension in the diagonal pair of limbs, and upon final common paths of flexion of the neck. And the concurrent stimuli simultaneously check other arcs from getting into active touch with the final common paths of extension of one fore limb and hind limb, namely, those of the seat of stimulations, and of flexion in the opposite fore limb and hind limb, and of retraction of the neck. Further, these reactions certainly receive reinforcement through the arcs of receptors in the muscles and through arcs arising in the receptors of the otic labyrinth. An instance of reinforcement of this very kind from muscular receptors we have already given (Lecture IV, p. 131).

Thus at any single phase of the creature's reaction, a simultaneous combination of reflexes is in existence. In this combination the positive element, namely, the final common paths (motor neurone groups) in active discharge, exhibits a harmonious discharge directed by the dominant reflex-arc, and reinforced by a number of arcs in alliance with it. The dominant reflex-arc in the instance taken is that from the nociceptors of the right hind foot. The reinforcing arcs are at this phase of the reaction certain direct extension arcs, certain proprioceptive arcs, and certain labyrinthine arcs. But there is also a negative element in this simultaneous combination of reflexes. The reflex not only takes possession of certain final common paths and discharge nervous impulses down them, but it takes possession of

the final common path whose muscles would oppose those into which it is discharging impulses, and checks their nervous discharge responsive to other reflexes. This negative part of the field of influence of the reflex is more difficult to see, but it is as important as the positive, to which it is indeed complementary. Therefore it is that the reflex initiated by one group of receptors while in progress excludes in various directions the reflexes of other receptors, although these latter may be being stimulated. In this way the motor paths at any moment accord in a united pattern for harmonious synergy, co-operating for one effect.

The notion, therefore, that we arrive at of such a motor reflex reaction is that it is referable to a constellation of congruous stimuli of which one is prepotent, and that the reaction taken in its totality gives the nervous intercommunications of the central organ a certain pattern, which pattern may ramify through a great extent of the central organ. This reaction has its positive side traceable as active discharge from a number of end-points of the nervous network, and its negative side symmetrically opposed to its positive and traceable conversely by check, depression, or absence of nervous discharge. Even in extensive reflexes of the bulbo-spinal animal it is probable that though great fields of the nervous centres are involved in the reaction at any one time, large parts are still left outside the reaction. This part of the neural network would therefore be indifferent to that particular reaction. That amounts to saying that it is open during the reaction to be thrown into activity by some concurrent and distinct other reaction. But this possible neutrality and discreteness of reflex reaction and its fields is probably far less in the intact higher vertebrate than in the lower or in the mutilated higher vertebrate.³⁰⁰ In the presence of the brain the knitting together of the whole nervous network is probably much greater than in its absence.

A question arises concerning the simultaneous combination of reflexes which is closely related to that regarding the grading of intensity of a reflex.

Some reflexes exhibit many grades of intensity under grad-

ing of intensity of stimulus. The flexion-reflex is an instance. There as the skin stimulus is increased the height to which the foot is flexed is increased. But it seems obvious that such an effect is not to be expected in all reflexes. Where, as, for instance, in the scratch-reflex, the foot has, in response to irritation at a certain spot, to be moved to that spot, it would defeat the use of the reflex for a strong stimulus to flex the limb further, so as to carry it beyond the spot required. And we see that as the scratch-reflex is increased in intensity the increase does not appreciably increase the amount of tonic flexion exhibited by the reflex, but spends itself in increasing the clonic beat of the reflex, which still oscillates about the same median position. When the scratch-reflex is elicited by simultaneous combination of two reflexes initiated from spots near together in the receptive field the tonic flexion underlying either reflex does not in my experience appear to sum with that of the other; the summation that appears seems confined to the more vigorous clonic beating of the combined reflex.

It seems therefore likely that in the simultaneous combination of reflexes the reinforcement that goes on, although it is sometimes expressed as greater amplitude of contraction, is not necessarily so expressed in all cases. Just as various type-reflexes exhibit extreme individuality of time-relations, intensity grading, etc., so also they exhibit in their mode of simultaneous combination individual differences of high degree.