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T H E S I S  
FOR THE DEGREE OF M.D.  
on  
R H Y T H M I C M O V E M E N T S  
A Contribution to the Physiology of the  
Central Nervous System.  
by  
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PART I.

I N T R O D U C T I O N .

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## I. I N T R O D U C T I O N .

### A. G E N E R A L I N T R O D U C T I O N .

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Of all the dynamic activities which are evidenced throughout the animal kingdom there is none so wide-spread nor is there any so fundamental as the act of rhythmic movement.

Such functions are present everywhere - from the pulsating vacuole of the unicellular organism to the beating mammalian heart - and they may persist in action through the whole existence of the organism, from the beginning of life to its end.

In the higher metazoa there are rhythmic functions some of which are continually in progress and the commencement and termination of which are coterminous with the boundaries of life. Such are the rhythmic movements of the intestine, of the heart and blood vessels, and of the act of respiration. These may progress throughout life without interruption. But some of them may be interrupted for shorter or for longer durations of time. To them may be added other rhythmic functions - the rhythmic reflexes so-called - which are evidenced in short periods of activity. Of these rhythmic reflexes the/

the scratch-reflex is one of the most common occurrence, and another is that rhythmic act of progression to the elucidation of some properties of which this thesis is devoted.

These great rhythmic activities - of the intestinal tract, of the vascular mechanism, of respiration, and of progression - are conditioned in different degrees by the central and by the autonomic nervous systems; and they may be arranged in a series the order of which is determined by the relative importance of the central nervous factor. This series corresponds to another possible one in which the rhythmic functions are arranged in accordance with the morphological characteristics of the tissue the movements of which express the rhythmic activity.

Sherrington has pointed out (19, p.312) that although a diffuse nervous system seems to be the only one in such invertebrates as Medusa, in the higher animals another - the "synaptic" - is developed. This system co-exists with the diffuse and in various places dominates it. Even in the highest mammals the autonomic system of the viscera, of the heart, and of the blood-vessels remains diffuse.

When attempting to arrange the rhythmic activities in an ordered series we may commence with those/

those of the hollow viscera - the intestines and the heart - which are least controlled by the central nervous system. In the case of the intestines the musculature is of the visceral type and the control of the central nervous system is perhaps at its lowest. The musculature of the heart is in closer approximation to that of the skeletal muscles, and the rhythmic mechanism is more under control than is that of the intestines.

Next in order may be placed the rhythmic act of respiration. The contractile tissue is here of the skeletal type, and the nervous mechanism is one of the central nervous system - synaptic. The act proceeds rhythmically and continuously, but it may be stopped for a short time by the activity of inhibitory centres. It may be remarked here that although in the mammal the skeletal muscle is the chief contractile tissue involved in the act, in lower vertebrates, such as the frog, there is in addition to the activity of the skeletal musculature of the mouth and throat and (in dyspnoea) of the flanks, an activity of a sheet of visceral muscle which covers the lungs and is a factor in the movements of the lungs themselves. (Kahn, II; Francois-Franck, 17, 18.)

Finally/

Finally we may place the rhythmic reflexes. These are again completely conditioned by the influence of the activity of the synaptic central nervous system upon an arrangement of skeletal muscles. But the acts are more under the influence of the higher centres. In the case of the scratch-reflex this is probably less so than in the case of the rhythmic act of progression.

We may say that there are two main types of rhythmic activity in the mammal. These are conditioned by the activity, on the one hand, of a diffuse nervous system and, on the other hand, of a synaptic nervous system. As an example of the latter we may take the act of respiration, and it the chief aim of this thesis to shew the close similarity thereto of the rhythmic act of progression.

#### B. PROGRESSION.

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The act of progression in the mammal is essentially one in which phasic movements of the limbs - in determined order - condition a passage of the animal through the environment by means of ordered and phasic backward thrusts of the various limbs in the periods during which they are in contact with the ground. The friction between the surface of the limb and that of the environment into/

into contact with which it comes is sufficiently great to prevent any very extensive backward slip of the limb, and the backward thrust is consequently translated as a forward movement of the trunk of the animal.

In reality the value of the incremental forward propulsion in each step is not necessarily large. A bird flying for a period without moving its wings glides down a long incline continuously gaining in speed until that speed may reach a maximum determined on the one hand by the value of the component of gravity at the angle which its flight makes with the perpendicular and, on the other hand, by the value of the resistance of the medium through which it glides. At the lowest point of the glide if it readjusts the slope of its wings it again ascends up another long incline. It starts upon its upward passage with the gained velocity and this gradually diminishes as the energy of its momentum is converted against gravity to the potential energy of its height from the ground. A point is then reached when the height becomes maximal and the momentum minimal, and then another downward glide is commenced. So the progression through the air continues, the movements being, as it were, the swings of a pendulum. But each leaves/

leaves the bird at a lesser elevation than before, and this potential energy is lost in part by the downward slip of the animal from the true path of the incline and in part by the effect of the friction of the air - evidenced in head-resistance. To replace it the bird must periodically beat its wings and thus actively ascend against gravity .

The act of progression in the walking mammal - for convenience we may take man - closely parallels the gliding of a bird, but here the sustaining force of the air pressure against the under surface of the wings is replaced by the thrusts of the limbs which prevent the trunk from falling to the ground. If the cycle be supposed to commence at a point when one limb is perpendicular the following act is really one in which the trunk falls forward and downwards. The foot is in contact with the ground and the centre of gravity of the body falls down a curve which is a portion of the circumference of a circle formed with its centre at the ankle and its radius of the length of the distance between ankle and centre of gravity. As the trunk falls it gains in velocity. But at the same time the other limb has been swung forward and its foot placed in contact with the ground in front. The trunk then begins to ascend upon another similar circumference until/

until it reaches another climax when the second limb is perpendicular. The act then repeats until the cycle is completed with the first limb again perpendicular.

The centre of gravity of the body thus rhythmically falls and rises, gaining in velocity during the fall and losing in velocity during the rise. Theoretically, then, once the animal has started off with a certain velocity the momentum should be conserved and during the act no work should be done. This might be so were the surface of the ground perfectly level the friction between foot and ground sufficiently great to prevent any backward slip of the limbs, the friction in the joints of the limbs infinitely small, and were there no resistance from the air. But as it is these various factors are such that the momentum is gradually and continuously transformed and must be as continuously replaced. This is done by the act of the animal in thrusting back its limbs whilst they are in contact with the ground.

Each cycle of movement in the phasic activity of any individual limb may be portioned into two distinct periods. These may be differentiated by the states of contact and of non-contact with the ground. During the first of these the distal parts of/

of the limb rest upon the surface of the ground; the weight of the animal is then partially borne by it; and simultaneously the limb is thrust backwards, but by remaining in contact with the same surface of the ground in effect thrusts the animal forwards. During the second period of the cycle a movement of the limb causes it to terminate its contact with the ground and be carried forward relative to the trunk until, at the end of the period, it is again placed upon the surface of the environment: while this part of the act is in being the weight of the animal is borne by certain of its other limbs.

During these phasic acts of the different limbs the balance of the neural centres is disturbed by two different kinds of peripheral stimuli.

In the first place the discontinuous contact with the ground and the synchronous distortion of the skin of the foot, determined by the weight of the animal then carried in part by the limb, condition changes in the activity of exteroceptive end-organs therein embedded and discontinuous augmentations and diminutions of the stimuli determined by them.

In the second place the backward and forward movements of the limb and the activity of the muscles/

muscles which condition them produce changes in the state of the proprioceptive organs situated in the muscles, joints, and tendons which take part in the act.

The act of progression is one richly coordinated. Yet it has long been known that movements of the hind limbs certainly those of progression may be present in the "late spinal animal." A mechanism confined to the lumbar part of the spinal cord is therefore sufficient to determine in the hind limbs an act of progression which is probably very nearly a normal one. As reflex movements of the limb, exactly similar to movements integrated in the act of progression, may be obtained by the artificial stimulation of exteroceptive or of proprioceptive end-organs, the suggestion has naturally arisen that the act of progression may be entirely determined by cyclic variations of the stimuli which arise in peripheral sense organs, and are themselves conditioned by the movements which they engender - in other words, that the act of progression is automatic and conditioned by the integration of reflex movements which follow each other successively, and each of which determines the stimulus which calls the following movement into being.

In discussing the nature of progression  
Philipppson/

Philippson (14) has laid stress upon the stimulation of the skin as a factor in the determination of the act. Before this Sherrington (9) had observed that, in the Spinal dog and cat, the ipsilateral flexion-reflex may be avoked, soon after the trans-section, by pressure so directed upwards upon the pads of the foot that the toe-joints are extended - the stimulus being comparable to the pressure of the ground in progression. But later, when the shock of the operation has passed the same stimulus will evoke the ipsilateral extension-reflex - the "extensor thrust" - if the stimulated limb be in a state of flexion. If it be extended the reaction is one of flexion as before. Philippson believes that this reflex plays an important part in the mechanism and determination of progression. At first sight this may appear improbable for, if the reaction is evoked alone when the limb is in flexion and if the stimulus evoke flexion when the limb is extended, then it might be expected to work in progression by producing flexion as it only occurs normally when the limb is extended and in contact with the ground. But these postures are passive ones, and it is perhaps possible that a posture of passive flexion is equivalent to one of active extension. In each case the extensor/

extensor muscles are tightened - either by passive stretching or by active contraction - and in the two states it is possible that their contained receptors are similarly activated. Thus the present author has demonstrated a reversal of reflex action as the hind limb is in different active states, similar to, but of opposite sense, that reversal obtained in different passive postures by Magnus (25, 26, 32, 33,) and others.

Philippson, then, supposes that the first contact of the limb with the ground evokes the extensor thrust. This reaction is reinforced by the crossed extension which accompanies the flexion of the opposite limb. These two determine an increase of pressure of the foot upon the ground, and this peripheral extero-ceptive stimulus then causes a reflex flexion of the same limb and an extension of the opposite limb which then, in its turn, is about to come into contact with the ground. The former limb is now flexed and carried forward while the latter is in contact with the ground, and the stretching of the skin thus caused in the inguinal region determines the appearance of extension in the flexed limb. This extension brings the limb on to the ground, where the contact determines the extensor thrust. And so the cycle begins again.

Philippson/

On this hypothesis it is, however, difficult to explain the mechanism of Freusberg's (4) "mark-time" reflex. There the "late spinal" dog, when suspended free from the ground, performs movements of progression with its hind limbs. Philippson thinks that here the crossed extension due to the ipsilateral flexion, combined with the inguinal stretching of the skin and with the action of association paths in the lumbar spinal cord, are sufficient to produce the phenomena in the absence of actual contact with the ground.

The difficulty in explaining this phenomenon has been emphasised by Sherrington (30). He points out that, in the intact animal (cat, dog), severance of all the sensory nerve trunks directly distributed to all four feet up to and above the wrists and ankles scarcely impairs the act of progression. He also notes that reflex stepping is not annulled, or even obviously impaired, by severance of all the various cutaneous nerves of the limb. And stretching of the prominent fold of skin which runs along the outer edge of the groin cannot be of essential importance in the act, because cocainisation of this region does not interfere with reflex stepping. The extensor thrust may also be abolished - by that division/

division of the sensory nerves of the foot described above - without noticeably changing the acts of the walk and the trot. He therefore concludes that the intrinsic stimuli for reflex stepping of the limb are not referable to any part of the skin of the limb.

In continuation of his work on proprioceptive reflexes (24, 27), Sherrington finds in the sensory end organs of the muscles themselves the seat of the intrinsic stimuli for reflex stepping (30). He considers that the mode of process in reflex walking is as follows: The spinal step is a rhythmic reflex which may be excited by continuous stimuli applied either to the cross-section of the divided spinal cord or to various peripheral points outside the limb itself. The generating stimulus is continuous, but the movement of the limb is determined by the alternate action of two antagonistic reflexes. The primary stimulus sets one of these in action. This act generates in that limb a proprioceptive reflex antagonistic to itself. The proprioceptive reflex interrupts the primary reflex, and in this interruption abolishes the stimulus which engendered itself. The primary reflex is then reconstituted and again calls forth the interrupting reflex, and so on. The secondary reflex is determined by the combination of three main factors - centripetal impulses from/

from the deep structures which are moved passively by the primary reflex (joints, etc.); centripetal impulses from the muscles which move actively in the primary reflex; and the central change which underlies "rebound". The phenomenon of "reflex reversal" and the "extensor thrust" may also play a part.

Of peculiar significance is this factor of "central rebound". Sherrington (16, 20) has noted that the flexion-reflex, for instance, is often terminated after cessation of the exciting stimulus by an active phase of extension; and that the individual muscles which are in a state of inhibition during the application of the stimulus contract suddenly after its termination. That this phenomenon is not due to a proprioceptive stimulus generated in the muscles which take part in that primary flexion-reflex — or at any rate is not solely conditioned by such a stimulus — is shewn by Sherrington's observation (27) that the rebound contraction — "successive spinal induction" — may be obtained in the de-afferented preparation.

Another point of interest and importance is the partial similarity of the act of progression with that of the scratch. Sherrington (30) has noted this similarity, and the present author has shewn (36) that in the anaesthetised rabbit the one state may/

may immediately follow upon the other, and that there is indication in some cases that the two may blend for a time. This partial similarity is suggestive. Sherrington (21) found that in the scratch-reflex the flexion of the thigh did not completely relapse during each brief extension of the phasic act - that there was always a certain amount of maintained flexion. In certain states, as the present author (29, 34) was able to shew for the guinea-pig, the two factors in the scratch may be separated. And of these two factors one is a state of maintained flexion while the other is a discontinuous inhibition of that state. In the scratching phenomenon described by the present author (23, 29) as occurring in guinea-pigs under anaesthesia there is an alternation of the state of scratching from one hind limb to the other. At any one time the state of maintained flexion complicated by rhythmic inhibition is accompanied in the crossed limb by a state of maintained inhibition of flexion. He has suggested that the rhythmic inhibition during maintained flexion and the maintained inhibition of flexion which immediately succeeds in the same hind limb may be expressions of one and the same activity; and that they may, in effect, be conditioned by variations in the mutual influence of interacting spinal centres.

centres. The suggestion in reality is that the locus of the inhibitory factor is central, and that it is not of essential peripheral origin from proprioceptive stimuli. For the scratch this is in accordance with a previous observation of Sherrington(21) that the de-afferented hind limb of the cat may be made to scratch. Although this is perhaps not conclusive - in view of the possible influence of stimuli which arise in the opposite hind limb - he and the present author have recently demonstrated at a meeting of the Physiological Society a cat in which scratching may be elicited although both hind limbs have been completely de-afferented.

Thus the rhythmic act of progression may be regarded as conditioned on the one hand by self-generated peripheral stimuli. If this view be taken the chief origin of these peripheral stimuli may be placed either in the skin or in the deep structures of the muscles and joints. It has been pointed out above that the extero-ceptive afferents in the skin may be eliminated without obviously impairing the act. If the "peripheral" theory of the intrinsic factors be held their origin must be placed in the proprioceptors of the limbs.

But on the other hand another view as to the conditioning of the act may be held, for it is possible/

possible to suppose that the rhythm is intrinsically of central origin and modified only by the peripheral factors. The similarity between the act of progression and the act of alternating scratching as it occurs in the guinea-pig under narcosis is great; and has suggested for some time to the present author that the act of progression may too be essentially a central and not a peripheral phenomenon. The proof that this is so has already been given in a short preliminary communication (39) and the experiments upon which it is based are given in greater detail in this thesis.

PART II./

PART II.

EXPERIMENTAL.

II. METHODS OF OPERATING AND OF RECORDING  
EMPLOYED IN THE PRESENT EXPERIMENTS.

---

In the experiments upon which this thesis is based the movements of progression have been investigated in rodents and carnivores, the greater number being cats.

Progression has been obtained in three different manners. The first of these is the simple process of narcotisation, aided in some cases by specific drugs. The second is the application of a stimulus to the spinal cord. And the third is the application of a peripheral stimulus either to the skin, or to one or more sensory nerves simultaneously.

The movements have been observed in different physiological preparations of the animals investigated - the differences being produced by curtailment of the central and peripheral nervous systems.

Four chief preparations have been used. These are:- the "normal" animal (under narcosis); the "decerebrate" preparation; the "high spinal" ("decapitate") preparation; and the "low spinal" preparation (otherwise decapitate).

These/

These chief conditions have been used as they are or with the additional complication of section of the lumbar posterior spinal roots on one or both sides (thus de-afferenting the recording limbs); or of removal of parts of the lumbar spinal cord itself.

The field of investigation of the movements of progression which may be produced in the above manners and in the above conditions has been confined to the hind limbs. In some cases their movements as a whole have been recorded, in other cases the movements have been studied as they occur in two individual antagonistic muscles - tibialis anticus and gastrocnemius - which together act in opposite directions upon the ankle joint. In the latter case all the other muscles of both hind limbs have been paralysed in the manner already described by the author (40).

Progression on stimulation of the cut surface of the spinal cord has been obtained by using the faradic stimulus in the unipolar method.

Progression as a reaction to peripheral reflex stimuli has been obtained by bipolar faradic stimulation of the ipsilateral and contralateral long saphenous nerves.

### III. PROGRESSION MOVEMENTS OF NARCOSIS

#### IN RODENTS.

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##### a. PROGRESSION IN RABBITS.

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The progression movements which occur during narcosis in the rabbit have already been described by the present author (36) and are here again briefly described only because of the interest which attaches to the hopping form of locomotion in these animals.

As observed in a normal rabbit in the state of ether or chloroform narcosis the phenomena take the form of rhythmic movements of the hind limbs. These are advanced and retired simultaneously, so that the acts are bilaterally symmetrical. At the same time the fore limbs may perform bilaterally alternate movements of a similar type. In fact, the hind limbs perform "hopping" movements while the fore limbs "run".

Graphic tracings of the movements of the hind limbs in this phenomenon demonstrate their synchronism/

FIG. 1.  
FIG. 4.

synchronism. The two limbs perform the same phases of the cycle simultaneously.

Graphic tracings of the isolated muscles demonstrate that the acts are produced by muscular contractions which are separated by shorter or longer pauses of rest. The pauses may be almost entirely absent.

FIG. 2.

In the rabbit scratching movements may also appear under narcosis and may immediately succeed the movements of progression. In records in which the two phenomena immediately adjoin each other the rhythm of the two appears to bear the simple relationship of 2:1. That is to say that the rhythm of the "beats" in progression is very nearly exactly twice as slow as that of the "beats" of the scratch (36).

FIG. 3.

FIG. 5.

FIG. 6.

The hopping form of progression peculiar to such animals as the rabbit is of interest to us in the first place because it more nearly approaches in form the movements of respiration than does the more common alternate running type of progression. The act of respiration is also one of bilateral symmetry.

But the fact that the movements of progression in narcosis in the rabbit are of the hopping type is of additional importance to us for it demonstrates that in these rhythmic acts in narcosis we are/

are really dealing with activities of the mechanism of progression. By simple inspection we may convince ourselves that the rhythmic movements of the limbs resemble those which occur in progression. But when, in the act under narcosis, these movements in the pair of hind limbs bear the same relationships to each other as in the normal progression in such different types as those of hopping and of running, then we may be convinced that the acts are fundamentally one and the same.

#### b. PROGRESSION IN GUINEA-PIGS.

In the guinea-pig the normal form of movements in narcosis is that of the "narcosis scratch". If, however, a solution of novocain be administered the rhythmic movements exhibited are those of progression. This enables us to compare in different experiments the "narcosis scratch" and the act of progression under narcosis in one and the same individual.

Records obtained by registering the movements of the two hind limbs in this state demonstrate that they are bilaterally alternate. Thus one hind limb/

FIG. 7.

FIG. 10.

limb performs the act of flexion while the flexion of the other is diminishing, and the climax of flexion in one limb coincides in time with the maximum of extension in the other.

While the rhythmic phenomenon is in process a peripheral stimulus - for instance pinching of the skin of the fold which passes from the abdomen to the front of a thigh - produces in the limb of that side a great augmentation in the amplitude of the rhythmic movements. These may be of as great an extent as double that which obtained before stimulation. Their rate is increased simultaneously. At the same time and in the contralateral hind limb there may be a diminution or even a complete abolition of the beats.

A similar stimulus applied to the skin of the lower quadrant of the abdomen produces upon the same side a great increase in the amplitude of the beats and a lesser increase in their rate. Upon the opposite side there is a slighter increase in amplitude. This bilateral augmentation of the extents of the movements is perhaps related to the bilateral flexion-reflex sometimes evoked in the normal guinea-pig by stimulation of the skin in this area.

The rhythm of the movements has varied in rate in the same guinea-pig at different times between the/

FIG. 9.

the extremes of 1.75 beats per second and 3.0 beats per second. The usual rate of rhythm has been 2.0 beats per second, and this has been remarkably regular. In this same individual the movements of the "narcosis scratch" were also recorded. The rhythm of the beats in this phenomenon in rate was about 8.0 beats per second. The rate varied between this and 7.0 per second. This rate corresponds very closely with the average of 7.5 beats per second obtained from a large number of different individuals (29). It seems to bear the simple relationship of 4:1 to the rate of the movements of progression in the same individual. If this is so it is of interest that the relationship should be 2:1 in the rabbit (where the progression is that of hopping) and 4:1 in the guinea-pig (where the progression is that of running).

IV./

IV. THE PROGRESSION MOVEMENTS OF NARCOSIS  
 IN THE CAT.

---

a. GENERAL DESCRIPTION OF THE MOVEMENTS AS  
 THEY OCCUR IN THE INTACT HIND LIMBS.

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In a certain proportion of cats subjected to the influence of a general anaesthetic, movements of progression occur at a certain depth of narcosis. In these experiments the anaesthetic used has usually been a mixture of ether and chloroform, sixty parts by volume of the former and forty of the latter (but sometimes equal parts by volume of both).

The movements may be very slight in extent. Then they are exhibited simply as slight alternate movements of the hind limbs. But in other cases they may be greatly exaggerated in extent and may be present as well in the fore limbs.

As regards the hind limbs the movements are of flexion followed by extension - or perhaps it would be more accurate to say, by relaxation of flexion. Palpation of the muscles of the leg demonstrates/

demonstrates that the chief activity is exhibited by the physiological flexors of the ankle-joint — tibialis anticus and other muscles. The extensors (gastrocnemius and others) commonly shew no activity.

The movements occur in the two limbs, and are then related in such a manner that flexion of one ankle occurs during relaxation of flexion of the other; and when the latter limb then exhibits flexion the first relaxes.

It sometimes occurs that the rhythmic movements are confined to one hind limb. In other cases after the appearance of a series of rhythmic alternate movements in both hind limbs the movements may cease for a time in one of them.

It rarely happens that the movements in the two limbs are nearly synchronous in the sense of being in the same direction at the same time.

It has been stated above that the extensors of the ankle may not obviously take part in the movements, but that still the act of extension (relaxation of flexion) may occur. At first sight these statements appear to be contradictory, for with the limbs lying upon the table there is no force such as gravity to give a resistance to the flexors. But if the ankle extensors act simply as inactive bands the contraction of the knee extensors besides directly extending/

extending the knee, will, in consequence of that movement, indirectly extend the ankle in virtue of the mechanical effect of the inactive ankle extensors.

Graphic records of the movements at the ankle during this narcosis progression demonstrate the relations of the movements in the two limbs and also their rhythm.

In a typical instance the curves traced during the movements of the two limbs are seen to be rhythmically discontinuous. Each remains for intervals parallel with the abscissa, but between these intervals it describes a sharp rise and fall. The pause which runs level with the abscissa denotes a state of relative extension of the joint. The rise of the curve which terminates the pause denotes a state of active flexion, while the following fall denotes a state of active extension or relaxation of flexion which again brings the limb to the initial posture of relative extension. There is usually no pause at the top of the interrupting "beats" of the movement. Relaxation of flexion succeeds flexion immediately. Sometimes there is a slight pause at this point, and the curve then remains for a short time parallel with the abscissa in a state of maintained

FIG. 11.

ed/1173/

state of maintained relative flexion. In the beats the fall is usually a movement of greater rapidity than the rise.

The relation between the movements in the two limbs is commonly such that the "beat" of one occurs during the state of rest of the other. The exact relationship depends upon the rhythm of the phenomenon. Where that is very slow and the rest period or pause is greater in duration than is the duration of a beat, there occur intervals during which both limbs are in a state of maintained relative extension. Thus the termination of one pause overlaps the beginning of a pause in the other limb. The whole movement of the beat in the first limb takes place and the succeeding pause commences while the pause in the second limb is still running. At this point again, both limbs are in the state of rest until the succeeding beat in the second limb terminates its pause: and so on.

Where the rhythm is faster and the duration of the beats and of the pauses similar, the initiation of a beat in one limb exactly synchronises with the termination of a beat in the other limb, and a pause in one limb synchronises with the movements of a beat in the other.

With still faster rhythms the interval of rest may become shortened. The apex of a beat in one/

one limb then corresponds in time with the mid point in a pause in the other limb.

Finally, the pause may disappear altogether. Then the apex of a beat in one limb corresponds in time with the point where termination of one beat is immediately succeeded by the initiation of the following in the other limb - this point may be regarded as a pause of infinitely short duration. But with very rapid rhythms, as will be shown later, there may be no such alternation of phase in the two limbs, and the apices of corresponding beats in the two limbs may actually synchronise.

In these experiments the rhythm has been found to vary considerably even in the same individual. The slowest movements observed have been at the rate of five complete cycles in one limb within a period of eight and a half seconds of time. This gives a rate of about 0.6 cycles per second. Rates as fast as 2.5 cycles per second have been observed under ordinary conditions, while in the state of asphyxia the rate has risen to one of 3.3 cycles per second and even higher.

In one and the same individual, as has been said above, the rhythm may vary greatly. Thus in/

FIG. 11.

FIG. 24.  
(3 beats per second).

in one instance on two succeeding days records were registered in which the rhythms were 0.6 and 2.0 cycles per second, while nine days later the rhythm was 1.0 cycles per second.

FIG. 11.  
FIG. 12.

The movements are not always regular. In some cases there may be a grouping of the beats. When this occurs two consecutive beats may be closer together than are the second of these and the beat immediately following it. The beats may be arranged in pairs with a shorter pause between the two elements of a pair, than between successive pairs. In other cases irregular duplications and triplications of the movements of the beats have been observed. In these cases the relaxation phase of a beat may not attain the position of rest but may be arrested by a superposed beat, and the relaxation of this too, may be similarly arrested. In these cases the superposed beats have their apices at the same level as the ordinary single beats. This irregular form has been observed in narcosis progression under chloroform. The pauses in the record of the other hind limb are correspondingly increased in duration synchronously with these superposed beats. Another irregularity which has been observed is the failure of beats, either permanent or temporary, in one of the limbs. This will be described in a separate section.

One other point may be referred to here.

In the "narcosis scratch" described by the present author (28, 29, 34, 36,) increase in the depth of anaesthesia gradually diminishes and finally abolishes the scratching movements which occur in narcosis in the guinea-pig and rabbit. With decrease in the depth of narcosis the movements increase in extent and then cease suddenly. The same course of events occurs in the case of narcosis progression.

b. UNILATERAL/

b. UNILATERAL PROGRESSION AS SEEN IN THE INTACT  
LIMB.

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It occasionally happens, as has been remarked before, that the movements of progression may be confined to one hind limb alone. This phenomenon may be a constant one, that is to say that the movements may appear alone in a certain hind limb throughout the whole experiment. Or it may be a temporary one; and in this case, during the registration of a series of movements which occur alternately in both limbs, the beats may suddenly fail for a space in one limb - then again to be resumed. Such records afford interesting data in reference to the rhythms of the movements of a limb when accompanied and when unaccompanied by movements in the other limb.

In the case of the constant variety of unilateral progression there is little to describe. It has been stated in the previous section that when the rhythm of the beats is very rapid there is often synchronism in the movements in the two limbs. In these circumstances very often the movements are comparatively slight in one of the limbs, and it is possible that the unilateral progression is a further stage/

stage of this phenomenon in which the movements have entirely disappeared in the one limb. In such records the rate of rhythm is always great, and it corresponds very closely with the rate in the synchronous movements.

Temporary abolition of the movements of progression may occur in long series of bilaterally alternate movements.

This abolition as a rule occurs without warning. The beats in one limb suddenly fail and there occurs a long pause during which the beats continue in the other limb. The pause is then terminated by the reappearance of the beats in the first limb and the earlier beats of the record after resumption are usually smaller in extent than the average, but the common extent is soon attained. The duration of the long pause is approximately equal to that of so many cycles. That is to say that it is approximately equivalent in duration to a simple multiple of the duration of a single cycle when the two limbs are acting together alternately. But this correspondence is only approximate for minuter investigation reveals the fact that the duration of the pause is smaller than this simple multiple of the duration of the cycle would be. At the same time the/

FIG. 13.  
FIG. 19.

FIG. 13.

the beats which continue to remain in being in the other limb become more rapid than is usual. This change of rhythm in such temporary unilateral progression may be slight. It may change from 0.75 to 0.9 cycles per second only. But in other cases it may be great - as great as a change from 1.5 to 2.5 cycles per second or even more.

FIG. 13.

The beats of the other limb which thus occur during a temporary abolition of the beats of a limb are often greater in extent than usual as well as being more rapid. This increase may persist for a short time after the resumption of the beats in the first limb, and then it gradually disappears synchronously with the attainment by these beats of their normal extent.

FIG. 13.

c./

c. THE EFFECT OF ASPHYXIA UPON PROGRESSION  
IN THE INTACT HIND LIMB.

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The effect of asphyxia, which may be readily produced by complete closure of the elastic trachea of the cat, may be discussed in connexion with three main changes which it conditions. These are: an increase in the rhythm of the beats in each hind limb; a change in the mutual relationship of the movements in the two limbs; and the production of a state of maintained flexion in the limbs.

With regard to the change in the rhythm of the beats two effects may be detected. It may be supposed, for example, that the beats are proceeding with regularity in the limbs. During this process the trachea is suddenly closed. There may then follow no change in the rhythm of the beats for some seconds. But it more usually happens that there is a slowing of the rhythm which makes itself evident within two seconds or less of the closure of the trachea. It may even occur that there is a complete cessation of the beats in both hind limbs for a period as long as twelve seconds. The slowing of the rhythm is slight, the change being, for instance/

FIG. 14.

FIG. 17.

instance, from 1.3 to 1.0 cycles per second, and the slowed rhythm lasts for about 9 to 12 seconds. The rhythm then begins to become faster (or at this point the beats commence again if they have ceased) and the change rapidly becomes marked. After this the increase in rhythm proceeds more slowly but still steadily and the beats may continue to become faster for as long as thirty seconds after closing the trachea. They may then be two or three times as fast as the beats before the closure. Thus a rate of 1.3 cycles per second before closure of the trachea may become one of 2.75 cycles or 3.0 cycles per second 25 seconds later; or one of 1.0 cycles per second may become one of 2.75 cycles per second.

This change in the rhythm is in great part conditioned by a gradual disappearance of the pauses which separate the termination of one beat from the point of initiation of the following one. These pauses become less and less until the initiation of a beat follows immediately upon the termination of its predecessor. But this is not the only factor in the increase of rhythm. The actual beats become of less duration, and this change may be as great as a shrinkage to three quarters of the duration which obtained before the commencement of asphyxia.

As regards the rhythm there are therefore two main phases. Of these the first is a slowing and it may be entirely absent, or it may be so exaggerated as to cause a temporary cessation of the movements. The second is a phase in which the rhythm of the beats is markedly hastened. It is never absent unless the beats at the commencement are already very fast in rhythm.

Synchronously with these changes in the rhythm of the beats changes in their extent occur. These changes are of two kinds - changes in the heights of the beats, that is to say in the amount of flexion when the beat culminates at that point when the state of active flexion passes over into that of relaxation of flexion; and changes in the level of the pauses between the beats or of the lowest points in the beats; that is to say, in the amount of relative extension at that point at which active flexion commences in a beat.

The beats may be supposed to be proceeding with regularity of extent. The trachea is then closed, thus commencing the state of asphyxia. At first the pauses between the beats persist and, as has been said above, become longer of duration. But their level remains the same as before. That is to say/

FIG. 14.

FIG. 15.

FIG. 16.

FIG. 17.

say that each hind limb in the intervals between its rhythmic movements attains to the same degree of relative extension that obtained before the closure of the trachea.

At the same time a change commences in the extent of the beats. These gradually become greater, and this increase in extent is obtained by the attainment of an increasingly greater degree of flexion at the summits of the rhythmic movements. The beats thus appear in the records progressively to increase in height while their lowest points remain at the same level. The point at which the beats attain their greatest absolute extent seems to occur usually when the rhythm has again become faster and the pause has just disappeared.

Thereafter the extent of the beats progressively decreases although the highest points continue to ascend. This relative decrease in the extents is conditioned by a lessening in the degree of relative extension which obtains at the lowest points of the beats. The levels of the pauses between the beats, or of the point at which one beat on cessation is immediately followed by the commencement of the succeeding beat if there be no pause, thus/

thus ascend from the abscissa in the curves of the graphic tracings. The highest points in the beats continue also to ascend, but the speed of this increase in height is slower than is the speed at which the lowest points ascend, and the beats therefore diminish in absolute extent.

Soon a point is reached at which the beats no longer continue to gain in height. Their summits then remain constant in level. But the points to which the curve falls between the individual beats continue to rise upon the tracing. At last a time comes when the lowest and highest points almost coincide. The beats, in short, become excessively small. Finally they disappear altogether as separate discontinuities upon the curve, and the tracing remains level at a point higher than that reached by the summits of the beats before the closure of the trachea - that is to say, it remains in a condition of marked maintained flexion.

If the summits of all the beats in such an experiment be joined by an imaginary line, and if the lowest points be joined by another, the beats may be regarded as lying between two irregular curves which denote the extremes of relative flexion attained at the top of the beats and of relative extension/

extension attained in the intervals between the beats or at their lowest points when no intervals of rest are present. Before the act of closing the trachea these two curves run parallel with the abscissa - that is to say that the beats are of constant extent and at the same time attain constant levels of relative flexion and extension. Shortly after the closure of the trachea both the curves begin to rise, but the latency of the curve of relative flexion is less than that of relative extension. While the curve of relative flexion is rising and during the latency of the curve of relative extension there is a period in which the beats increase in height and in extent. The rise of the two curves is at first rapid and then more slow. Thus when the curve of relative extension commences to rise the beats at once begin to decrease in extent although their heights may still continue to rise. The curve of relative flexion then attains its maximum but the curve of relative extension still continues to rise so that there is then a period in which the beats remain of constant height but of ever diminishing extent. Finally the curve of relative extension comes to coincide with that of relative flexion. At this point the/

the beats disappear as such and are replaced by a state of maintained flexion.

Irregularities in this course of events occur. Immediately after the closure of the trachea the two curves may fall slightly, and the fall of the curve of relative flexion may be greater than that of relative extension so that the beats may slightly diminish in height. The beats may be even abolished and then their reappearance is conditioned by the shorter latency of the curve of relative flexion. The curve of relative flexion also may fall before the beats are abolished by the coincidence of the two curves. But more commonly the curve of maintained flexion continues to ascend after the abolition of the beats.

FIG. 17.

FIG. 14.

The temporal relations of the rhythms of the two limbs during asphyxia are of interest.

During the normal narcosis progression before the closure of the trachea the rhythms on the two sides are equal and the beats are so related that the summit of a beat in one limb falls mid way in the pause between beats in the other limb. With the state conditioned by the closure of the trachea not only do the rhythms change in the separate limbs but the/

the relation between the acts in the limbs also do. In the first period after the closure of the trachea, when the rhythm slows in both limbs and the beats increase in extent, the relation between the bilateral movements remain the same. There is exact alternation. Thereafter a change occurs. It is easiest to describe this by stating the relative positions in the one curve at which the points of climax - the apices - of the beats in the curve of the other hind limb fall.

In the first period these points fall midway between the beats of the first limb. When the rhythm begins again to become faster the points begin to fall to one or other side of the mid line. That is to say that the rhythms begin to differ in two limbs. For the purpose of description it does not matter to which side they fall - let us say that they become more advanced. With the increasing rates of the two rhythms the points advance still further. Instead of falling in the pauses between the beats they fall upon the descent of the beats, and as the pauses disappear and this advance still proceeds, the points occur at ever higher levels on the descent of the beats - instead of coinciding with their/

FIG. 14.

FIG. 15.

their points of termination. The points may then come to coincide with the apices of the beats and then to advance still further, falling down on the ascents of the beats. Or they may begin to retrograde on the descents of the beats - that is to say, to retreat instead of advance. If they come to coincide with the lowest points of the beats the movements are then again alternate. In either case - whether the points of climax of the beats in the other limb continue to advance or commence to retreat - a period occurs when they coincide with the apices of the beats in the limb we are considering. When this occurs the movements in the two limbs are no longer alternative but are synchronous - flexion and extension phases occurring simultaneously in the two limbs.

These then are the chief phenomena which occur in the state of narcosis. The rate of the movements in the two limbs first becomes slightly slower than is normal and then become markedly more fast - the latter being the predominant phenomenon of the two: the extent of the beats becomes at first greater and then lesser than normal - this finally resulting in a cessation and a state of maintained flexion/

flexion: and the relationship of the movements in the two limbs changes from one of truly alternate rhythm to one of true synchronism - there being an intermediate swinging of the rhythmic relationship between these two states.

Before passing to consider other questions in relation to this phenomenon of narcosis progression, three additional observations may be made.

The first of these is the effect of asphyxia upon the movements of the limbs when the progression is already of the synchronous type.

This phenomenon occurs but rarely. There may be no alteration of the state of synchronism or there may be a slight alteration, the beats then not being exactly synchronous. The rhythm in the two limbs - already faster than usual - becomes slightly more rapid.

The second observation which may be recorded is the effect of asphyxia in the phenomenon of unilateral progression. It has been noticed here - in a case in which the movements were fast - that there may be but little change in the rhythm.

The third observation concerns the production of the movements of necrosis by the state of asphyxia/

asphyxia.

It sometimes happens that, when the movements of progression have occurred in a cat under narcosis but have then ceased to occur, the production of the state of asphyxia may bring them into being again. The appearance of the phenomenon is then very similar to that described above when the first effect of the closure of the trachea is to abolish the movements. Some time after the closure of the trachea - perhaps as long as thirty seconds - the beats appear. They appear usually in one limb only, they may be confined to that limb throughout, and they are at first very slight. They soon become comparatively large in extent (but are commonly not so large as normal) and their rhythm is slow. The rhythm rapidly becomes fast and the course of events is then the same as in normal circumstances under asphyxia.

The movements, as has been said above, are often confined to one limb alone. Sometimes they appear late in the curve of the other and are of very small extent. Even if they do not so appear that limb may still exhibit a curve of rising maintained flexion which may become very marked synchronously with the emergence of the beats of the other limb in the state of maintained flexion.

FIG. 16.

FIG. 17.

d. PROGRESSION IN THE HIND LIMBS DURING  
RECOVERY FROM ASPHYXIA.

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In the climax of asphyxia the movements of progression as discontinuous rhythmic acts have disappeared and been replaced by a state of maintained flexion. If the state of asphyxia is terminated at or about the point at which cessation of the rhythmic movements takes place there may be a recovery of the movements of narcosis progression.

But if the asphyxia be continued longer the maintained flexion begins gradually to diminish and recovery of the movements does not then follow the cessation of asphyxia. In this phenomenon there is little to describe. The maintained flexion reaches a maximum and then continues to diminish until the limb comes to its posture of rest.

But, if the asphyxia is not so long continued, in some cases a resumption of the movements of progression may follow its cessation.

There is at first the state of maintained flexion in both hind limbs. This is long sustained after the cessation of the asphyxia - the opening of the trachea. The maintained flexion may remain for as long as twenty seconds or more. It may be broken/

FIG. 16.  
FIG. 17.

FIG. 14.  
FIG. 15.

broken from time to time by short series of abortive beats. In rare cases there may be no complete absence of the beats in one of both limbs - shallow irregularities then persist throughout the period of maintained flexion.

To take a case in which the maintained flexion is complete:- After one or two abortive attempts the beats finally appear again permanently in one limb and are shortly accompanied by beats in the other. The rhythm of these is faster than the fastest rate which occurred before the appearance of the maintained flexion, and the beats are either synchronous or very nearly so. At that point at which the beats reappear the level of maintained flexion has fallen considerably from that level which was attained shortly after the cessation of the beats in asphyxia.

As the reappeared beats persist they change in extent and rhythm while at the same time the temporal relationship between the beats in the two limbs also changes.

In the first place the beats gradually increase in absolute extent. This increase is conditioned by two factors. The heights of the beats increases/

increases and the lowest points attained also become lower. The curve of relative flexion (the line joining the summits of the beats) having reached a maximum begins to fall again slightly, but the curve of relative extension seems to fall gradually until it reaches a minimum which is then maintained.

During all this time the rhythm of the beats slows and at the same time the relation between the rhythms in the two limbs changes. From complete, or almost complete, synchronism the relationship gradually changes to true alternation, one series of beats gradually advancing in time in relation to the other.

The phenomena of the recovery from asphyxia in fact reproduce in reverse order those of the establishment of asphyxia. And the condition gradually attains a point at which the beats again have the normal extent and rhythm and the normal bilateral relationship of rhythms.

e. NARCOSIS PROGRESSION AFTER SOME LESIONS  
OF THE NERVOUS SYSTEM.

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The movement of progression in the intact hind limbs under narcosis may persist and be recorded after certain lesions of the central and peripheral nervous system.

Of these the first which we may consider is the act of decerebration.

In one experiment the act of progression was in evidence for some time before the cat was decerebrated. The movements continued after the decerebration and were recorded fifteen seconds after the infliction of the lesion. The movements were then present in both hind limbs and were synchronous, whereas they had been alternate before. The movements were reduced in extent and were more so in one limb than in the other. As the record proceeded the movements became alternate. The most remarkable change was in the rate of their rhythm. This was markedly faster than before decerebration. In the record before the act, the rhythm had been about 1.2 beats per second. After the act the rhythm was 2.6 beats per second. The movements entirely disappeared 40 seconds after the decerebration.

FIG. 19.  
FIG. 20.

The/

The movements of progression under narcosis may persist even after local injury to the spinal cord in the lumbar region.

FIG. 22.  
FIG. 23.

Thus in another experiment well marked movements of progression had been recorded in the intact animal under narcosis. Less than twenty minutes thereafter the lumbar spinal cord was completely transected at the level of entry of the most caudal fibres of the sixth pair of post-thoracic posterior spinal roots. This lesion severs the spinal centres for the extensors of the ankle (gastrocnemius), which are in the segment of the cord caudal to the lesion, from the centres for the flexors (tibialis anticus), which remain in connexion with the rest of the central nervous system. In making this lesion the lower segment of the cord was destroyed and removed. Movements of progression in the limbs had been in action just before the infliction of the lesion and they persisted after it. Three minutes after the act of transection the movements were recorded and at the same time it was determined by palpation that the tibialis anticus was taking part in them and that the ankle was thus in action.

In a record taken twenty minutes before the infliction/



infliction of this lesion, the movements of narcosis progression were well marked, of large extent and truly alternate. After the lesion, at first the movements were irregular, but they soon became regular. They were then strictly alternate, but of comparatively small extent. The rhythm was not markedly different from that which obtained before the lesion. It was then about 0.95 beats per second. After the lesion, and when the movements had become regular, they were of a rhythm of 1.0 beats per second.

A further lesion may be inflicted upon the lumbar spinal cord, in that a portion of one side may be removed. In the above experiment, after the lumbar cord had been destroyed, from the level of the upper margin of the seventh segment downwards, the left side was further ablated in the 4th, 5th and 6th segments. After this lesion, which removes the centres of the flexors of the ankle on one side (including that of tibialis anticus), the movements of progression still persisted in the ankle of the side upon which the spinal cord still remained in these segments. Palpation revealed the fact that the tibialis anticus muscle was taking part/

FIG. 23.B.

part in the movements. The rhythm seemed to be faster than before, and the movements to be small in extent. An attempt was made to register them. The beats were extremely small, but were present. At the time of registration they were of a rhythm of about 1.0 beats per second.

The movements of progression under narcosis have also been observed before and after section of the lumbar posterior spinal roots.

In one experiment very marked movements occurred in the intact animal. These were rather fast in rhythm. All the lumbar posterior spinal root fibres from the level of the third pair downwards were then cut intradurally upon the left side. Shortly thereafter movements of progression in the limb of the uninjured side were registered. They were still of large extent, but were of slow and irregular rhythm.

In another experiment all the lumbar roots, both anterior and posterior, were cut upon the left side intradurally from and including the third left lumbar spinal roots downwards. Good records of progression were obtained before and after the lesion. With regard to the extent of the beats/

FIG. 17.  
FIG. 18.

FIG. 17.  
FIG. 18.

beats there was little difference. They were, of course, not present in the limb of the same side as the lesion. The rhythm of the beats, which before the lesion was about 0.85 beats per second, became 1.05 beats per second.

In this experiment the effect of asphyxia was recorded before and after the section of the lumbar roots. In either case similar phenomena were observed. This was one of the instances in which the immediate result of the closure of the trachea was a cessation of the movements, and in which these then reappeared and became faster in rate. These phenomena were observed in records before and after the lesion, and differed in no marked manner.

f. MOVEMENTS OF PROGRESSION UNDER NARCOSIS  
IN ISOLATED MUSCLES.

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So far the movements of progression have been described as they occur in the intact hind limbs. They have also, however, been recorded as they occur in individual isolated muscles, and it is then of interest to examine the relationships of the movements in them with the similar movements of the intact hind limbs in the same individual.

It/

It may be remarked that in the preparation of the individual muscles the one hind limb is entirely out of action by motor paralysis, while of the other limb only the recording muscles are left to function.

In one experiment the movements of progression were registered before the preparation of the individual muscles, and in the intact hind limbs. They were then of good extent, were regular, and of a rhythm of about 1.6 beats per second.

After the preparation of the individual muscles (tibialis anticus and gastrocnemius), the movements persisted and were recorded as they occurred in them. They were confined to the flexor - tibialis anticus - and the extensor - gastrocnemius - exhibited no movement. The appearance of the rhythmic acts in the flexor exactly paralleled in the record the appearance of the acts in the intact limb. The rhythm was the same. At different points the beats occurred either with or without intervening pauses. In the former case, the termination of the act of relaxation in the flexor muscle was succeeded by a period of maintained relaxation, which, in its turn, ceased on the commencement of the act of active flexor contraction. The contraction of/

FIG. 24.

of the flexor in the first part of the beat reached a certain limit, and then passed over immediately into flexor relaxation which, when it had again reached the level of complete relaxation, terminated with the state of maintained relaxation. At another time, and in another record, the beats had no intervening pauses of maintained relaxation. Active relaxation of flexion then immediately succeeded active contraction, but was immediately succeeded by the active contraction without pause. The phase of contraction was slower than that of relaxation. ¶ The effect of asphyxia was studied as before. The immediate effect of closure of the trachea was a slight lengthening in the period of the beats. This was quickly succeeded by an increase in the rapidity of the rhythm. The intervening pauses became shorter. Occasionally grouping of the beats occurred as the asphyxia proceeded. A beat would, as it were, be added and take the place of a pause. The groups in which beat succeeded beat without pause became then greater in number of beats, and more frequent, so that the pauses came to be the exceptional occurrences. Finally, and with regularity, beat succeeded beat without pause and the rhythm/

FIG. 24.

rhythm continued to become faster, until the movements ceased in the full asphyxial effect.

During this time, a change had taken place with regard to the extents of the beats. At first, the level of the points of relaxation between the beats remained constant. At the same time, the levels attained at the tops of the beats continued to ascend. Then there was a slight fall, and shortly after this the levels of relaxation between beats commenced to ascend. Finally, with the complete cessation of the beats, there was a state of maintained contraction of the muscle which continued for a short time to become greater, and was, in extent of contraction, greater than the extreme contraction seen in any beat.

It will thus be seen that the phenomena exactly paralleled those present in similar movements in the intact limbs. Another reference may, however, be made to the grouping of beats referred to above.

It has been said that there is, immediately after the commencement of asphyxia, an appearance as if occasionally an adventitious beat was interposed between two ordinary beats, and then replaced the normal pause. This is not quite an accurate statement/

statement of the phenomenon, although in the records the appearance is very much as if this were true. What happens is this:- After a series of beats, in which there are regular pauses, has occurred, suddenly the cessation of relaxation in one beat is immediately followed by the contraction of another beat without pause. The termination of this is then followed by a third beat - with or without pause - and this third beat appears to occupy the position in the tracing that it should have occupied had there been no interposed beat (the second beat being called for convenience an "interposed" one). But, as a matter of fact this is not so, for the exact measurement of the curve demonstrates the fact that the third beat falls markedly later than it should have done, had there been no interposed beat. In other words, there is in the rhythm a delay, following the appearance of a beat out of place. The third beat does not occur in its normal position, nor does it follow the second at the usual interval.

In one instance the phenomena of recovery from asphyxia were observed in a tracing of the narcosis progression in individual muscles.

The/

The state of maintained flexor contraction then showed occasional abortive series of shallow beats. Soon undoubted movements of progression occurred in the flexor. These were irregular, of slower rhythm than before the asphyxia, and of smaller extent.

The extensor played no part in the phenomena of asphyxia or of recovery therefrom. Throughout it remained inactive.

v./

V. PROGRESSION MOVEMENTS FOLLOWING CENTRAL  
STIMULATION IN THE CAT.

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a. ELECTRICAL STIMULATION OF THE CUT SUR-  
FACE OF THE UPPER LUMBAR SPINAL CORD:  
PROGRESSION IN THE INTACT HIND LIMBS.

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In these experiments the upper cut surface of the more caudal lying (lumbar) segment of the spinal cord has been stimulated electrically in the unipolar method after transection of the spinal cord at the level of the XIIth thoracic segment in the decerebrate cat.

In the low spinal preparation electrical stimulation applied under these conditions sometimes evokes rhythmic movements of the hind limbs similar to those of progression.

The effect of the stimulation may be simply a maintained bilateral flexion which dies away in both hind limbs on the cessation of stimulation. Very often, however, during the period of stimulation a rhythmic movement in each hind limb replaces the bilateral/

FIG  
1

bilateral flexion. This is irregular, but the beats which compose it are alternate and their rhythm is not faster than the rhythms seen in narcosis progression during asphyxia, although it is faster than the normal rhythm of the narcosis movements. This rhythmic movement further resembles the narcosis progression in asphyxia in that the levels of the upper and lower points in the beats ascend as the stimulus is continued.

Even in cases where there is no breaking of the maintained flexion during stimulation into rhythmic components the rhythmic movement may appear as a sequence of the cessation of stimulation, while in the cases in which the rhythmic movement commences during stimulation it may be continued thereafter. These rhythmic movements may at first be comparatively regular and alternate, but soon they become very irregular in rhythm and extent.

b. ELECTRICAL STIMULATION OF THE CUT SURFACE OF THE SPINAL CORD: PROGRESSION IN THE INDIVIDUAL MUSCLES.

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In these experiments the muscles, tibialis anticus and gastrocnemius, have been prepared in the manner already described; their movements in response to electrical stimulation of the cut surface of the spinal cord have been recorded in the low and high spinal preparations, and in the latter preparation also in the de-afferented condition.

In the first place we may examine the phenomena in the low spinal preparation (otherwise de-cerebrate).

In the records that of the flexor - tibialis anticus - may exhibit rhythmic discontinuities of contraction during the electrical stimulation of the cut surface of the lower thoracic spinal cord. Immediately after the initiation of stimulation there commences a state of maintained contraction, but this shortly is broken by a complete or a partial relaxation/

FIG. 25.

FIG. 26.

FIG. 27.

FIG. 28.

FIG. 29.

FIG. 29.

relaxation and is then reconstituted. The relaxation and reconstitution of contraction proceeds rhythmically. Thus the record in appearance is split up into a series of rhythmic beats. These are of regular rhythm the rate of which is about 1.5 beats per second. There may, or there may not, be pauses between the point of cessation of relaxation and the point of initiation of the succeeding contractions in the beats; and, although the summits of the beats are usually pointed, there may sometimes be short plateaus there.

The lowest points in the beats do not usually coincide with the level of the position of rest of the muscle (its "post mortem" length). That is to say that there is usually a certain amount of maintained contraction even at the lowest levels of relaxation during the rhythmic movements. The amount of this maintained contraction may be considerable. With the onset of "fatigue" caused by periodic repetition of the stimulus, the amount of maintained contraction at the lowest points of the beats becomes greater. The beats thus become smaller for their summits do not then increase in height. The stimulus has been applied for periods of 10 seconds and the/

the beats have persisted throughout; but the cessation of stimulation has in every recorded case been followed by immediate cessation of the phenomenon. The muscle, after perhaps one additional beat, at once relaxed to its length of rest.

In the case of the extensor muscle there was no observed movement except in one record. In this instance one very slight contraction took place. It corresponded in time with a phase of relaxation in the flexor record.

FIG. 29.2.

In the second place we may examine the phenomena in the high spinal preparation (decapitate) in which the afferent fibres of the muscles are in action.

There was in the record little not observed in those taken from the low spinal preparation. The rhythm of the beats was, however, more irregular. Its rate was between 1.8 and 2.0 beats per second. There was a greater degree of maintained contraction at the level of the lowest points of the beats, and no movement was observed in the curve traced by the extensor.

In the third place we may examine the records obtained from the high spinal preparation (decapitate)/

(decapitate) in which the afferent fibres of the recording muscles are destroyed. It will be remembered that although the progression movements of narcosis may occur in the uninjured hind limb after section of the posterior root fibres upon one side of the lumbar spinal cord yet that they have not been observed to take place in the limb of that same side.

In an experiment of this nature the posterior lumbar spinal root fibres were destroyed upon the side of the recording muscles, in the sixth post-thoracic segment and in all other segments lying more caudal. The recording muscles were thus de-afferented and all other muscles in the two hind limbs either de-afferented or put out of action by motor paralysis.

Stimulation of the cut surface of the cervical spinal cord - the stigmatic electrode being applied to the dorsal part of the antero-lateral column of the same side as the recording muscles - gave a well marked rhythmic response of the flexor muscle. The rhythm of the beats was regular and of a rate of about 1.1 beats per second. If the stimulus was continued, let us say for a period of 15 seconds, the rhythm became slower in rate. There was /

FIG. 25.

FIG. 26.

FIG. 27.

was a certain amount of maintained contraction of the flexor muscle at the lowest points of the beats, but it was not of great extent. On cessation of stimulation the response ceased. But if a beat was then in action it was completed. That is to say that a beat in process at the point of cessation of stimulation was not cut short. Immediately after the initiation of the reaction the beats were comparatively small in extent but as the reaction proceeded they became gradually larger until a maximum was reached or until stimulation was stopped.

As a rule the extensor - gastrocnemius - exhibited no movement. But in one instance the tracing recorded from this muscle exhibited small beats. In time these corresponded with the intervals between the beats of the flexor: the point of commencement of the beat of the extensor coinciding with a point midway on the downstroke of a flexor beat.

The effect upon the reaction of increasing the strength of stimulation in successive reactions was of interest. With a minimal stimulus the reaction was rhythmic and there was almost no maintained contraction of the flexor at the level of the lowest points in the beats. As the strength of stimulus was gradually increased there was still a rhythmic response /

FIG. 26.

FIG. 27.

response but with a marked degree of maintained contraction. Later, there was a reaction like that of a pure flexion-reflex but with slight irregularities in the plateau of maintained flexion. A further increase of strength of stimulus abolished these irregularities. Up to this point the extensor exhibited no movement. But a still greater increase in strength of stimulus produced a marked extensor rebound contraction on cessation of stimulation. This effect of abolition of the rhythmic response on increase of strength of stimulus was not a "fatigue" effect for a strong stimulus which evoked nothing but unbroken maintained flexion did not prevent an immediately succeeding weak stimulus from evoking the rhythmic effect.

The area of the cut surface of the cervical spinal cord described above was that stimulation of which most effectually produced the rhythmic act of progression. Similar stimuli applied to the ipsilateral and contralateral posterior columns of the cord also gave a rhythmic response.

Weak stimuli applied to the dorsal part of the contralateral antero-posterior column of white matter evoked a reaction in which the chief activity was a maintained contraction of the extensor - the flexor /

flexor usually not acting. A flexor rebound contraction in some cases followed the cessation of stimulation. As the strength of stimulus was increased a flexor contraction appeared. This was of long latency and in the latency there occurred a contraction of the extensor which disappeared on the commencement of the flexor contraction. This flexor contraction was rhythmic or irregular. With further increase of strength of stimulation the flexor contraction became regular and maintained. Its latency became short; and, at the same time, the extensor did not act at all.

VI. PROGRESSION MOVEMENTS FOLLOWING CENTRAL  
STIMULATION IN THE CAT.

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MECHANICAL STIMULATION OF THE SPINAL  
CORD.

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Movements of progression have been obtained in these experiments also by mechanical stimulation of the spinal cord. As these movements have been better marked than any others save those in the intact hind limbs under narcosis, and as they have been observed in a great variety of conditions, they are here described in this separate section of the thesis.

The most efficient mechanical stimulus has been found to be a rapid division of the lower thoracic spinal cord with one cut of a sharp pair of scissors. In a large number of decerebrate preparations this procedure releases marked movements of progression which exhibit several interesting phenomena.

Irregular movements resembling progression have also been observed to take place both in the intact /

intact hind limbs and in the individual muscles upon crushing the upper end of the lumbar segment of the spinal cord after transection. In these cases, which may be dismissed in this paragraph, the movements are irregular in rate and rhythm and alternate. They are in many cases undoubtedly movements of progression. But they are not so well marked as those about to be described. In some instances they may be exhibited by the extensor alone; in others by the flexor without concomitant movement of the extensor.

A. IN THE DECEREBRATE PREPARATION.

If the spinal cord is rapidly severed in the decerebrate preparation at or about the level of the caudal thoracic segments, and the movements of the individual muscles - tibialis anticus and gastrocnemius - registered, the record exhibits three main phases.

Immediately after the act of severance there is a period - the first phase - characterised by maintained flexion; that is to say, by maintained contraction of the flexor and by absence of movement in the extensor. There is sometimes evidence of extensor relaxation, and sometimes of slight extensor contraction /

FIG. 30.

FIG. 41.

FIG. 44.

contraction. In the flexor record there is immediately a rapid contraction of the muscle which thus rises into a state of great maintained contraction. This may last for 12 seconds or more, but towards the end it is broken by partial relaxations. These become greater but occur at irregular intervals, after each partial relaxation the maintained flexion being at once reconstituted.

The second phase is characterised by complete rhythmic relaxations of the flexor contraction. the flexor record is composed of rhythmic beats. These are at first rather irregular in extent and rhythm and succeed each other without pause in relaxation between the beats. As the phase continues the beats become regular in rhythm and pauses appear between them at the level of their lowest points which coincide with the position of rest of the muscle before the application of the mechanical stimulus. There appear at the same time movements of the extensor.

It may be supposed that the record is one in which there is relaxation of the extensor in the first phase. Immediately after the first relatively complete relaxation of the flexor there ensues a complete reconstitution of its contraction which at once passes over into relaxation again. Synchronously with /

with this passage from contraction to relaxation in the flexor curve there occurs the first movement of the extensor. This is a sharp contraction followed by relaxation. It resembles the extensor rebound contraction seen on the cessation of a peripheral stimulus which evokes a flexion-reflex, and on its cessation the curve of the extensor remains at the level of rest. At the next similar point in the flexor curve the same phenomenon reappears in the extensor tracing, and so the condition continues. But, as the phase proceeds, the extensor relaxations become less. The extensor beats, in fact begin to exhibit a certain degree of maintained contraction in the intervening pauses. At the same time the rapidity of the extensor relaxations in the beats remains constant, but the rapidity of the upstrokes diminishes considerably. As the beats of the flexor record slow in the rate of their rhythm and exhibit intervening pauses in relaxation there is a maintained contraction of the extensor in the corresponding intervals. The phase merges with the succeeding one in an imperceptible manner. There is a slowing of the rate of the movements and a diminution of the extents of the flexor beats with a corresponding accentuation /

accentuation of the maintained extensor contraction in the intervals. The phase may be of a duration as long as one minute or more.

The third phase is characterised by a cessation of the flexor movements and a state of maintained contraction of the extensor. The flexor beats having become slow suddenly diminish in extent and become much slower. This lengthening in rate of their rhythm is produced by an increase in the duration of the intervening pauses. Synchronously with these slowed beats there are relaxations and reconstitutions of the maintained contraction of the extensor. The relaxations are comparatively rapid movements and they commence in time markedly before the commencement of contraction in the flexor beat. The reconstitutions of extensor contraction, on the other hand, are comparatively slow. The phase terminates in a state of absence of the beats in the flexor record and of maintained contraction in the extensor record. This gradually fades away, the process perhaps taking one or two minutes in some cases.

For convenience these three phases may be termed the first phase or that of maintained flexion; the second phase, or that of "balance"; and the third phase, or that of maintained extension. Variations in /

in the phenomena exhibited in these three phases occur in the records.

In the first place the record may be one of maintained flexion in its entirety. This may be looked upon as one in which the first phase is exaggerated. There is then usually no movement of the extensor throughout the record. At this point of application of the stimulus there is a sudden contraction of the flexor and the ensuing state of maintained flexor contraction soon reaches a maximum, after which it gradually dies away. There may be irregularities in this maintained contraction. But the partial relaxations and succeeding reconstitutions of contraction are slight, and of very irregular rhythm. The duration of this phenomenon may be greater than one minute.

Intermediate between this type of the phenomenon and what may be termed the "normal" form is a type in which there appears to be predominantly throughout a state of maintained flexion, but in which that is more broken by relaxations of flexor contraction. The beats thus constituted are of great irregularity of form, extent, and rhythm. They appear more to resemble the flexor contraction of the flexion-reflex. The tracing appears as if composed /

composed by the addition of irregular flexor reflex contractions. In the extensor record there are beats of short duration although they may be of comparatively great extent. They correspond in time - both in their contraction and relaxation phases - with the period of relaxation of the flexor contractions. There is in these records no evidence of the terminal state of maintained extensor contraction; and, as the extensor movements strongly resemble the movement in extensor rebound, it looks as if there were two factors in the normal extensor phenomenon of this act.

Yet another irregular form is perhaps a type which more nearly resembles the normal than this does. Here the first phase may run a normal course (save that there may be a certain amount of maintained contraction of the extensor synchronous with the maintained flexor contraction). The second phase also may be comparatively normal although the beats may be rather irregular. Towards the end there may be considerable regularity of the flexor beats, and in the pauses between them there may be evidence of maintained contraction of the extensor. But on the cessation of the second phase the flexor goes again into maintained contraction and there is no evidence of /

FIG. 21.

of extensor contraction at all.

In the three phases of comparatively normal records there may also be certain degrees of irregularity.

In the first phase there may be irregularity of the state of maintained flexion. This may be almost entirely absent in its maintained form. In these cases the rhythmic relaxations of the contraction of the flexor appear almost at once after the section of the spinal cord. They are for a short time irregular, but the regular beats of the "balanced" phase may then appear within 4 seconds of the infliction of the lesion. In other cases the relaxations may appear in the curve of maintained flexor contraction in the first phase, but may again give place to maintained contraction before finally the complete relaxations of the second phase commence.

Variations of the behaviour of the extensor muscle in the first phase also occur. In some records there may be little or no evidence of movement of gastrocnemius. In other records there may be evident relaxation of the muscle in this phase and this may perhaps be regarded as the typical phenomenon exhibited by the extensor. It more rarely happens that this muscle exhibits marked contraction synchronous /

FIG. 35.

FIG. 30.

FIG. 33.

synchronous with the maintained contraction of the flexor. This may occur, for instance, in such a case as that in which the maintained flexor contraction is of less duration than usual and in which the beats appear very soon in the record. But it may also occur in records in which the maintained contraction of flexor is of long duration and great extent. There may be a brief initial relaxation of extensor but this is soon succeeded by an active contraction which increases in extent as the record proceeds. If there are isolated incomplete relaxations and reconstitutions of the flexor contraction these may be accompanied in the extensor record by brief additional contractions which resemble extensor rebound contraction. As a rule however the extensor relaxes or shews no movement throughout the first phase, and its first movement in the record is then at the beginning of the second phase when it begins to exhibit these reboundlike contractions which synchronise with the flexor relaxations.

In the second phase of the phenomenon variations in the flexor and in the extensor curves may also occur.

In the flexor tracing, whereas the typical reaction is one in which the beats are of regular extents /

FIG. 21.  
FIG. 35.

extents and rhythm with level intervening pauses in relaxation, irregularities in their extent, in their rhythm, and in the occurrence of the pauses may occur.

To take the last of these irregularities first: It sometimes occurs that the incidence of the beats is not so arranged that they are regularly disposed with equal durations between their points of initiation, but that there is such an arrangement that the beats are in groups of two with no pause between but with a short pause intervening between the groups. It then commonly happens that the second beat in the pair is slightly smaller in extent than the first and at the same time markedly shorter in duration - about half as long. Greater irregularity of rhythm may also occur. In some cases there may be a great variation of the durations of the intervening pauses. This is usually accompanied by irregularities of the extents of the beats, and it is such that the shorter beats are followed at shorter intervals by the ensuing beat than are the beats of greater extent. But this rule is often broken in the curves.

Another variation is seen in the average rate of rhythm in the different records. In typical examples of the second phase the rate of rhythm is about /

FIG. 35.

FIG. 21.

FIG. 30.

FIG. 37.

FIG. 37.

about 1.0 to 0.7 beats per second. But the rate of rhythm may be as slow as 0.3 beats per second. This slowing is seen usually at the termination of the second phase. In some records the rate of rhythm has been extremely fast - 3.0 to 3.5 beats per second - and these rapid beats, although irregular in rate and in extent as well as in the completeness of some of the intervening relaxations, have been continued for durations as long as 45 seconds.

Irregularity in the extents of the beats in a record may be great. Although commonly there is comparative regularity in the levels reached at the summits of the beats, in some records these levels may shew great variation. It may then happen that the extent of the beats suddenly is reduced, and that in the succeeding beats there is a gradual growth in extent until a maximum is reached, when the process may be repeated. In other cases, and at other parts of the same record, there may be no observable rule in the variation of the extents of the beats.

Variation of the extensor movements may also occur in the records. These seem to be related to the flexor irregularities.

Where the flexor record is of that type in which /

FIG. 21.  
FIG. 30.

which the beats occur in groups of two without pause between the constituent beats of the group but with a pause between the groups the extensor record may shew corresponding irregularities. These may be such that the termination of contraction - the summit of the first, or larger, beat of the group is accompanied in the extensor record by a sudden contraction. This does not occupy the whole time of the relaxation of the flexor. It terminates in a short and level plateau which lasts only as long as the remaining portion of the flexor relaxation. The plateau is terminated by the commencement of the relaxation of the extensor contraction, and the point of initiation of extensor relaxation corresponds in time with the termination of the relaxation of the first beat in the flexor group and the commencement of the contraction of the second beat. The relaxation of the extensor movement is a slower movement than the contraction, and it lasts for the whole of the contraction phase of the second flexor beat and terminates shortly after the commencement of relaxation of the flexor. There then commences another extensor movement, but this is smaller than the foregoing and of slower contraction. Its contraction phase lasts through the flexor pause, which then occurs, and ceases /

FIG. 37.

ceases just before that point at which the first beat of the following flexor group commences its contraction. The extensor then slowly relaxes - the relaxation synchronising with the contraction phase in the flexor - until a point just after the appearance of flexor relaxation, at which point the sudden contraction of the extensor as first described repeats itself - and so the phenomenon proceeds.

The behaviour of the extensor during the phenomena of the second phase may be summarised by saying that when the flexor beats follow each other without pause the extensor performs a sharp movement of short duration, the contraction phase of which commences in time just after the commencement of relaxation in a flexor beat, while the commencement of relaxation of the extensor movement falls in time just before the commencement of the next flexor contraction. The whole of the extensor contraction and a part of its relaxation then falls within the period of relaxation of a flexor beat. But when the flexor beats follow each other with intervening pauses the extensor movements are commonly shorter in extent and slower in phase. The initiation of the extensor movement then occurs shortly after the commencement of flexor relaxation and during it. The contraction ceases /

ceases shortly before the following flexor contraction. The phase of extensor contraction thus corresponds more or less nearly with the flexor pause, and the relaxation phase with the ensuing flexor contraction. Although usually slow, the extensor contraction may occasionally be a rapid movement.

When the flexor beats in the records are of slow rhythm and with long pauses intervening between them the second type of extensor movement may be the only one to be exhibited. When the flexor beats follow each other rapidly and without intervening pause the extensor may exhibit only the first type of movement. This may also be seen alone in the irregular forms which seem to be composed of movements like the movements in flexion reflexes. When the flexor exhibits in places pauses and in other places no pauses then both types of extensor movement may be present in the records.

In the third phase of the reaction there is usually a marked maintenance of extensor contraction. This is broken by partial relaxations with following reconstitutions of contraction. These occur synchronously with the slow and small flexor beats which may still persist into the third phase. The extensor relaxation commences considerably before the /

FIG. 32.

FIG. 30.

FIG. 33.

the flexor contraction, and the phase of relaxation ceases shortly after the commencement of flexor relaxation or even after the termination of it. Finally the flexor beats cease and there is maintained extensor contraction. This extensor phenomenon may be regarded as an exaggeration of the second of the types of extensor movement in the second phase described above. But variations occur.

Thus the flexor beats may disappear before the disappearance of the extensor relaxations and reconstitutions of contraction, or these may occur when the flexor beats fail although the beats may afterwards reappear. In any case the diminution of the flexor beats in extent does not seem to be accompanied by a diminution of the extent of the extensor relaxations.

In some instances the maintained extension may not appear. Even a maintained flexion may take its place. In other cases it may be present but rapidly disappear.

It has been stated above that in some instances rapid transection of the lower thoracic spinal cord is followed by a state of maintained flexion alone, and that this gradually disappears without any phase either of progression (balanced phase) or of maintained /

FIG. 21.  
FIG. 33.  
FIG. 21.

maintained extension. It may be asked whether a reaction purely of maintained extension is ever met with. This phenomenon has been observed but not in the normal decerebrate cat on section of the spinal cord.

Before passing to the other conditions and preparations in which this form of progression is obtained it may be stated that the movements have been observed and recorded in the intact hind limbs. In these records the movements at the two ankles commenced with maintained flexion and ended with maintained extension while between these there was a phase in which movements of progression occurred in the two limbs. On termination of the phenomenon in one record there appeared to be a state of maintained flexion at the knee when the ankle was in maintained extension. The movements of progression were irregular. At times they were synchronous in the two limbs, and then a large beat in one limb accompanied a small one in the other, while a small beat in the first would accompany a large one in the second limb. When the beats were more regular, later in the record, there was true alternation of them.

B./

B. IN THE HIGH SPINAL PREPARATION.

A sudden section of the spinal cord in the lower thoracic region of the high spinal preparation converts the condition of the lumbar centres from a "decapitate" to a spinal state, and at the same time may evoke movements of the isolated individual muscles.

A maintained flexion - characterised in the tracings by contraction of the flexor and absence of movement, or relaxation, of the extensor - may be the only result of the stimulus. This gradually dies away and the curve ends without demonstrating extensor contraction. But there may be an appearance of beats upon the curve of flexor contraction. These are then of slight extent and irregular incidence.

In other instances there may be a more marked demonstration of beats in the flexor curve and, at the same time, there may be evidence of extensor contraction. In one instance there was an extensor contraction of maintained type shortly after the infliction of the transection - the flexor contraction then waning rapidly - but later there was a balanced phase and the curve finally ended with maintained extension. In this case there were beats in the second /

second phase. These were irregular in rhythm and extent, and there were synchronous movements in the extensor tracing similar to those in the decerebrate preparation.

C. IN THE LOW SPINAL PREPARATION.

A rapid transection of the spinal cord in the decerebrate condition often releases movements of progression as has been described above. The interesting question then arises - whether or no a second transection at a lower level will again release such movements. This second lesion is, of course, performed upon the low spinal preparation; and in some cases it has been followed by a third and a fourth - each at a level more caudal by one spinal segment than that which preceded it.

In these instances movements of progression have been the exception. The rule is a maintained flexion in response to the stimulus. In one instance, however, movements of progression have occurred.

In this case the movements recorded were those of the intact hind limbs and the second transection was performed at a level about 3 mm. caudal to the first which was in the lower thoracic region of /

of the spinal cord. It was followed by a short maintained flexion, then a rhythmic balanced phase, and finally by a state of maintained extension in both hind limbs. In the second phase of the phenomenon the beats were irregular in form, in extent, and in rhythm. At one point they were alternate in the two hind limbs. At another they were synchronous. In their appearance and in the rate of their rhythm they nearly resembled the rhythmic beats elicited in response to electrical stimulation of the cut surface of the cord after the first transection. They were more rapid than were the beats of the second phase at the first transection.

In another instance in which also the movements of the intact hind limbs were recorded, there was alone maintained flexion. In this instance there had been very regular movements under narcosis before the first transection, and irregular movements in response to that transection.

In an instance in which the movements of the isolated individual muscles were registered the first transection was performed at the level of the entry of the first post-thoracic pair of posterior spinal roots and it evoked a very irregular reaction in which there was evidence of beats in the second phase. /

phase. The second transection was just caudal to the entry of the second post-thoracic pair. There was evoked a reaction at first of maintained flexion and then of maintained extension. The appearance was as if the second phase had been omitted. A third transection was then performed just below the level of entry of the third post-thoracic pair of roots, and evoked a reaction of maintained flexion.

In another case in which this experiment was repeated the first transection - between the entries of the first and second post-thoracic spinal roots - evoked a reaction of maintained flexion alone. Subsequent transections between pairs II-III, III-IV, IV-V also evoked maintained flexions, in the last instance there being also a synchronous maintained contraction of the extensor.

D. IN THE DE-AFFERENTED PREPARATION.

The possible occurrence of movements of progression after abolition of the afferent nerves of the muscles is a question of some interest and importance in the problem of the intrinsic factors in the act of progression.

In these experiments the muscle afferents have /

have been divided by section of all the post-thoracic roots from the level of the upper fibres of the sixth downwards upon the side of the recording muscles.

This removes the afferents of the recording muscles as well as those of other muscles in the leg. All the other muscles of both hind limbs were then paralysed by section of their motor nerves or of their tendons. Thus no proprioceptive stimuli - normally engendered in the limb during the act of progression - were in action. The majority of the experiments have been performed in preparations in which the condition which obtained before the spinal transection was the decerebrate. In one of these experiments all the post-thoracic posterior spinal roots were cut upon the recording side. In one other experiment the condition before the spinal transection was the high spinal.

In that experiment in which the preceding condition was the high spinal the only reaction to the spinal transection was a maintained extension - evidenced by contraction of the extensor. There was no movement of the flexor. But it must be stated that there had previously been a failure of the flexor act in the ipsilateral flexion-reflex, and subsequent to the transection the ipsilateral stimulus also failed /

FIG. 41.

FIG. 44.

failed to evoke flexor contraction. Undoubtedly there had here been a preceding paralysis either of the flexor centre or of its peripheral mechanism.

That instance in which all the afferents were divided also exhibited predominantly a maintained extension. This was preceded by a short act of maintained flexion, and the maintained extension was broken at intervals as if there were concomitant beats of the flexor, although these were absent in the record.

All the other experiments demonstrated rhythmic acts of progression of unusual excellence.

In the first phase there has been observed a greater tendency to an initial maintained extension than has been the case in the "normal" experiments. The first act after the production of the lesion is then a flexor contraction. This may be of short duration and in its termination be succeeded by the maintained extensor contraction which persists for a time unbroken. The flexor maintained contraction then re-appears and the extensor contraction wanes. There shortly follow the flexor relaxations which constitute the beats of the balanced phase. There may, however, be no marked movement of the extensor in the first phase; but on the whole it may be said to be characterised /

characterised by shortness of duration and by the presence of maintained extensor contraction in greater or in less degree.

The third, or final, phase is characterised by the usual maintained extensor contraction. As the flexor beats at the end of the second phase decrease in extent the concomitant extensor relaxations remain of nearly constant value. These relaxations then persist for a time after the total disappearance of the flexor beats. On the whole the phenomenon of maintained extensor contraction in the third phase occur with greater regularity than in the "normal" - that is, not de-afferented - condition.

In the second, or balanced, phase phenomena of some interest have been observed. The flexor beats have occurred with greater regularity of form, extent, and rhythm than has usually been the case in preparations not de-afferented. At the same time the movements of the extensor have been unusually well marked.

The phenomena of the extensor movements in the second phase seem to be controlled by two factors. At first there may be little or no maintained extensor contraction, but there are single contractions of that muscle - each of comparatively short duration. In /

In these the upstroke of contraction is a rapid one. It synchronises in its initiation with a point just later than the summit of a beat in the flexor record, and this upstroke terminates before the flexor relaxation has reached its lowest level. The termination of the upstroke is succeeded by a short plateau of maintained contraction which lasts as long as the remainder of the relaxation of the flexor beat. At the termination of the flexor beat there is a pause in relaxation, and this is accompanied in the extensor record by a slow relaxation which finally ceases in the next extensor movement which synchronises with a point just after the summit of the next flexor beat. During the latter part of the extensor relaxation there, therefore, occurs the upstroke of the flexor movement, but this does not determine any synchronous change in the extensor curve. In some instances an extensor movement may not accompany the relaxation phase of a flexor beat. This seems to occur when a flexor beat of smaller extent and duration than usual follows the preceding flexor beat at a shorter than usual interval of time. When the duration of the relaxation phase of a flexor beat is greater than usual the plateau of the extensor movement may be increased in duration.

As the second phase continues a change occurs /

occurs in the phenomena exhibited by the extensor. At first there is an ever decreasing extent of relaxation after each plateau of contraction. That is to say that there is a gradual increase in the amount of maintained extensor contraction at the level of maximum relaxation. When this reaches a certain degree an additional movement appears in that portion of the curve of relaxation which synchronises with the contraction phase of a flexor beat. At a point which falls in time a little before the point of initiation of the flexor contraction there commences an acceleration in the rate of the extensor relaxation, and this continues until, just after the summit of the flexor beat, the extensor contraction appears. There thus seems to be a small additional relaxation of the extensor.

With an increase in the duration of the pauses between the flexor beats, which appears towards the end of the second phase, the synchronous relaxation of the extensor during these pauses reaches a maximum and then decreases. The curve of relaxation then appears to rise again just before again falling in the additional relaxation synchronous with the flexor contraction makes its appearance. This second rise reaches its greatest extent at the end of the second phase. /

phase. At that period, even although the flexor beat is of good extent and comparatively slow fall, the plateau of the extensor movement disappears. There is a more rapid relaxation than before, and this soon reaches its climax. There is then a gradual rise which terminates again, in a relaxation phase just before a flexor beat. If this is small in extent there may then be no extensor movement during the flexor relaxation of the type described above. The relaxation of the extensor lasts throughout the whole period of the flexor beat, and at its termination gives place again to the slow extensor contraction which continues until a point just before the next flexor beat. The extensor curve then proceeds in this manner. There is a slow extensor relaxation which commences before and lasts during the flexor beat. It ends at a point nearly synchronous with the termination of the flexor beat and there gives place to a slow contraction which persists until the commencement of the next slow relaxation.

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VII. MOVEMENTS OF PROGRESSION WHICH FOLLOW  
PERIPHERAL STIMULATION.

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Rhythmic movements which closely resemble - sometimes completely resemble - the movements of progression may be evoked in response to peripheral stimulation.

The stimulation applied in these experiments has usually been the electrical - the application being of faradism to the long saphenous nerve, a purely afferent nerve peculiar to the hind limb. In some instances in which the movements of the intact hind limbs were recorded the stimulus has been a mechanical one applied directly to the skin of the limb or to the skin of the parts about the root of the limb.

The movements of progression have followed immediately upon the application of a simple reflex stimulus - that is to say, of a stimulus applied to one or other long saphenous nerve. In other cases the movements have followed upon the cessation of such a stimulus. In such instances the phenomenon may be termed one of "rhythmic rebound" (40), and it does not then occur during the actual application of the /

the stimulus.

It sometimes occurs that, although the movements do not occur either during a simple reflex stimulus or at its cessation, they may yet occur during the simultaneous application of two such stimuli to the respective ipsilateral and contralateral long saphenous nerves.

These different conditions have been observed to evoke movements of progression in the decerebrate and low spinal preparations - both "normal" and "de-afferented".

a. SIMPLE STIMULI : LOW SPINAL PREPARATION  
- NORMAL AND DE-AFFERENTED.

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In the low spinal preparation movements of progression are extremely rare as a response to simple stimulation of an afferent nerve.

Immediately after transection of the spinal cord, and when the condition of the preparation is still in the third phase described above, it sometimes happens that a stimulus may evoke an irregularly rhythmic reaction which resembles the movements of progression. This has been observed to take place in the case of a contralateral stimulus. Here there was /

was a more or less evenly maintained contraction of the extensor evoked in response to the stimulation. This was however broken by relaxations and reconstitutions of the contraction. Synchronous with these there were slight contractions and relaxations of the flexor. The whole appearance of the record suggested the part of a progression record, evoked in response to rapid transection of the spinal cord, in which the flexor beats finally die out.

A similar phenomenon, but uncomplicated by flexor beats, has been observed in the de-afferented preparation immediately after it had been rendered a low spinal preparation by the rapid severance of the lower thoracic spinal cord. In this instance there had been a marked third phase of maintained extensor contraction in the record taken during spinal transection, and this reflex response resembled the third phase after the disappearance of the flexor beats but before the extensor record had ceased to exhibit the rhythm relaxations and reconstitutions of contraction.

Mechanical stimulation of the upper part of the caudal segment of the spinal cord in the low spinal preparation evokes a reaction of maintained extension - thus reproducing the state seen in the third /

FIG. 42.

third phase of the phenomenon which follows the transection. During the condition thus induced a peripheral stimulus may evoke a reaction which exactly resembles the phenomena of progression - as seen, for instance, in the balanced phase of the records taken during transection.

This method is the most effective in the production of progression movements in the low spinal condition by the application of a simple reflex stimulus. But it may be remarked that it is perhaps not correct to class this with the progressions evoked in response to simple reflex stimulation as there are really two stimuli used - the central and the peripheral. This criticism of course also holds good in respect to the experiments described immediately above.

In these cases the stimulus applied peripherally evoked the flexion responses. This, when applied during the condition of maintained extensor contraction, evoked a flexor contraction which was at the same time accompanied by extensor relaxation. For a brief duration of time the flexor contraction was maintained, but was thereafter broken by relaxation, partial or complete. The termination of relaxation was immediately succeeded by a movement of re-constitution /

FIG. 38.

reconstitution of flexor contraction, but the next relaxation was separated by a pause in relaxation from the commencement of the next reconstitution. Thus the reaction was divided into beats and the pauses between these became gradually longer.

In the extensor record there had been at first relaxation alone. This was soon broken by movements the contraction phases of which fell in time slightly behind the summits of the flexor beats. These resembled more or less completely the first of the extensor types of movement described as present in the records of transection of the spinal cord.

The termination of the stimulus was in some cases followed by re-establishment of maintained extensor contraction, the curve of this being broken although there were no flexor beats present.

In this experiment the contralateral stimulus evoked the comparatively rare crossed flexion-reflex, and the contralateral stimulus was the most efficient in evoking these movements of progression in the state of maintained extension. The ipsilateral stimulus, which evoked the ordinary ipsilateral flexion-reflex, did not give the rhythmic movements during stimulation - maintained flexor contraction then obtained throughout - but was succeeded by a  
"rhythmic /

"rhythmic rebound" in the flexor record. This then gave place to the state of maintained extensor contraction.

In the low spinal preparation in which movements of the intact hind limbs have been recorded mechanical stimulation of the skin about the perineum has evoked movements of progression in the limbs. These movements have approached, in form and in rhythm, very nearly to the movements of progression evoked in the same experiment as effects of the electrical stimulation of the cut surface of the spinal cord.

b. SIMPLE STIMULI : DECEREBRATE PREPARATION,  
NORMAL AND DE-AFFERENTED.

---

In the normal decerebrate preparation rhythmic responses have occurred with greater frequency in answer to simple reflex stimuli than in the low spinal condition.

Ipsilateral stimulation, instead of evoking the ordinary reaction of flexor contraction maintained during the period of stimulation, has resulted in these cases in a rhythmic flexor response.

In one experiment the reaction was at first a maintained flexor contraction, but this was suddenly interrupted by a series of rhythmic partial relaxations /

FIG. 45.

relaxations each of which was succeeded by reconstitution of contraction. These were regular in form and rhythm; the rate of rhythm being about 2 beats per second. The extensor record exhibited no indication of movement.

In another experiment this phenomenon was more complete. The flexor contraction was rhythmically interrupted from its commencement. The beats were regular in form, extent, and rhythm - the rate being about 1.5 beats per second. The relaxations of the flexor contraction here also were incomplete. In one record there were very slight irregularities upon the tracing described by the extensor.

The third stage in completeness may be illustrated by another experiment. In this case a minimal ipsilateral stimulus evoked a very slight flexor contraction. This had a long latency and was of short duration - less than a second. In the extensor tracing its appearance was accompanied by relaxation which shortly gave place to maintained contraction. A slightly stronger stimulus called up a flexor response which was composed of four well marked beats. These were complete in the extents of their relaxation phases, and there were pauses between them. In the extensor curve there were relaxations which synchronised with the flexor beats. In the /

FIG. 31.

the intervals corresponding to the flexor pauses there were slow reconstitutions of the state of maintained extension. This increased in value as the phenomenon proceeded. In the case of the first beat the reconstitution of extensor contraction was rapid, the upstroke of the movement corresponding to the relaxation of the flexor. After the final flexor beat, and when the stimulus was still in process of application, the extensor entered into a state of maintained contraction markedly greater than that which obtained before the application of the stimulus. Stimuli of greater value evoked reactions of similar appearances.

When the stimulus is applied upon the contralateral side the response may also be rhythmic and similar to the movements of progression.

This phenomenon may occur in the contralateral flexion-reflex - a reaction of comparative rarity. It then exhibits the same variations that occur in the ipsilateral flexion-reflex. Thus there may first be maintained flexor contraction which is broken later by partial relaxations. The flexor beats - accompanied in this instance by extensor relaxations - may be complete in their relaxations but without intervening pauses, and their disappearance may be accompanied by marked maintained extensor /

FIG. 46.

FIG. 34.

extensor contraction.

But rhythmic reactions may also appear when the contralateral response is the usual crossed extension-reflex. Here the first effect of the stimulus is to procure a maintained contraction of the extensor. As the stimulus continues there suddenly appears a rhythmic contraction of the flexor and this is accompanied in the extensor record by a relaxation of the maintained contraction and then by extensor reconstitutions and relaxations of contraction corresponding to the flexor beats. The flexor beats may then be complete in their relaxation or only partial. They fail suddenly and there then appears a marked state of maintained extensor contraction.

In one experiment the sartorius muscle - a flexor of the knee and hip joints - was used instead of the flexor and extensor of the ankle joint, and the crossed great sciatic nerve was stimulated. In this case well-marked rhythmic movements of the muscle were recorded. These were of a regular rhythm, the rate of which was about 1.8 beats per second. The preparation was decapitate, and movements of progression under narcosis before decapitation varied in rate of rhythm between 1.2 and 2.6 beats per second under the influence of asphyxia.

FIG. 47.  
FIG. 50.56.

In the decerebrate de-afferented preparation rhythmic responses have been observed to be more or less similar to some of the forms which occur in the normal decerebrate preparation.

FIG. 51.

c. COMPOUNDED STIMULI : LOW SPINAL  
PREPARATION.

---

Even although neither the ipsilateral nor the contralateral stimuli produce rhythmic effects in the low spinal preparation yet when they are applied synchronously the resultant reaction may be rhythmic and may resemble in certain of its features the movements of the act of progression. In this condition the rhythmic movements have been badly marked in the flexor but have been clearly present in the extensor record.

The phenomena as they occurred in one experiment may be described. The simple contralateral stimulus evoked a reaction in which an even maintained contraction of the extensor was the only positive activity. In the same manner the ipsilateral stimulus evoked alone a contraction of the flexor. This shewed a state of "fatigue" - that is to say that the contraction was not evenly maintained throughout the period of stimulation, but fell towards the end of it. /

FIG. 60.

FIG. 61.

FIG. 62.

FIG. 60.A.

FIG. 60.B.

it. The contralateral stimulus was then applied, and during its administration an ipsilateral stimulus was added. The maintained extensor contraction of the contralateral reaction was at once relaxed, but shortly thereafter was partially reconstituted, then again relaxed - and so on, thus constituting rhythmic beats. There were no beats in the flexor act. This soon vanished as the stimulus proceeded. The rate of rhythm of the extensor movements was about 1.0 beats per second.

FIG. 60.c.

One minute later the two stimuli, of the same strength as before, were applied at the same moment and kept in action for the same length of time. The first response was an act of flexor contraction. This was succeeded in time by a rhythmic act of extensor contraction the latency of which was greater than in the pure contralateral extension-reflex. Its rate of rhythm was slightly greater.

FIG. 60.d.

A reaction in which the commencement of the ipsilateral stimulus preceded that of the contralateral was then registered. In this a rhythmic extensor contraction was also evoked after the commencement of the contralateral stimulus.

Another reaction in which the ipsilateral stimulus was applied for a time during the application /

FIG. 62.

application of the contralateral changed the constant contraction of the extensor to a rhythmic reaction during the period of its application only. After the cessation of the ipsilateral stimulus, and when the contralateral stimulus was still in process of application, the extensor again went into unbroken maintained contraction.

In all these instances the extensor movements were composed of slow relaxations and slow reconstitutions of contraction. They resembled the movements of the extensor in the third phase of the movements of progression evoked by rapid spinal transection.

d. COMPOUNDED STIMULI : DECEREBRATE PREPARATION.

---

In the decerebrate preparation various combinations of ipsilateral and contralateral peripheral stimuli in temporal relationship have been observed to be accompanied by rhythmic movements in the recording muscles. These may be described separately.

In one instance a contralateral stimulus evoked a simple crossed extension-reflex in which the contraction of the extensor was simple in form and unbroken. /

unbroken. Immediately thereafter a record was taken in which an ipsilateral flexion-reflex preceded a contralateral stimulus - the two stimuli not running synchronously but an interval of one second intervening between the point of cessation of the ipsilateral stimulus and the point of commencement of the contralateral. The contralateral stimulus then evoked a response in which extensor contraction appeared first in time but was shortly succeeded by three definite flexor beats. Each of these was accompanied, during its phase of contraction, by a relaxation of the maintained extensor relaxation; whilst, towards the end of the phase of flexor relaxation, there was a re-establishment of the extensor contraction. This became great in extent after the final flexor beat, and was thus continued until the cessation of the stimulus.

In another experiment, although the ipsilateral stimulus evoked a simple flexion-reflex, and the contralateral a simple extension-reflex, when the two stimuli ran concurrently the extensor response was rhythmic. It resembled the rhythmic extension described in the preceding section of this thesis.

In a third instance a series of records of reactions in response to compounded stimuli was taken, the /

the value of one stimulus being progressively changed. The contralateral stimulus when applied alone gave a marked simple extensor contraction. In each reaction it was applied for ten seconds, and after it had run for four seconds an ipsilateral stimulus (flexor contraction) was applied for four seconds. The contralateral stimulus, therefore, ran for two seconds after the termination of the ipsilateral. In consecutive records the ipsilateral stimulus was progressively decreased in value while the value of the contralateral was kept constant. In the first reaction the cessation of the ipsilateral stimulus was succeeded by two marked flexor beats. These resembled the movements of flexor rhythmic rebound, although this was not a phenomenon present when the ipsilateral stimulus was applied alone, and each was accompanied by relaxation and subsequent reconstitution of the extensor contraction. In subsequent reactions the value of the ipsilateral stimulus was progressively decreased, and in none was this phenomenon present.

In the decerebrate condition a maintained flexor contraction may be rhythmically broken during the application of a concurrent contralateral stimulus. This phenomenon has not been observed in the other conditions.

As /

FIG. 57.

As an example of this phenomenon the following experiment may be described. The ipsilateral stimulus - which evoked a simple flexor contraction - was applied for a period of about ten seconds.

During this period an ipsilateral stimulus was applied for about four seconds - its termination falling about two seconds before the termination of the ipsilateral stimulus. Although the response to the contralateral stimulus when it was applied alone was one of simple extensor contraction, when given during the application of the ipsilateral it evoked at first an augmentation of the flexor contraction. After this augmentation had run for about two seconds the extensor began to contract and at the same time the flexor contraction curve shewed rhythmic irregularities.

The extensor contraction rose steadily in extent until the cessation of ipsilateral stimulation produced a relaxation of it. Throughout it demonstrated slight irregularities - the relaxations corresponding in time to the reconstitutions of flexor contraction. On the cessation of the contralateral stimulus the flexor contraction again became evenly maintained.

In another reaction of the same experiment an ipsilateral stimulus was made to interrupt a contralateral. The maintained contraction of the extensor /

extensor was reduced during this interruption, and it was rhythmically broken. At the same time there was a flexor contraction which also exhibited beats the movements of which were of the opposite sense, at any one time, to those of the extensor irregularities. This was also seen in another experiment.

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VIII /

VIII. A COMPARISON OF VARIOUS MOVEMENTS  
OF PROGRESSION.

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In one and the same individual movements of progression have been registered and examined in different conditions. Thus the movements of progression under narcosis may occur in an individual from which afterwards a record of progression is obtained on dividing the spinal cord. We may therefore compare the different forms of progression dealt with in this thesis.

In Section IV, sub-section 'e' of this thesis the movements of progression under narcosis after different lesions of the nervous system have already been described and will not be further noticed here. In the succeeding sub-section ('f') the movements of progression in narcosis were also examined in experiments in which they were first recorded in the intact hind limbs and then in the isolated muscles of one hind limb after paralysis of the other.

In some experiments movements of progression have been obtained in two or in all three of the main /

main types described here. That is to say - in narcosis; on stimulation of the spinal cord; and on stimulation of the peripheral afferent nerves, or in any two of these. It will be most convenient to describe certain of these experiments in detail.

EXPERIMENT XXVII. reactions 1161 - 1237,

17:iii:II. Decerebrate cat, muscles prepared and spinal cord divided later in the experiment.

In the decerebrate state a simple ipsilateral stimulus evoked a reaction of maintained flexion which was succeeded by a rhythmic after-discharge. the rate of the beats, which were "incomplete", was about 2.0 per second. A simple contralateral stimulus evoked the crossed flexion-reflex, and cessation of stimulation was followed by a marked rhythmic rebound the rate of the beats, which were "complete", being about 2.0 per second. Compounding of a subliminal ipsilateral stimulus and a contralateral one gave a more complete flexor contraction than when the contralateral stimulus ran alone. If then the contralateral stimulus was stopped the flexor contraction persisted as if the ipsilateral stimulus had become effective, but it was broken by incomplete rhythmic relaxations - as if the rhythmic rebound of the /

FIG. 36.  
FIG. 37.  
FIG. 38.

the contralateral reaction was attempting to break through. The rate of these was about 1.5 beats per second. A peculiar feature of the rhythmic flexor rebounds which followed cessation of a contralateral stimulus was their tendency to occur in pairs the second constituent of which was smaller than the first.

On rapid division of the spinal cord in the lower thoracic region a good record of the "balanced" phase of progression was secured. This had the same characteristic of paired beats seen in the case of the rhythmic flexor rebound. The beats in a pair had a rhythm of about 1.5 - 2.0 beats per second, but the total rate of rhythm estimated over several pairs of beats was about 1.2 beats per second.

FIG. 37.

In the low spinal condition the simple ipsilateral flexion-reflex was followed by an "incomplete" rhythmic rebound evidenced by alternate contraction in the two antagonistic muscles. The rate of this was about 2.0 beats per second.

A quarter of an hour after the division of the spinal cord the upper end of the lower segment was stimulated mechanically. This resulted in a state of maintained extensor contraction. While this was in being a contralateral stimulus was applied. This evoked at first maintained flexor contraction /

contraction which was accompanied by extensor relaxation. Soon the flexor contraction became completely rhythmic while the stimulus was still running. Accompanying the flexor relaxations in this act there were extensor contractions. The rate of rhythm was about 1.0 beats per second, and the general appearance of the tracings was similar to that progression recorded after section of the spinal cord, save that the beats were not paired.

Twenty minutes after the division of the spinal cord this experiment was repeated. A simple ipsilateral stimulus evoked a flexion-reflex which was followed by a rhythmic rebound the beats of which were much less incomplete than before. They were, indeed, nearly complete. A simple contralateral stimulus evoked a rhythmic response which was complete from the beginning.

EXPERIMENT XXXVII. reactions 1667 - 1750,  
19:iv:II. Cat decerebrate and muscles prepared,  
cord cut in course of the experiment.

During the preparation of the animal progression was recorded in narcosis. It was unilateral, being confined to the left hind limb. The movements were regular and the rate of rhythm was 1.6 beats per /

FIG. 28.

FIG. 29.

FIG. 30.

FIG. 31.

per second.

In the decerebrate preparation and before the division of the spinal cord rendered it a low spinal one, ipsilateral peripheral stimulation of the long saphenous nerve evoked a completely rhythmic reflex. There were rhythmic contractions of the flexor which were separated by intervals and the rate of which was about 1.25 beats per second. These were accompanied by synchronous relaxations in the extensor record.

FIG. 31.

On rapid division of the spinal cord in the lower thoracic region a well marked reaction of progression was obtained and recorded. It demonstrated all the three typical phases, but the beats in the balanced phase were rather irregular. The rate of their rhythm was about 2.5 beats per second.

FIG. 30.

After this, electrical stimulation of the cut surface of the lower segment of the divided spinal cord evoked a rhythmic response of the flexor. There was not complete relaxation between the beats, which were of a rate of about 1.5 beats per second.

FIG. 29.

It will be noted that here the rate of the rhythmic movements in narcosis and on stimulation of the spinal cord is almost exactly the same.

EXPERIMENT LIV. reactions 2393 - 2417, 3:vii:II.

Decerebrate cat, muscles not prepared but movements of intact hind limbs registered, spinal cord cut later in experiment.

Under narcosis there were well-marked bilateral movements of progression. These were regular and of a rate of about 1.2 beats per second. On division of the spinal cord in the lower thoracic region there was not a very well-marked "balanced" phase in the reaction. The beats were about 2.0 per second in rate.

EXPERIMENT LV. reactions 2418 - 2457, 4:vii:II.

Decerebrate cat, intact hind limbs, cord cut in experiment.

On division of the spinal cord in the lower thoracic region there was a record, the "balanced" phase of which exhibited rhythmic movements of a rate of about 1.2 beats per second.

Electrical stimulation of the cut surface of the spinal cord evoked a reaction which was rhythmic and of a rate of about 3.5 beats per second.

Mechanical stimulation of the skin in the region of the anus evoked a rhythmic reaction the rate of the beats of which was about 1.5 beats per second.

On /

On cutting the lower segment of the spinal cord again near the first lesion a rhythmic reaction with a rate of about 2.0 beats per second was evoked. Mechanical stimulation of the cord evoked a similar response.

These different reactions appeared on inspection to have many points of similarity.

Experiment LVII. reactions 2461 - 2472.

5:vii:II. Decerebrate cat, muscles prepared, and spinal cord cut later.

Under narcosis there were well-marked movements of progression. These were very regular, of a rate of about 1.1 beats per second, and were recorded continuously for about 190 seconds.

After decerebration narcosis progression still continued, and was of a rate of about 2.6 beats per second.

On division of the spinal cord, the isolated muscles then recording, there was a good record of progression in which the rate of rhythm in the "balanced" phase was about 1.3 beats per second.

EXPERIMENT LX. reactions 2607 - 2648,

14:vii:II. Decerebrate and de-afferented preparation, cord cut later, muscles prepared as before.

Under narcosis good records of the progression /

FIG. 19.  
FIG. 20.  
FIG. 21.

FIG. 24

progression movements in the intact hind limbs and in the isolated muscles were obtained. These showed no essential difference, and the rate of rhythm was about 1.6 beats per second. In the case of the isolated muscles it was about 1.5 beats per second. There were no gastrocnemius movements.

The muscles were then de-afferented by division of the appropriate posterior spinal roots. On cutting the spinal cord in the lower thoracic region a good record of progression was obtained. The "balanced" phase was of long duration. The beats were of a rate of rhythm about 0.9 per second. The flexor contractions were very much greater in amplitude than in the records of the movements of the flexor muscle in the narcosis progression. Their extent was about twice as great. At the same time there were marked movements of the extensor. In other respects there was a great similarity between the records of progression during narcosis and on division of the cord.

EXPERIMENT /

EXPERIMENT XXXIII. reactions 1541 - 1632,

10:iv:II. Decerebrate cat, muscles prepared as usual, cord cut in experiment.

Simple reflex stimuli - ipsilateral and contralateral - evoked reactions, at cessation, of rhythmic rebound. The rate of rhythm of these, which were of the "complete" type, varied. In the case of contralateral stimuli the rate was of between 1.0 and 2.0 beats per second. The rate of the rebound after the ipsilateral stimuli was about 1.5 beats per second. In either case the general form of the rhythmic movements in the flexor and extensor muscles approached very nearly to that which was subsequently seen in the record on cutting the spinal cord.

In one instance on contralateral stimulation the ordinary extension reaction was interrupted during the period of stimulation by a rhythmic flexor movement. The flexor beats, of a rate of about 1.0 per second, were accompanied by relaxations of the extensor contraction.

On division of the spinal cord in the lower thoracic region a good record of progression was obtained. In the "balanced" phase the beats were rather irregular in rhythm and in amplitude. The rate of their rhythm varied in different places from about 1.25 to about 1.5 beats per second, but towards the end /

FIG. 48.

FIG. 49.

FIG. 50.

FIG. 50.

end of the phase became much slower. In their form they approached very nearly to the form of the beats in the rebound records. This was so in the case of the movements of both antagonistic muscles.

EXPERIMENT XLIX. reactions 2063 - 2116,  
16:vi:II. Decerebrate and de-afferented preparation, muscles isolated as usual, spinal cord cut in experiment.

FIG. 39.  
FIG. 40.  
FIG. 41.  
FIG. 42.

On division of the spinal cord in the lower thoracic region a good record of progression was obtained. In the third phase of the reaction, and also at the end of the second or "balanced" phase, there were marked rhythmic relaxations of the maintained contraction of the extensor muscle. These commenced before the accompanying flexor contractions, and they persisted in the record after the cessation of the flexor movements. Their rate of rhythm decreased from about 0.75 to about 0.5 beats per second.

Shortly after this a contralateral stimulus evoked a rhythmic extensor contraction. The rate of rhythm of this reaction was about 0.7 beats per second, and the general appearance of the reaction was almost exactly similar to that of the movements of the same muscle in the third phase of the progression record.

EXPERIMENT /

EXPERIMENT LXXXIV. reactions 3289 - 3308,  
16:xi:II. Decerebrate cat, muscles isolated as  
usual.

Under narcosis there were good movements of  
progression. Those had the usual characteristics  
and were of a rate of rhythm of about 1.0 beats per  
second.

After decerebration and on two occasions an  
ipsilateral stimulus produced a rhythmic flexion re-  
action. The beats were "incomplete", and of a rate  
of about 1.5 beats per second.

EXPERIMENT XC. reactions 3437 - 3459,  
30:xi:II. Decapitate cat, sartorius muscle prepared.

FIG. 16.

Under narcosis progression movements of the usual  
kind occurred. Their rate varied from about 1.0 to  
about 2.2 beats per second.

After decapitating stimulation of the con-  
tralateral great sciatic nerve evoked a rhythmic re-  
sponse of the sartorius muscle the rate of which was  
about 2.0 beats per second. Their formation closely  
resembled that of the beats in a rhythmic response  
of tibialis anticus.

EXPERIMENT /

EXPERIMENT XV. reactions 629 - 738, 17:ii:II.

Decerebrate cat, muscles prepared in the usual manner, spinal cord cut later in the experiment.

A simple contralateral stimulus evoked a rhythmic flexion reaction the beats of which were sometimes complete and varied in rate from 2.0 to 3.0<sup>^</sup> beats per second. There was in some cases a rhythmic rebound. This was incomplete, and the rate of the beats was about 2.0 per second.

In this experiment there was a good record of progression registered after division of the spinal cord. The rhythmic movements in the "balanced" phase were present in both muscles. The flexor movements, which were regular in amplitude and rhythm, had a rate of about 0.8 beats per second.

EXPERIMENT XXIV. reactions 961 - 1054,

14:iii:II. Decerebrate cat, muscles prepared as usual, spinal cord cut later but movements not then recorded.

Before division of the spinal cord simple and compounded reflex stimuli evoked rhythmic reactions. Compounded reflex stimuli, which when applied alone evoked in that period simple maintained contractions and relaxations of the isolated muscles, produced /

FIG. 34.  
FIG. 35.

FIG. 34.A.  
FIG. 34.B.

FIG. 35.

FIG. 46.  
FIG. 47.

produced rhythmic responses in both muscles. This was especially seen when a contralateral stimulus was applied during the period of application of an ipsilateral. The rhythmic movements were of a rate of about 0.8 beats per second. At a later period in the experiment simple contralateral stimuli evoked a rhythmic response in both muscles. This was especially the case after an ipsilateral stimulus had just been applied. The flexor movements were well-marked and were accompanied by relaxations of the extensor. Their rate varied between about 0.8 and 1.0 beats per second.

After division of the spinal cord a contralateral stimulus still evoked a rhythmic response. The movements in the flexor muscle, of a rate of about 0.3 beats per second, were not well-marked.

EXPERIMENT XXV. reactions 1055 - 1147,  
15:iii:II. Decerebrate cat, muscles prepared as usual, spinal cord not divided.

At one period in the experiment contralateral stimuli when applied alone evoked a rhythmic response in both muscles. The movements were well-marked but varied in rate of rhythm. This rate was about 2.0 beats per second.

Later in the experiment, when simple ipsilateral /

FIG. 46.  
FIG. 47.

FIG. 56.  
FIG. 57.  
FIG. 58.  
FIG. 59.

FIG. 56.

ipsilateral and contralateral stimuli gave maintained reactions, if an ipsilateral stimulus was applied during the application of a contralateral and then stopped a rhythmic rebound occurred, the rate being about 1.5 beats per second. Still later in the experiment a contralateral stimulus if applied during an ipsilateral evoked a rhythmic flexor and extensor response, the rate of the beats being about 2.0 per second. The extensor contraction did not appear at once, and it was only on its appearance that the flexor beats occurred. Still later an ipsilateral stimulus if applied during the application of a contralateral gave a rhythmic response of about 1.7 beats per second.

FIG. 57.

FIG. 59.

EXPERIMENT XLVII. reactions 1993 - 2015,  
13:vi:II. Decerebrate cat, muscles prepared as usual and the extensor de-afferented. The flexor was not de-afferented.

FIG. 51.  
FIG. 52.  
FIG. 53.  
FIG. 54.  
FIG. 55.

In this experiment rhythmic responses were evoked on application of simple ipsilateral and contralateral stimuli. Rhythmic rebounds followed the cessation of the stimulus in each case. It is therefore possible to examine in one and the same record rhythmic reflex reactions and rhythmic rebounds.

In /

In either case there were well marked flexor contractions and these were similar in amplitude, regularity and rate of rhythm (about 0.5 - 0.6 beats per second).

EXPERIMENT XLVIII, reactions 2016 - 2062,

15:vi:II. Decerebrate cat, both muscles prepared as usual and de-afferented, spinal cord not cut.

In this experiment on one occasion there was a rhythmic response to a simple ipsilateral stimulus. The rate of rhythm was about 1.0 beats per second. In the same experiment rhythmic rebounds occurred. These had a rate of rhythm of about 1.2 - 1.5 beats per second.

PART III.

· C O N C L U S I O N S .

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IX. CONCLUSIONS.

In reviewing the experimental evidence presented in this thesis some difficulty arises in the selection of the best manner of presenting the facts. From an examination of the experiments there seems to be little doubt that the conclusion may be drawn that the different forms of rhythmic movements here described are essentially one and the same - variations of the movements of progression.

That these movements occur after the isolated muscles have been de-afferented seems to place the intrinsic stimuli for progression in the centres themselves and not in the peripheral mechanism as previous observers have done.

If this be true an interesting problem arises in the question of the causation of the phenomenon of rhythm; and an interesting speculation arises in the question of the similarity of the rhythmic movements of progression and of respiration.

We may also draw certain conclusions regarding the mutual relationships of the centres from the/

the experimental evidence, and these conclusions may guide us in examining the question of the origin of the intrinsic factors in the production of the rhythmic movements.

In a manner similar to that sketched above we may pass to the consideration of the different conclusions to be drawn by discussing first the similarity of the different types of rhythmic movement which occurred in the experiments.

a. THE SIMILARITY OF THE DIFFERENT TYPES OF  
RHYTHMIC MOVEMENT.

---

The three chief forms of progression examined here - narcosis progression, progression following stimulation of the spinal cord, and progression evoked by peripheral reflex stimuli either directly or as a "rebound" and when the stimulus is either simple or compounded with another - shew similarities in their rate of rhythm and in the form of the curves obtained from the recording muscles or intact hind limbs.

The/

The rate of rhythm seems to vary between a rate of about 0.5 beats per second and one of about 3.0 beats. But the greater number of records have a rate of between 1 and 2 beats per second.

The average rhythm in the three chief forms of progression is about 1.5, 1.7 and 1.1 beats per second respectively. There is thus but little difference between them, and what difference there is points to a rather slower rate in rhythmic movements produced reflexly than in those seen in narcosis or evoked on stimulation of the spinal cord.

This rate - about 1.5 beats per second - is too slow for the beats of the scratch-reflex. In the cat that rate is about 5 beats per second (Sherrington, 19). The comparatively slow rate of the beats with which we are dealing makes it practically certain that they are those movements of progression; and the similarity of the rates in the different conditions makes it practically certain that the movements are fundamentally the same in all.

Another reason for supposing that the movements are those of progression and not of the scratch reflex is their character when they are examined in both limbs. The bilateral alternation of the beats is/

is sufficient to exclude the possibility that they are connected directly with the scratch-reflex.

That the movements are essentially the same in all the conditions in which they have been examined is shewn also by the similarity of their forms in the graphic records.

The first point which we may notice is that the movements are essentially discontinuous flexions each of which is succeeded by a state of flexor relaxation and thus separated from its successor. In the narcosis progression of the isolated muscles the extensors may shew little or no movement, although we may assume that the postural tonus of the extensors is inhibited during the flexor contraction and re-established during its relaxation.

In the progression which is obtained on rapid division of the spinal cord in the lower thoracic region the movements of the flexor muscle exactly resemble those which have been recorded in the isolated flexor muscles under narcosis; but the amplitude of the movements is commonly greater, and may be very much greater. The similarity between the movements is sufficient to enable us to draw the inference that the two rhythmic phenomena are of similar kind.

This/

This form of progression also varies from the narcosis type in that there is often a marked extensor factor.

The forms of progression which are called up by the application of peripheral stimuli - whether simple or compound - have, in many cases, exact similarity to the other forms of progression. Where the rhythmic movements appear in the extensor they may exactly parallel the similar movements which occur in some of the records of progression after stimulation of the spinal cord.

In a similar manner the progression movements may resemble each other when the reflex stimulus is simple and when it is a compound one; and the movements may also resemble each other when they occur directly during the application of the stimulus and when they occur as a "rhythmic rebound" on cessation of stimulation.

Finally, the fact that the rhythmic movements have the same characteristics as the movements of progression in the normal animal - being bilaterally synchronous in the rabbit and bilaterally alternate in the guinea-pig and (usually) in the cat - makes it practically certain that they are movements of/

of true progression. They are expressions of the activity of one and the same mechanism; an activity which is called forth in different manners.

b. THE INTRINSIC FACTORS IN THE ACT OF PROGRESSION.

---

In the first place we may conclude that the mechanism which conditions progression in the hind limbs is located in the lumbar spinal cord. This conclusion has been drawn before from the experiments of Freusberg (4) who first described the "mark-time reflex" in the late spinal dog. A mechanism sufficient to condition rhythmic acts which scarcely differ from those in the normal animal must lie in the grey matter and peripheral mechanism of the lumbar centres. It is true that in the normal act the activity of the lumbar centres must be controlled by the activity of other and higher centres, but the intrinsic factors in progression may be sought in the lumbar centres.

The experiments in which the stimulation of the spinal cord in the de-afferented preparation produced/

produced rhythmic progression movements shew that the phasing of the acts of progression is determined neither by the peripheral skin stimuli nor by the self generated proprioceptive stimuli of the muscles which take part in them.

The division of the spinal cord generates an arrhythmic stimulus. This causes the contraction of certain limb muscles. Of these the recording muscles are the only mobile parts of the two limbs in the preparation used. The characteristic alternating contraction of the two antagonistic muscles cannot be conditioned by their own contractions and the consequent setting up of a series of refractory phases in the activity of the centres by means of the stimulation of an afferent apparatus contained in the muscles, because the afferent nerves which arise in these muscles were put out of action by the conditions of the experiment. Not only must the locus of the changes which condition the rhythmic phenomenon in progression be in the spinal cord, but the mechanism which determines them must also be central.

There are therefore two points of interest in connexion with the mechanism of progression -- the question of the nature of the central changes in activity/

activity, and the question of the part played in the act by the proprioceptive mechanism. The stimuli which arise in the skin probably play but a small part in the act, and then are of importance in certain of its types only, and not in all of them.

The mechanism of progression therefore in this resembles the mechanism of respiration in that its rhythmic activity is conditioned intrinsically by rhythmic activities in the centres of the nervous system and not by the "selbststeuerung" of a peripheral nervous mechanism. The question of the nature of the rhythmic central activities - the question, that is, of the intrinsic origin of the rhythm - will be considered later. We may look for a moment here at the question of the part played by the proprioceptive peripheral mechanism, and in this connexion it is of interest to compare the effect of stimulation of the vagus in respiration with the effect of stimulation of the muscle afferents in the spinal limb reflexes.

Sherrington (23) has pointed out that the electrical stimulation of the proximal end of the cut nerve of an extensor muscle itself produces a reflex contraction of the group of limb flexors and a reflex relaxation/

relaxation of the group of limb extensors. Electrical stimulation of the proximal cut end of a nerve of a flexor muscle produces again reflex contraction of the flexors and reflex relaxation of the extensors. That the muscle itself to which the nerve passes acts with its own group is shewn by experiments in which the motor nerve is carefully split and one half only cut and stimulated.

The mass of muscle afferents in a limb on stimulation therefore evoke the flexion-reflex; but occasionally, as Sherrington has also shewn (22), the stimulation of an extensor motor nerve may evoke a response of extension and not of flexion. This may be seen in the case of the knee extensors. If the nerve to vasto-crureus be split and one half faradised, and if the limb be in a posture of full flexion at the knee, then the first effect of the stimulation may be a slight extension of the knee; but if the posture be one of extension the effect is at first reflex relaxation of the extensor - flexion.

In the case of the vagus nerve and respiration a somewhat similar state exists. Hering and Breuer (3) found that inflation of the lungs produced reflex expiration, and collapse of the lungs reflex inspiration./

inspiration. As both reactions disappeared after section of the vagi they accounted for them by the presence of inspiratory and expiratory nerve fibres in the vagus nerve. In support of this it was subsequently found that not only inspiratory but also expiratory effects might be produced by appropriate stimulation of the vagus nerve trunk. If we look upon inspiration as equivalent to flexion, Traube's discovery of the inspiratory effect of faradic stimulation of the trunk of the vagus (1, 2) may be paralleled by the flexion effect of faradic stimulation of any of the muscle afferents in a limb. And Grützner's (5) statement that certain forms of stimuli such as the ascending constant current always evoke expiration may be likened to the discovery of Sherrington and Sowton (35) of the effect of weak ipsilateral stimuli produced by a varying constant current in evoking an ipsilateral extension-reflex.

It is now generally held that the chief effect of the vagus in normal respiration is an inhibitory one upon inspiration. This receives support from the experiments of Boruttau (7, 12) and of Alcock and Seemann (15) who found a negative variation in the vagus current only during dilatation of the/  
the/

the lungs and not during collapse of the lungs. It is difficult to reconcile this with the inspiratory effect of faradic stimulation of the vagus trunk except by regarding that as an abnormal effect incomparable with the adequate stimulus of the vagus endings in the lungs, but perhaps analogous to the nociceptive Hexion-reflex in the limbs.

It is possible that in the same manner the adequate stimulation of the muscle afferents of a limb produces the extension-reflex and not the Hexion-reflex which is obtained on faradic stimulation. It may appear illegitimate to base this view upon an hypothetical comparison, but it may be remarked that Sherrington's discovery (22) of "plastic tonus" seems to give some support to the view that extension-producing proprioceptive afferents play a greater part in the conditioning of limb reflexes than might be suspected from the results of faradic stimulation of nerve trunks only.

In the spinal dog also as Sherrington has shewn (30 pp. 75, 76) that, if the animal be held vertical and with one hind limb supported in the posture of flexion at the hip, the "mark-time" reflex does not occur. It immediately commences with an act/

act of contralateral flexion if that limb be allowed suddenly to drop. The extension thus produced gives a proprioceptive stimulus which evokes contralateral flexion and probably therefore also ipsilateral extension. Passive shortening of the knee extensor also evoked a reflex ipsilateral act of extension (Sherrington, 27).

It may be taken that the muscle afferents of a limb exercise an influence in the act of progression as does the vagus in the act of respiration; but the limb proprioceptive mechanism cannot be the intrinsic seat of the rhythm of the act.

There can be no question of its importance nor of its suitability to augment the central mechanism. It cannot, however, be regarded as determining the refractory phases in the act. Its part must be regulative - not causative.

A purely central mechanism of progression ungraded by proprioceptive stimuli would clearly be inefficient in conditioning the passage of an animal through an uneven environment. Were the animal passing across a perfectly level plain a central mechanism might drive it with precision; but such a mechanism unaided would be inefficient if the level  
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of the ground were broken. When a carnivore stalks its prey over uneven ground every step must be regulated by the posture of the limbs as they then are in contact with the ground. This posture varies somewhat at every step, and the value of a given act must vary with the changing postures. Each step may differ a little from all others, and each must be graded to its conditions if the whole progression of the animal is to be efficient. The hind limb, which at one time is somewhat more extended when it is in contact with the ground, in another step may be more flexed; but the forward thrust which it gives as its contribution to the passage of the animal must be of a comparatively uniform degree in each consecutive step. This will occur only if it is graded by the posture of the limb when in contact with the ground, and by the duration of its contact with the ground. The grading can be brought about by proprioceptive stimuli alone. Of these we must regard the proprioceptive stimuli from the muscles themselves as the most important, and the part which they play is essentially the regulative - not the causative.

c./

c. THE PROBLEM OF CENTRAL RHYTHM.

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If the possible effect of a peripheral "Selbststeuerung" may be excluded - as it must be both in the case of respiration and of progression - the explanation of the rhythmic act must be looked for in the central mechanism.

In the case of respiration it has been assumed that there is a constant stimulus - the "blood stimulus" - and that the rhythm is explicable on the assumption of a "refractory phase" which is set up in the discharge of the centre stimulated. "The specific intrinsic factors of the respiratory centre are then: (1) the specific excitability for the respired gases; and (2) the alterations in this excitability conditioned by the kind and manner of their rhythmically changing activity (refractory phase, relative infatigability)". (Baglioni, 41).

According to Verworn (10) rhythmic discharge and the refractory phase may be explained in a manner somewhat as follows:- In the normal circumstances the two metabolic processes (anabolism and katabolism)

katabolism) balance in the labile biogen molecules of the neurones. If their activity be raised the process of katabolism is greater than that of anabolism. If the period of heightened activity is a short one, the balance is soon regained by the "Selbststeuerung" of metabolism. But if it continues the ganglion cell discharges and thus becomes temporarily inexcitable, recovers, discharges again and again becomes paralysed - and so on. The two factors which he postulates for the production of the paralysis are the diminution of convertible bodies and the accumulation of the products of katabolism. He uses the term "Ermüdung" for the paralysis caused by the accumulation of waste materials, and the term "Erschöpfung" for the paralysis due to the exhaustion of its material. The first primarily paralyses dissimilation, the second assimilation. After a discharge there is left in the neurone partially broken down biogen molecules. These cannot discharge further. Assimilation takes place by the building up of oxygen molecules and of simple nitrogen-free atom complexes into the biogen molecules. The result is again the labile biogen molecule which is capable of discharging in dissimilation. After a discharge there is therefore/

therefore a period during which further discharge is impossible and in which assimilation takes place.

This explains a phenomenon of refractory phase, and may be used to give an explanation of rhythmic activity in response to a continuous stimulus.

This "biogen theory" - really a theory of the metabolic nature of rhythmic activity - to a certain extent resembles the much older one of Ewald Hering (6, 8) in its explanation of refractory phase. Hering said that in so far as living matter is wholly unaffected by external stimuli its assimilation and dissimilation may be termed "autonomous", and when the autonomous assimilation and dissimilation are equal there is a state of "autonomous equilibrium"; but external stimuli may affect this equilibrium either by increasing assimilation or dissimilation. These, when re-inforced by external stimuli may be termed "allonomous". After allonomous dissimilation has been in process the living matter is less capable of functioning and there is a greater disposition to assimilation and a lesser to dissimilation - the living matter tends to return to a state of autonomous equilibrium. The greater this tendency is the longer has dissimilation proceeded. Thus in stimulation/

stimulation a balance of equilibrium is again attained - allonomous equilibrium.

Against the "metabolic" view of the nature of rhythmic activity some weighty considerations may be urged.

In the first place, as regards the respiratory centre, it is at any rate difficult to admit the assumption of a mechanism, the energy of which becomes so completely exhausted as it is necessary to assume for this theory. And again, the respiratory centre - which might be supposed to be peculiarly affected by narcotics and by nutritional changes - in reality seems to be more resistant to them than are the spinal reflexes which shew less tendency to rhythm.

In the case of the mechanism of progression there seems to be a fatal obstacle to the view that the origin of the rhythm is essentially metabolic. It has been shewn in these experiments that a contralateral and an ipsilateral peripheral stimulus may each, when applied singly, evoke an arrhythmic response in the limb muscles; but when applied together they may evoke the rhythmic act of progression. Here the rhythmic activity is not an intrinsic/

intrinsic property of either of the two antagonistic centres. In neither does a continuous stimulus set up a refractory phase antagonistic to itself. The rhythm must arise in the interference of two antagonistic activities. As such it cannot be intrinsically metabolic, but must be a property of the mutual relationships of the centres.

This points, then to some other explanation than the metabolic for the rhythm of progression, and it is probable that we will not be far wrong in assuming that in the case of respiration and of other rhythmic activities of the nervous system another explanation than the metabolic is the correct one. This does not necessarily deny the correctness of the biogen theory in explaining the origin of the discharge of a centre. It is quite possible that each centre discharges rhythmically and that this rhythm may be conditioned in the manner which is assumed in the biogen hypothesis - but that the rhythm is so great in rate and small in the amplitude of its variations that for our purposes we may regard it as a constant flow equivalent to the continued propagated disturbance in a nerve artificially and continuously stimulated. The truth of the biogen hypothesis in explaining/

explaining this discharge is here neither affirmed nor denied.

In a discussion of the nature of rhythmic activity McDougall's theory must be mentioned (13, 23, 37). This is really a theory of inhibition which he uses to explain rhythmic activity.

He rejects the "metabolic" theory of inhibition associated with the names of Hering and Verworm - arguing that it is based upon a fundamental fallacy (13). "For the theory of inhibition of Hering and Verworm is simply the assumption that inhibitory stimuli act by causing increase of assimilation, and so preventing in some utterly mysterious and, in fact, miraculous manner the liberation of energy which results from dissimulation, and is the specific vital manifestation of the substance of muscle and nerve".

In place of this theory of inhibition he gives his well-known "drainage" theory.

In the first place, he postulates as a concept the idea of the nervous impulse as a flow of "neurin" down the nerve fibres. In explaining the inhibition caused in some cases by the stimulation of an afferent nerve which evokes one type of reflex during/

during the stimulation of another afferent which evokes an antagonistic reflex he supposes that each afferent divides into two and that each branch passes to one of the two antagonistic centres enervated in these reflexes. Of these two branches the one which passes to the centre which is activated has less resistance to overcome at the synapse which separates it from the centre. Each of the two antagonistic centres has therefore a branch of each of the two different afferent nerves impinging upon it, but the resistance of the two synapses between it and the branches differs. When one of the afferents is stimulated the neurin in it flows chiefly to the one centre, and, in a lesser degree, also to the other. In the case of the first centre the flow of the neurin across the synapse lowers the resistance of that synapse and at the same time also that of the other synapse between the same centre and the branch of the other afferent nerve. This fall in resistance in the second synapse at this level drains off the neurin from that afferent, so that the second centre obtains less. This explains the reciprocal inhibition of the one muscle in the simple reflex. In a similar manner if the second afferent be stimulated the/  
the/

the resistance of its synapse at the centre inhibited in the description above will be reduced, and it will then drain off the neurin from the first afferent. This explains the inhibition of a reflex contraction on throwing in an opposite reflex. He supposes that the resistance of a synapse is decreased by the charging of the neurones between which it mediates, and is increased by the fatigue that results from the continued transmission of the impulse.

He uses this theory to explain alternating reflexes. In this explanation he supposes that the one afferent neurone is continuously stimulated. At first it discharges into its more peculiar centre and thus inhibits the antagonistic centre by drainage. Fatigue soon sets in and raises the resistance of the synapse which its impulse crosses. This resistance soon rises to such a height that the afferent neurone more easily discharges into the antagonistic centre. It then drains its first and more peculiar centre and activates the centre which indirectly it usually inhibits; but fatigue then sets in at this synapse and, the first synapse having presumably become refreshed, it again discharges into the first centre and inhibits the second - and so on.

There/

There are several grounds upon which this theory may be attacked. For instance, if two equal stimuli are applied to two afferent nerves which evoke opposite reflexes in a pair of antagonistic muscles both muscles at one and the same time should contract, for each afferent will discharge into its more peculiar centre and drain the other. The resistance of the synapses will not be relatively altered, although they will fall, and the greater flow of neurin caused by the stimuli will be expressed by heightened activity of the two muscles; but although both muscles may contract the phenomenon is by no means so general as it must be if the theory is correct. The fact also that both muscles occasionally contract simultaneously in the simple reflex (Graham Brown 40) cannot be explained by this theory.

Against this theory may chiefly be urged an observation which I have made previously (40) and which I have supported by additional evidence in this thesis - namely, that the inhibitory relaxation may appear before the accompanying excitatory contraction in a pair of muscles. According to the "drainage" theory of inhibition that antagonistic muscle which relaxes should do so a little after the contraction of/

of the other muscle. At the very earliest it should begin to relax at the moment when the other begins to contract. It not uncommonly happens that the relaxation may occur as much as half a second or more before the contraction of the antagonistic muscle, and it appears to me that this raises a fatal objection to the drainage theory, and to the concomitant explanation of rhythmic activity.

d. THE THEORY OF NEURAL BALANCE.

In the place of these theories of rhythmic activity I suggest the following which may be termed the "theory of neural balance."

It may be presumed that the central portions of the motor neurones which form the "final common paths" to the two antagonists form together the primary centre. These two neurones may be termed respectively the extensor ("E") and the flexor ("F") primary "half-centres". Each of them may be supposed, besides activating its respective muscle, to/

to inhibit the other half-centre, (Figure).

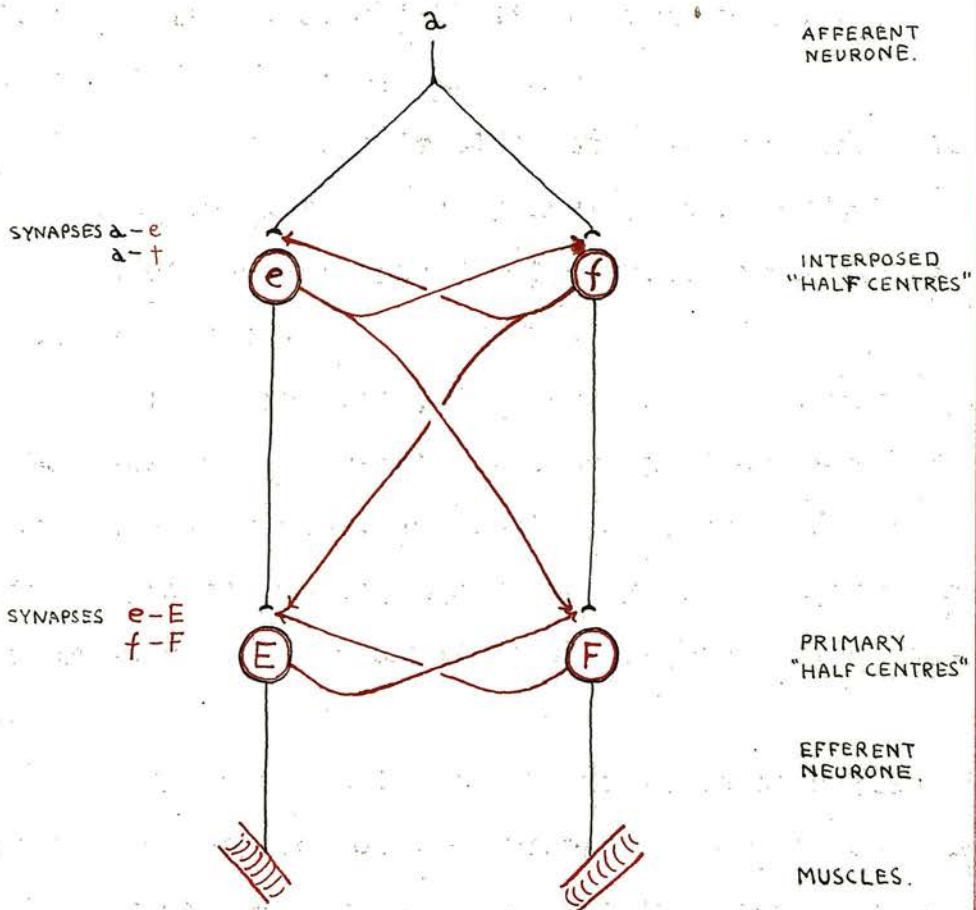


FIGURE.

"INHIBITORY" PROCESSES IN RED.  
 "EXCITATORY" PROCESSES IN BLACK.  
 FOR CONVENIENCE THE APPLICATION  
 OF INHIBITION IS PLACED AT THE  
 SYNAPSE.

Each/

Each of these primary half-centres may be supposed to be affected in an excitatory manner by an "interposed" half-centre. The two interposed centres ("e", "f") also mutually inhibit each other, and, in addition, also inhibit the primary half-centre which they do not activate.

The afferent impulse for rhythmic movements is supposed to play with very nearly equal effect upon each of the interposed half-centres in a purely excitatory manner.

It is presumed, further, that the resistance at a synapse decreases with the passage across it of an excitatory impulse, and that the value of an inhibitory process acting against a synapse progressively decreases with the duration and degree of the process.

The first point which arises in connexion with this conception of the arrangement of the centres may be termed the "principle of the progressive augmentation of excitation".

If the primary half-centres mutually inhibit, an excitatory process which falls upon one of them (say "E") - besides facilitating by the reduction of its synaptic resistance - will raise the activity/

activity of that half-centre (E) and thus will decrease the activity of the other (F); but that activity (F) is in part manifested by inhibition of the first half-centre (E). It is therefore less inhibited - that is, more activated - and thus it (E) again inhibits the second half-centre (F) in a greater degree, and again reduces the inhibitory effect upon itself (E) of that second half-centre (F) - and so on.

But if it be assumed that the process of inhibition is progressively retarded in a manner corresponding inversely to the facilitation of excitatory impulses at the synapse - that is to say, if a process of "inhibitory fatigue" be assumed - a balance will be struck in this progressive augmentation of excitation.

We may now use this conception in explaining the phenomena of rhythmic activity. For convenience we may leave out of consideration the balanced "interposed half-centres" and assume that a double excitatory impulse falls upon the primary half-centres.

If the excitatory value of that part of the afferent impulse which falls upon one half-centre, (let/

(let us say "E") is slightly greater than that which falls upon the other, then the first half-centre (E) will be activated against the inhibition of the other (F), and the value of this excitation will rise by progressive augmentation until balanced by inhibitory fatigue. When this point of balance is reached the process of inhibitory fatigue continues and thus reduces the value of the inhibition of the second half-centre (F) by the first (E). There will then set in the opposite process - progressive diminution of excitation in the first half-centre. This process is the reflexion in the first half-centre of the process of progressive augmentation of excitation which then sets in in the second half-centre and continues until the balance is again attained at the other end of the scale. Thereafter there is a progressive diminution of excitation in the second half-centre (F) accompanied again by progressive augmentation of excitation in the first (E). And so the process continues rhythmically, if the afferent excitation falls with very nearly equal value upon each of the antagonistic half-centres.

In such a scheme, however, the process of inhibition must of necessity fall in time behind that of

of excitation - the difference of time being that taken to traverse the inhibitory paths from one centre to the other.

To give an explanation of the occasional occurrence of anticipatory relaxation in the rhythmic act we may use the conception of the interposed half-centres; and we may assume that the relation between the synaptic resistances between the afferent neurone and the interposed half-centres (a - e; a' - f) and between the interposed and the primary half-centres (e - E; + - F) varies.

If that resistance be greater between the interposed and primary half-centres than between the afferent neurone and the interposed half-centres then inhibitory relaxation will occur in time before excitatory contraction in the antagonistic muscle.

If this be so the reversal of activity by inhibitory fatigue will occur first between the interposed half-centres - that is to say, between these half-centres upon which the components of excitation have the greatest value. The result of this will be that the excitatory effect of one interposed half-centre upon its primary centre will be decreased at the same time that the excitatory effect of the other interposed/

interposed half-centre upon its primary half-centre is increased; but the greater resistance of the synapse over which this activity has to pass in the second instance will prevent the immediate manifestation of this increased activity, while the decreased excitation of the other half-centre will be immediately manifested. At the same time, the inhibitory effect of the interposed half-centre which is now becoming active upon the opposite primary half-centre will be added to the decrease of its excitation by its own interposed half-centre - and thus the precedence of inhibitory relaxation over excitatory contraction may be explained.

That in the conditioning of rhythmic activity a "double" activation of the antagonistic centres plays a part seems to be shewn by evidence here given - such evidence as the production of a rhythmic act by the compounding of two arrhythmic effects as in the experiments on the compounding of simple peripheral stimuli; or the evidence given by the "balanced" phase after division of the spinal cord where the maintained fusion is compounded with a maintained extension, and it is by no means unlikely that even in the simple reflex there may be a "double"/

"double" effect - for evidence given by the author (40) shews that sometimes simultaneous contraction of the antagonists may occur.

SUMMARY/

SUMMARY.

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1. In these experiments movements of progression have been studied in the intact hind limbs and in the individual muscles of rodents and cats in different circumstances. These are:-
  - a. In narcosis.
  - b. On stimulation - electrical and mechanical - of the spinal cord.
  - c. On stimulation of the afferent nerves.
2. In rodents - guinea-pigs and rabbits - and in cats, the movements under narcosis have the general characteristics of the normal forms of progression. Thus in rabbits, the normal progression of which is that of hopping, the movements are bilaterally synchronous. In guinea-pigs, they are bilaterally alternate - the progression being normally that of running. While in cats they are sometimes bilaterally synchronous and sometimes bilaterally/

bilaterally alternate - the normal progression being sometimes that of running and sometimes that of the gallop.

3. In the cat, the narcosis progression may persist for long periods. Sometimes the movements may disappear for a time in one hind limb, and the movements which persist in the other then become faster.
4. Asphyxia produces a marked change in these movements. At first the beats may diminish slightly in extent and become slower. This phase soon passes and then the beats of the act become greater in extent and faster in rhythm. The highest points progressively rise, and soon a rise in the lowest points of the beats also occurs. This rises faster than the rise of the highest points and finally the beats disappear leaving the limb in a state of maintained flexion. If the asphyxia is then stopped, the reverse phenomena occur until the beats again become normal in extent and rhythm. The relations of the beats in the two limbs also vary during this asphyxia phenomenon. As the rate of rhythm/

rhythm increased the beats cease to be accurately alternate in the two limbs, and finally come to be bilaterally synchronous.

5. The individual flexor - tibialis anticus - demonstrates the same general phenomena as the intact limb. The flexor beats become faster and finally end in a state of maintained flexion.
6. In the individual muscles the flexor act is the chief positive activity in the narcosis progression. The extensor of the ankle - gastrocnemius - rarely shews movement.
7. The movements of progression in narcosis, besides occurring in normal animals, have also been observed in the decerebrate cat. They have also occurred in the cat after removal of the lower part of the lumbar spinal cord containing the extensor centres for the ankle, and then even after the additional removal of the ankle flexor centres of one side of the spinal cord.
8. Progression movements have been obtained on stimulation of the cut surface of the spinal cord. These have been observed in the low and/

and high spinal preparations, as well de-afferented as normal. The rhythmic effect is almost always seen alone in the flexor, although also seen occasionally in the case of the extensor at the same time. Weak stimuli give a rhythmic response and stronger stimuli a more continuously maintained flexor contraction, until the strongest stimuli give arrhythmic flexor contractions. This effect is not due to fatigue for a weak stimulus repeated will then again give a rhythmic flexor response.

9. Rapid division of the spinal cord in the decerebrate preparation in the lower thoracic region is the best method of producing progression movements by central stimulation.
10. Three main phases occur in the response. The first of these is characterised by a state of maintained flexor contraction, and absence of extensor contraction. Towards the end of this phase irregular partial relaxations of the flexor response occur.
11. The second - or "balanced" - phase is characterised by regular flexor beats. These are usually/

usually separated by pauses in maintained relaxation, and the extensor contracts during the flexor relaxation and in the pauses.

Towards the end of this phase the extensor begins to exhibit an interrupted state of maintained contraction, and the flexor beats diminish in size and become slower.

12. The third phase is characterised by a state of maintained extensor contraction. At first, this is interrupted by phases of relaxation which synchronise with the final flexor beats. The relaxations persist for a short time after the final disappearance of these. The phase ends in unbroken maintained extensor contraction.
13. At the beginning of the third phase the extensor relaxations often occur in time markedly before the accompanying flexor contractions.
14. These same phenomena occur in de-afferented preparations.
15. Various irregularities in the reactions occur and these are described in the text.
16. In the normal and de-afferented preparations simple stimulation of afferent nerves may evoke/

evoke movements of progression.

17. In the low spinal preparation these are best obtained if a state of maintained extension be first produced artificially by mechanical stimulation of the spinal cord, and if then a flexion reflex be evoked.
18. In the decerebrate preparation - where there is already a background of extension - stimuli which evoke the flexion - reflex sometimes give a rhythmic reaction.
19. In either of these preparations, but more particularly in the decerebrate, simple stimuli on their cessation may evoke a rhythmic rebound reaction.
20. Stimuli which evoke antagonistic reflexes - extension or flexion - when compounded together may give a rhythmic response in both muscles, although when given separately they evoke arrhythmic contraction in their respective muscles.
21. An examination of all these different rhythmic activities in these different conditions and preparations demonstrates that they are one and all fundamentally the same - activities of/

of the mechanism of progression. Their rhythm - which varies from about 0.5 to about 3.0 beats per second - must be conditioned intrinsically by the central mechanism and not by the peripheral, for the movements may occur in the de-afferented preparation.

22. In the conclusions a parallel is drawn between the rhythmic activity of progression and that of respiration, and it is shown that in many respects the two are similar. A theory - the "theory of neural balance" - to account for rhythmic movement is outlined.

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