

On Some Results of Studies in the Physiology of Posture

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PART I

The study of the physiology of movement is of old origin. Movement affords many points of attack for research because by movement changes in the condition of the body or its parts occur, which attract the attention of the observer and can be recorded and measured. This is not the case when posture is studied. Here we have to deal with a constant condition without apparent changes, so that our desire for causality is not stimulated, and we therefore do not immediately suppose that active processes are at work. In consequence of this the physiology of posture is of relatively recent date and many facts to be described in these lectures have been discovered by still living physiologists during the last 40 years, among whom Sherrington must be named in the first place. The chief result of these investigations is that posture is an active process, and is the result of the cooperation of a great number of reflexes, many of which have a tonic character. Many parts of the central nervous system contribute to the function of posture; the importance of the spinal cord and the brain-stem we understand up to a certain limit, whereas the activities of other parts, especially of the cerebellum and basal ganglia, are still obscure.

For the purpose of these lectures I class postural activities under the following headings:

1. *Local static reactions*, in which only one part of the body – e.g., one limb – is concerned.
2. *Segmental static reactions*, which involve one segment of the body – e.g., both hind-limbs, both forelimbs, or the neck.
3. *General static reactions*, in which more than one segment or even the whole body comes into action.

The aspects of these general static reactions vary considerably in accordance with the part of the central nervous system which governs in different experiments the posture involved. We can thus distinguish: a) static reactions of the oblongata animal (decerebrate preparation), in which the spinal cord is in functional connexion with the medulla oblongata only; b) static reactions of the mid-brain and thalamus animal, in which in addition to the bulb the mid-brain centres also take an active part; c) static reactions of the intact animal, in which the cortical centres cooperate.

The importance of the cerebellum and of the basal ganglia will not be discussed in these lectures.

LOCAL STATIC REACTIONS

The limbs of mammals, as of other vertebrates, are built up of bony segments, linked by a complicated arrangement of ligaments and moved and fixed by muscles; fasciæ also play a rôle. The whole system is easily movable in different directions. Our problem is to explain how such a movable limb is at times used as an *instrument* for very different purposes (such as scraping, scratching, fighting, etc.) and moved freely in all joints, whereas at other times it is transformed into a stiff and strong *pillar*, which gives the impression of being one solid column, able to carry the weight of the body. Experiments have shown that this is accomplished by a series of local static reflexes.

We were confronted in the laboratory with this problem during the investigation of decerebellated animals, which had been operated upon by Dr G. G. J. Rademaker, and of which the condition of muscle-tone had to be followed during the course of many months. It soon became evident that this was not a simple task, and that the state of tone of a limb at any given moment depended greatly upon the way in which the tone is investigated. If, for instance, a dog is lying down in the lateral position and the resistance of one forelimb against passive flexion is measured with the hand and fingers flexed, often no resistance can be felt. But if the latter are extended and pressure exerted against the pads of the foot, then the

forelimbs become strongly extended and can hardly be flexed at all. The same difference can also be demonstrated in intact animals. We therefore decided to make a more detailed investigation of these reactions. In addition to Dr Rademaker, Dr R. Schoen (Würzburg) and Dr E. A. Blake Pritchard (London) took part in this research, Dr Schoen experimenting on the general conditions for these reflexes and on a graphical analysis of the muscles of the forelimbs, while Dr Pritchard investigated the hind-limb in the same way.

The best way to evoke this static reflex is to press against the pads of fingers or toes and to dorsiflex the hand or the foot. Then the limb becomes more or less stiff, and is, in the prone position of the animal, able to carry the weight of the body.

Two different stimuli cooperate in evoking this reflex:

1. The *proprioceptive* stimulus evoked by the dorsiflexion of the distal parts of the limbs (fingers and hand, toes and foot). These proprioceptive influences can be isolated by cutting the local sensory nerves for the skin of hand and foot. They disappear after cutting the tendons of all plantar or volar flexor muscles to the distal part of the limb.
2. The *exteroceptive* stimulus evoked by the contact of the pads of the feet with the ground. If a decerebellated dog be placed in the supine position with the head ventroflexed by 90°, then the hind-limbs are usually flexed in all joints. A very slight touch to the pads of the foot is sufficient to evoke a strong tonic extension of the whole hind-limb, even if dorsiflexion of foot or toes is carefully avoided by keeping the fingers only just in contact with the foot. It appears as though the slowly extended foot were being drawn after the receding finger by some magnetic force. The reflex has therefore been called the 'magnet reaction.' As soon as the finger is removed, the limb goes back into flexion. The exteroceptive stimulus can be isolated by cutting all the tendons to the foot or hand and disappears only after severing the sensory cutaneous nerves to the foot.

The static response ends and the whole limb is loosened and becomes free for movement by the removal of the two above-named stimuli, which takes place as soon as the limb in the standing animal is lifted from the ground; but, as is usual in very important functions, an active process cooperates. As soon as the distal part of the limb is flexed in the volar or

plantar direction, the limb is reflexly loosened and prepared for movement.

We call the whole process the *supporting reactions*. The passing from the flexible condition to the stiffness of a support is called the *positive supporting reaction*, whereas the loosening of the limb is called the *negative supporting reaction*.

A. The Positive Supporting Reaction

This reflex can be studied in the intact animal as well as after extirpation of the whole cerebrum or cerebellum. It is also present in certain stages of general narcosis. The following description is based especially upon the findings in the forelimbs of cats. The results on the hind-limbs will only be mentioned if necessary. The effective stimulus for this reflex is stretching of the flexor muscles of fingers and hand. The deep flexor muscle of the fingers alone is sufficient to evoke the reflex. But also other flexor muscles can serve this purpose. The exteroceptive stimuli from the pads of the toes cooperate to the same effect.

1. The *anatomical arrangement* plays only a rôle of secondary importance for the establishment of the supporting reaction. Formerly there was a general belief in the importance of the ligaments for the fixation of the joints, but at present there is a tendency to believe that the tonic activity of muscles is the most important factor.

That the arrangement of ligaments cannot explain the supporting reflex follows from the fact that in cats and dogs during ordinary standing all three main joints of the hind-limbs are semiflexed, and can be moved from the resting position in both directions. Also in man in easy standing the ligaments of the leg are only of secondary importance. The muscles have the function of supporting each part of the limb and the body as a whole. For that purpose they are brought into tonic contraction by impulses from the central nervous system. The supporting reaction is reflex. This is already proved by the fact that simple pressure against the pads of the foot is sometimes sufficient to evoke the reflex by exteroceptive stimulation. The following observations point in the same direction.

In the first hours after extirpation of the forebrain the supporting reaction is absent in spite of the presence of sufficient muscle tone. The post-operative shock has suppressed the reflex in an animal, which can right itself and even walk. Several weeks or months after severing the posterior roots to a fore- or hind-limb the movements are fairly well restored, and it is possible, by changing the position of the head, to increase the tone of

the desensitised limb; in spite of this no trace of a supporting reaction can be felt. In deep narcosis it is impossible, by changing the position of its most distal part, to transform the limb into a supporting pillar.

All these facts show that the anatomical arrangement alone, even if the muscles have some tone, cannot explain the supporting reaction.

One arrangement deserves special attention: the two-joint muscles. A part of the flexors of hand and fingers stretched during standing takes its origin from the medial epicondyle of the humerus, and can extend the elbow. In doing this the biceps is stretched and, if this muscle comes into tonic contraction, it can extend the shoulder, which in turn stretches the *caput longum* of the triceps, so that contraction of this muscle can extend the elbow. Simultaneous contraction of biceps and triceps fixes not only the elbow, but also the shoulder. In the completely relaxed limb under deep narcosis or immediately after death this mechanism does not act, only extension of the elbow can be evoked by extension of the shoulder; but in the normal animal or when, after death, the muscles become rigid from rigor mortis, the two-joint muscles exert their influence. For this effect therefore reflex tension of the muscles is a necessary condition.

From the foregoing remarks it follows that the anatomical arrangement by itself cannot explain the supporting reaction, but constitutes the mechanism through which the physiological processes can play their rôle.

2. Of great importance are the *myotatic reflexes* of Liddell and Sherrington. These authors found in decerebrate preparations tonic reflex contractions caused especially in the extensor muscles by even slight stretch of the muscle. The increase of tension is confined to the muscle, which is stretched, and even one part of a muscle can show this purely proprioceptive reflex, if this part only is subjected to stretch. According to Forbes, Cobb, Fulton and Liddell, contraction may be confined to only a part of all the fibres of a muscle, just sufficient in number to counterbalance the stretch, or to carry the weight which causes the increase of tension. If these muscle-fibres become fatigued, other fibres go into contraction, and alternation of the active fibres makes it possible for the muscle as a whole to be indefatigable during myotatic activity. The reflex begins with a stretch and an increase of tension, and continues as maintained tension at a constant, increased length. The weight being thus just counterbalanced by the particular muscle-fibres in action at the moment, the others are prepared to move the limb or body, just as smoothly as if no weight at all was present.

This myotatic reflex comes into play in the flexor muscles of hand and

fingers, which are stretched during standing by the dorsiflexion of these parts of the limb, and therefore react by increase of tension. In other muscles of the limb also, especially in the extensors of elbow and shoulder, if they become stretched during static activity, myotatic reflexes may cooperate with the direct supporting reflexes.

But besides these myotatic reactions many other reflexes cooperate in the supporting function.

3. According to Liddell and Sherrington, the myotatic reflexes in the decerebrate preparation are limited to the stretched muscles, or parts of muscles. This is not the case with the supporting reaction in normal or thalamus animals. If in experiments with graphic registration one or other flexor tendon to the hand or to one or more fingers is severed from its insertion and connected with a recording lever, it is seen to contract, although not stretched, when the hand and toes are dorsiflexed. In the course of the experiments the contraction of all the different flexor muscles during the static reflex has been in turn recorded. These facts show that the extension of the flexor muscles during standing sets up reflexes, which tend to bring into play the whole group of flexor muscles on the fore-arm, and that we have to deal with synergistic reinforcement of tonic contraction.

4. How do the *extensor muscles* react in the positive supporting reaction? They are not stretched at all. In a long series of marvelous investigations it has been shown by Sherrington that in ordinary *movements* antagonistic muscles obey the law of reciprocal innervation. Also in the experiments of Schoen reflex flexion of the hand was accomplished by contraction of the flexors and simultaneous relaxation of the extensors; and reflex extension of the hand (e.g. in the crossed extension reflex) by contraction of the extensors with relaxation of the flexors. But as soon as the supporting reflex was evoked by pressure against the pads of the sole and by dorsiflexion of hand and fingers, then there was a simultaneous contraction of both flexors and extensors. The functional grouping of the antagonistic muscles differs totally in the supporting reflex from that in ordinary movements: the antagonistic muscles exert a synergistic function and the result is *fixation of the joint*.

5. The elbow also becomes fixed.

- a) The fixation against flexion is accomplished by mechanisms differing according to the various possible positions of the fore-

limb. In the first place, as mentioned above, the flexors of fingers and hand, especially the flexor digitorum profundus, take their origin from the epicondylus medialis humeri, and will therefore, if stretched during standing, cause fixation of the elbow directly by myotatic reflexes. In the second place dorsiflexion of hand and fingers gives rise to reflex contraction of the triceps. In the third place, stretch of the triceps evokes a myotatic reflex upon this muscle, and finally, if in the supporting reflex the biceps is stretched (by flexion of the shoulder) this also gives rise to a reflex contraction of the triceps.

- b) The fixation against extension is secured by a reflex contraction of the biceps caused by the dorsiflexion of hand and fingers, reinforced by a reflex, taking its origin in the stretched triceps.

All these different reflexes cooperate, reinforce, and, if necessary, replace each other, so that standing under very different positions of the joints becomes possible.

6. The fixation of the elbow, as far as the biceps and the long head of the triceps are concerned, depends also upon the position and fixation of the shoulder-joint, as described above. The shoulder is fixed in the first place by these two double-joint muscles and in the second place by the shoulder musculature itself. For this joint also simultaneous contraction of flexors and extensors has been demonstrated. It may be mentioned that in the experiments of Schoen the supraspinatus muscle was very sensitive to the exteroceptive stimulus of touching the pads of the fingers.

7. The whole mechanism of fixation in the hand, elbow, and shoulder-joints would not be of any value for standing if there were not also a strong muscular fixation of the scapula to the thorax. The strong and broad mass of the levator scapulæ and the serratus, which are inserted on the scapula and take their origin from the neck region and the lateral parts of the thorax, form on both sides a bearing girth, by which the forepart of the body is slung between the two supporting pillars. The rhomboidei, connecting the vertebral column with both scapulæ, hold these bones in position and make the bearing function of the levator scapulæ and serratus effective. At the same time the pectoralis muscle and the latissimus dorsi fix the humerus to the trunk and secure the two pillars against abduction. If under certain conditions the levator scapulæ and serratus should give way, the pectoralis and latissimus on both sides can form a second bearing girth, which can also carry the thorax.

If the thalamus animal is hanging prone in the air, these shoulder muscles are usually tonically contracted. Standing on the ground increases this tone by reflexes evoked by dorsiflexion of the toes and exteroceptive stimuli of the finger-pads.

This short review, which naturally must be very incomplete, is sufficient to show how complicated is the system of different reflexes, which makes it possible to stiffen one limb and to transform it into a supporting pillar.

B. The Negative Supporting Reaction

Besides the disappearance of those conditions which evoke the positive supporting reaction, active processes take an important part in interrupting the positive reaction and inducing the negative phase. The active stimulus is not exteroceptive. The limb in the negative phase is usually removed from the ground. The volar flexion of fingers and hand in the forelimbs or plantar flexion of the toes in the hind-limbs is the effective stimulus. The reflex disappears in the forelimbs after cutting all tendons of the extensor muscles of hand and fingers. In the intact limb it is evoked by stretching these extensors. In consequence of this there is a reflex relaxation of the extensor muscles of the proximal joints, which has been demonstrated by Schoen in the case of triceps, serratus anterior, and levator scapulæ. At the same time the flexors of the shoulder contract. The relaxation of serratus and levator scapulæ can be seen also to follow flexion of the elbow or even of the shoulder.

In this way the whole limb, especially the shoulder, is loosened and becomes free for movements.

The foregoing description shows the importance of local static reactions.

SEGMENTAL STATIC REACTIONS

It will be sufficient to illustrate the segmental static reactions by some examples only. A very simple instance is given by the crossed extension reflex. In the standing animal the weight of the hind part of the body is carried by both hind-limbs and the weight of the fore part of the body by both forelimbs. A painful stimulus applied to one limb evokes the ipsilateral flexion reflex, by which the stimulated foot is removed from the neighbourhood of the stimulus. The crossed limb, therefore, has to carry the weight of the fore or hind part of the body alone. This is made possible by the increased supporting reactions as described above, but is aided by the crossed extension reflex, which causes increased tone in the extensor

muscles of the limb.

Another instance of segmental static reactions is afforded by the so-called 'Schunkelreflex,' which can easily be demonstrated in the fore- or hind-limbs of normal animals as well as after extirpation of the cerebellum or the forebrain. Suppose that the animal (dog or cat) is standing on the table and one – e.g., the right – forelimb is lifted up by the negative supporting reaction. The extensor tone of this limb is continuously tested by slight passive flexions of the elbow. The hand of the observer moves the thorax of the animal towards the right; then one feels an increased extensor tone of the elbow, and finally the limb is completely extended and able to prevent the fore part of the body from falling towards that side. The same reflex can be demonstrated in the hind-limbs and is also present in man, especially when we are standing on one foot and move towards the other side. Then the extension of the crossed knee is inevitable, and gives the subjective impression of being at least partly voluntary. But in animals the reflex is very active after complete extirpation of the cortex cerebri.

The reflex is not evoked by changes in the position of the head, neck, and vertebral column. The stimuli arise in the main from the adductor muscles, which are stretched by moving the body in the lateral direction. The reacting limb can be completely desensitised by cutting all the posterior roots carrying impulses from this limb; desensitisation of the standing limb, on the other hand, abolishes the reflex.

A similar reflex is present if the body be moved forwards or backwards. After lifting up one forelimb the forward movement of the thorax causes the limb, which has been lifted up, to be extended and moved forwards, so that it prevents the body from falling.

The static 'meaning' of this latter reaction is evident, but besides that the reaction also comes into play during walking and running. This shows that the same reflex can be used for the maintenance of equilibrium and for the purpose of walking.

These and other segmental static reactions, in which stimulus and effect are not confined to the same limb but to the same segment, show the interconnexion of separate parts of the body in static functions.

GENERAL STATIC REACTIONS

In general static reactions more than one segment of the body, even the whole body, is concerned. Many examples will be given in the course of these lectures. A fundamental condition for every static reaction is that the animal shall stand or at least be able to stand. In the preceding section this was supposed to be the case. At the present moment we have to

answer the question: Which part of the central nervous system must be present for standing?

The classical experiments of Goltz and Sherrington have demonstrated that a *spinal animal* can perform very complicated movements. If in a dog the spinal cord be divided in the thoracic region, after some months a great number of reflexes can be evoked in the limbs: ipsi-lateral flexion and extension reflexes, a crossed extension reflex, rhythmic movements resembling walking and running or galloping, the scratch reflex, movements of hind-limbs and tail exactly similar to those which normal animals perform during defæcation and micturition. Under certain conditions even a flexor tone of long duration may be present in such a limb – e.g., when an ulcer on the foot develops; but in spite of all these very complicated and adapted innervations, no static tone is present, and the limbs cannot carry the weight of the hind part of the body: they give way after a very short time. The same is true for a spinal animal in which the cervical cord has been cut. All four limbs are under these conditions deprived of static tone.

In the ‘decerebrate’ preparation the state of affairs is quite different. In these animals the brain-stem has been cut across somewhere between the plane of entrance of the eight nerves and the foremost part of the mid-brain. It has been shown by Sherrington that after decerebration the ‘decerebrate rigidity’ develops, which is characterised by a strong tonic contraction of the ‘antigravity’ muscles – viz., the extensors of the limbs and back, the elevators of neck and tail, and the closing muscles of the jaw. The antagonists of these static muscles, the flexors, have either a very slight tone or even none at all. If placed on its feet the decerebrate preparation will stand, that is to say, the strongly extended limbs will carry the weight of the body, but owing to the isolated and exaggerated contraction of the extensors the posture of the animal becomes abnormal and is deprived of the smoothness which is seen in intact animals. Sherrington has shown that ‘decerebrate rigidity’ is a reflex phenomenon. The chief stimuli arise in the proprioceptive sense organs of the contracted muscles themselves. Later experiments have shown that, besides this, other sensory stimuli cooperate, arising from the crossed limbs, from the neck region, the labyrinths, the fifth nerves, the skin, etc. After cutting the cervical posterior roots and extirpating the labyrinths the neck muscles can still develop pronounced decerebrate rigidity. It is possible to provide the completely deafferented limbs of a decerebrate animal with a fair amount of tone by stimuli from other parts of the body. Experiments of Bazett

and Penfield have shown that after decerebration the rigidity may last for weeks.

The reflex behaviour of the decerebrate animal differs from that of the spinal animal in a characteristic way. Under both conditions the flexor muscles perform reflex contractions of short duration after stimulation of an appropriate afferent nerve. The extensor muscles of the spinal animal also respond by short contractions. In the decerebrate preparation the reflex response of the extensor muscles is prolonged, and shows sometimes very long after effects.

The peculiarities of the decerebrate state will become still more evident when we later describe the different behaviour of animals with intact mid-brain.

A. GENERAL STATIC REACTIONS OF THE DECEREBRATE PREPARATION

The essential condition for these experiments is that the hind part of the bulb has been left in functional connexion with the spinal cord. The presence or absence of the cerebellum is not essential; the presence of the oral part of the bulb, the pons, and the caudal part of the mid-brain causes the preparation to show a greater variety of reflexes, but does not contribute to the fundamental phenomenon in question.

General static reactions in the decerebrate animal can most easily be induced by changing the position of the head. This was discovered by chance. Many years ago I prepared a decerebrate cat with cross section of the low thoracic cord, in order to study some reflex reactions of the tail muscles. For this purpose I brought the animal from the lateral into the supine position and noticed to my surprise a slow but very strong 'pathetic' extension of the forelimbs, which disappeared when the animal was again placed upon its side. Other changes of position evoked also tonic reactions of the forelimbs. Subsequent repetitions of the same experiment showed that various animals reacted differently. A long experimental analysis, in which I was joined by my friend and collaborator, De Kleyn, was necessary until we understood the phenomenon completely. As usual the result was comparatively simple. It is possible, by giving to the head different positions, to change the distribution of tone in the whole body musculature, and, as far as decerebrate preparations are concerned, especially in the above-named group of antigravity muscles. The most striking reactions appear in the extensors of the limbs and in the neck muscles. The effects observed are the result of combined reflexes from the labyrinths and from proprioceptive neck-receptors, and as the relative strength of these two influences varies from animal to animal, the

different results of subsequent experiments can be understood. In this way it is possible to impress upon the whole body different adapted attitudes by changing only the position of the head. These reflexes therefore may be called *attitudinal reflexes*.

Every change of the head implies two different factors:

1. a change in the position of the head in relation to the body by which the neck-receptors are stimulated; and
2. a change of orientation of the head in space, which brings the labyrinths into play.

These facts allow us to study the two sets of reflexes separately.

1. Tonic Neck Reflexes

In order to study the tonic neck reflexes upon the limb muscles without interference with the labyrinth reflexes it is necessary to extirpate the vestibular organs. This has been done by a method devised by De Kleyn without any lesion of the muscles on the basis cranii. After this operation the influence exerted by changes of the position of the head become independent of the orientation of the head in space. Only changes in its relation to the body cause tonic reflexes and these reflexes are now unequivocal, all animals reacting in the same sense.

Rotation of the head causes extension of the fore- and hind-limbs, towards which the jaw is rotated ('jaw-limbs'), and relaxation of the limbs, towards which the vertex is rotated ('skull-limbs'). Inclination of the head towards one shoulder causes extension of the fore- and the hind-limbs towards which the nose is inclined ('jaw-limbs') and relaxation of the limbs on the other side ('skull-limbs'). The general rule for rotation and inclination therefore is that the jaw-limbs are extended and the skull-limbs flexed. Dorsiflexion of the head causes, in all mammals except the rabbit, extension of the forelimbs and relaxation of the hind-limbs. Ventroflexion of the head causes flexion of the forelimbs and extension of the hind-limbs. In rabbits dorsiflexion of the head causes extension of all four limbs, and ventroflexion of the head causes flexion of all limbs. In all mammals with the exception of the rabbit, movement of the head in different directions is followed by opposite reaction of one pair of limbs as compared with the other. Relaxation of the four limbs in all mammals is given only by pressure upon the lower part of the cervical vertebral column in a ventral direction (vertebra prominens reflex).

The afferents for these reflexes (with the only exception of the vertebra prominens reflex) take their course through the three uppermost cervical

posterior roots. The centres of the tonic neck reflexes have been localised in the first and second cervical segments.

2. Tonic Labyrinthine Reflexes

These reflexes can be studied separately after excluding the neck reflexes. This can be done either by cutting on both sides the three first cervical posterior roots or by immobilising head, neck, and thorax by a strong plaster-jacket, so that no movements of the head in relation to the body are possible, while the forelimbs are left unrestrained and can be moved freely. If such a preparation be brought into different positions in relation to space the extensor tone of all four limbs always changes in the same sense. There is only one position in which the extension becomes maximal: the supine position with snout about 45° above the horizontal plane. The extensor tone diminishes to a relative minimum if the animal is brought into the prone position with snout about 45° below the horizontal plane. The minimum and maximum positions differ, therefore, by 180° . In all other positions in space the extensor tone is intermediate between these two extremes. These reflexes are not evoked by movement but depend upon position. They are independent of angular acceleration and last as long as a certain position is kept. Only such changes in the position of the head are effective as change in its angle in relation to the horizontal plane.

The labyrinthine origin of these reflexes is proved by the fact that they disappear after bilateral labyrinth extirpation. A delabyrinthised decerebrate cat in which the neck has been immobilised by a plaster bandage, can be brought in all possible positions in space, without any changes in the tone of the limb muscles.

The tonic labyrinthine reflexes arise from the otolithic organs. In mammals it is not possible to prove this by isolated extirpation of the otolithic maculæ or of the ampullæ of the semicircular canals, for this cannot be done without opening the peri- or endo-lymphatic space, and therefore definitely disturbing the vestibular function. Another method was, therefore, used. Following a technique first devised by Wittmaack, guinea-pigs under ether were centrifuged for a short time at high speed. Then the otolithic membranes are detached by the action of centrifugal force, whereas the canals with ampullæ and cristæ remain intact. In each case a microscopic investigation must be made, and this must show that the ampullar nerve-endings and the canals are intact, that all four otolithic maculæ are completely deprived of their otolithic membranes, and that these four membranes can be found, remote from them, inside the endolymphatic

space. This last point is of importance, because it proves that the detachment of the membranes occurred *intra vitam* and not as a result of faulty fixation or cutting of the section for examination. Only from experiments with complete histological evidence may definite conclusions be drawn.

In such animals all labyrinthine reactions evoked by angular or rectilinear acceleration are present, but all reflexes resulting from position have disappeared, including the tonic labyrinth reflexes upon the limb muscles. These reflexes, therefore, depend upon the otoliths.

The position of the otoliths in relation to the skull has been carefully investigated by De Burlet and his pupils in the anatomical department of the University of Utrecht. The results of their measurements have been used for the construction of models (guinea-pigs, rabbit, monkey, man).

The two maculæ utriculi are situated approximately in the same plane, which is nearly horizontal, when the animal carries its head in the normal position. The two maculæ sacculi are not at all in the same plane; they form as far as their chief portion is concerned an angle of rather less than 90° with the utricular maculæ. With normal position of the head the two maculæ sacculi face towards the lateral side.

If the head of a rabbit is brought into the maximum position for the tonic labyrinthine reflexes the saccular maculæ have no characteristic position, whereas the utricular maculæ are lying in a horizontal plane. In the maximum position, in which the extensor tone of all four limbs has reached its highest value, the otolithic membranes exert a pull on the macular epithelium. In the minimum position for the extensor tone, the maculæ stand again horizontal with the otolithic membranes pressing upon the epithelium. The conclusion is that the *tonic* labyrinthine reflexes are evoked from the utricular maculæ. This is confirmed by the fact that after unilateral labyrinth extirpation the maximum and minimum positions for the tonic labyrinth reflexes remain unchanged, which would be impossible if the maculæ concerned in these reflexes did not lie in the same plane.

In the position in which the extensor tone of the limbs is maximal, the otoliths pull on the utricular maculæ. The conclusion that the maximum of stimulation in the macular epithelium is induced, not by the pressing, but by the pulling otolith, is proved to be sound by observations on saccular reflexes, a part of which will be mentioned later.

The centres for the tonic labyrinthine reflexes upon the limb muscles have their position in the hind part of the bulb, behind the plane of entrance of the eighth nerves.

Besides the tonic utricular reflexes on the limb muscles there are also

tonic utricular reflexes on the neck muscles, which follow in general the same laws. The only difference is that every utricular macula sends impulses to the limbs of both sides and to the neck muscles of the crossed side only. As a consequence of this unilateral labyrinth extirpation is followed by no change in the tonic labyrinthine reflexes upon the limbs, but evokes the well-known turning of the neck, which has been described by all previous observers. This rotation and inclination of the head causes secondary tonic reflexes upon the limb muscles. The connexion of the labyrinths with the limbs is, therefore, a double one:

1. by tonic labyrinthine reflexes directly upon the limbs, and
2. by tonic neck reflexes upon the limbs indirectly through labyrinthine influences upon the neck.

3. Combinations of Tonic Labyrinthine and Neck Reflexes

If both sets of reflexes are present, they cooperate so that the tone of every single muscle depends upon the algebraic sum of influences derived from proprioceptive end-organs in the neck and from the utricular maculæ. If, therefore, the triceps muscle of the right elbow derives increased tone from the labyrinths and from the neck, the elbow will be strongly extended; if this muscle gets diminution of its tone from both sources the elbow will relax, but if the muscle tone is increased from the labyrinths and decreased from the neck the result depends upon the relative strength of these influences. If the labyrinthine reflexes predominate the elbow will be extended, if the neck reflexes are stronger it will be flexed, and if both reflexes are of the same strength the angle of the elbow will not change at all.

This cooperation gives rise to very characteristic attitudinal reactions of decerebrate animals. Place a cat in the prone position upon the table and flex the head ventrally, then the labyrinths come into the minimum position and all four limbs will tend to relax. The neck influences cause relaxation of the forelimbs and extension of the hind-limbs. Both groups of reflexes, therefore, cooperate in the forelimbs, which show distinct relaxation, whereas the hind-limbs may not change at all, because the influences from neck and labyrinths act in opposite senses. If with the prone position of the animal the head is bent dorsally the resulting removal of the labyrinths from the minimal position causes extension of all four limbs. The neck reflexes evoke extension of the forelimbs and relaxation of the hind-limbs. The combined effect is strong extension of the forelimbs and only slight changes in the hind-limbs. Head movements, therefore, in a

ventral and dorsal direction have a very strong influence on the forelimbs, whereas the reaction of the hind-limbs is much weaker.

Still more complicated is the effect of head rotation with the lateral position of the animal. In this case I shall describe only the effect upon the forelimbs. If with the right lateral position of the animal the head is rotated so that the vertex is below, then the labyrinths are in maximum position, which gives rise to strong extension of both forelimbs. In respect of the neck reflexes the uppermost forelimb is 'jaw-limb' and will be extended, whereas the lowermost forelimb is 'skull-limb' and will be flexed. Both influences cooperate for the uppermost forelimb, which is strongly extended. The behaviour of the lowermost forelimb is different according as one or the other reflex preponderates. With stronger labyrinthine reflexes it is extended. With stronger neck reflexes it relaxes. When the strengths of both groups of reflexes are equal, it remains unchanged. The reaction of the lowermost forelimbs to rotation of the head with the lateral position of the animal affords, therefore, the possibility of determining in a given animal the relative strength of both sets of reflexes. If, now, with the same lateral position of the body the head be rotated with the vertex uppermost, then the labyrinths come into the minimum position and both forelimbs will tend to relax. In the upper forelimb this relaxation is reinforced by the neck influence (skull-limb). In the lower forelimb it is counterbalanced by the neck influence (jaw-limb). With preponderant labyrinthine influences the lower forelimb is relaxed; with preponderant neck reflexes it is extended. In every case with the right lateral position rotation of the head evokes very strong and unequivocal reactions of the left (upper) forelimb, whereas the reactions of the right forelimb are weaker and of indefinite direction. Now, the animal is placed in the left lateral position and again the head is rotated. The same rules can now be applied with this difference only, that the upper forelimb is now the right one. In this case the right forelimb will react strongly and the left forelimb may not move at all. It becomes evident that one and the same rotation of the head causes with the right lateral position of the animal strong relaxation of the left forelimb, and with the left lateral position strong extension of the right forelimb. This instance shows clearly that the same movement of the head in relation to the body may, with different spatial positions of the body, evoke very different reactions. But in spite of these complications, which were very amazing at the time when the experiments were started, it has been possible to explain all reactions, observed in more than a hundred experiments, in which the head was moved about the three chief axes with each of the six main positions of

the body in space by the combined action of utricular and neck reflexes.

The attitudinal reflexes are called tonic, because they last as long as the head keeps a certain position. They are practically indefatigable. After unilateral labyrinth extirpation in rabbits the turning of the neck lasts until the animal dies. Also the tonic neck reflexes upon the limbs evoked by this head rotation can be demonstrated as long as the animal is alive. On the other hand, every change in position of the head is followed immediately by the corresponding change in the attitude of the whole body. The influence of the tonic attitudinal reflexes is very strong upon the muscles of the proximal joints, shoulder and hip, elbow and knee; on the distal joints of hand, foot, toes, and fingers the action of these reflexes is much less pronounced.

The mechanism as a whole acts in such a way that the head leads and the body follows. The attitudes impressed upon the body by a certain head position in the decerebrate preparation closely resemble the natural attitudes shown by the intact animal during ordinary life.

4. Attitudinal Reactions in Intact Animals and in Man

This leads to the question of the presence of attitudinal reflexes in normal animals with intact central nervous system. In most mammals they are present and can easily be demonstrated. In the normal rabbit dorsiflexion of the head in the sitting animal causes tonic extension of the forelimbs; head rotation with the rabbit in the supine position evokes extension of the jaw-limbs and relaxation of the skull-limbs.

It is not necessary that the head movements shall be passive. The same laws hold good when the animal performs active head movements. As these depend very often upon stimuli transferred to the animal by way of the distance receptors (eye, ear, nose), it is possible to impress upon the body of the animal different attitudes from distant points of the environment. A cat which sees some food lying on the ground flexes the head in the ventral direction, and this causes the forelimbs to relax so that the snout is moved towards the food; but if a piece of meat be held high up in the air the optic stimulus causes dorsiflexion of the head. This evokes strong extension of the forelimbs without marked extension of the hind-limbs. The body of the animal is not only focused on the meat, but is also brought into a position which is optimum for the springing reflex, so that by a strong sudden simultaneous extension of the hind-limbs the animal can reach the meat.

The activity of the vertebra prominens reflex can be watched in a cat or dog creeping into a hole. In doing so, the animal brings its head close

down to the ground with resulting relaxation of all four limbs, so that the belly lies flat upon the floor.

Many other instances of the action of attitudinal reflexes in intact animals have been observed. A striking difference between the reaction of the decerebrate and the normal animal is that in the decerebrate preparation the flexor muscles, which have no tone, do not take part in the reaction or respond only very slightly. In the intact animal the flexor muscles also, as will be shown later, have tone, and react to the tonic neck and labyrinthine reflexes. In this they follow the law of reciprocal innervation. Increase of extensor tone is associated with diminished flexor tone and vice versa. In this way the attitudinal reflexes of intact animals are much smoother than the stiff and always exaggerated attitudes of the decerebrate preparation.

In monkeys during their ordinary movements it is not easy to detect the presence of attitudinal reflexes, which, on the other hand, can with certainty be demonstrated in the decerebrate or narcotised animals.

In man also the presence of attitudinal reflexes in ordinary life is not striking. Good pictures and statues give the impression of being natural, if the body is represented according to the laws of attitudinal reflexes. If these laws are not obeyed we get the impression of a dead body or of a caricature. But the complexity of human movements during ordinary life usually obscures the simple attitudinal reactions. In a certain percentage of babies, however, the influence of head rotation upon arms and legs can be seen.

Under pathological conditions the presence of attitudinal reactions in man may become evident, especially when disease has interfered with the function of the higher parts of the brain. Very diverse pathological conditions give rise to the appearance of these reflexes, which are now used by neurologists for diagnostic purposes; head rotation especially causes extension of the jaw-limbs, sometimes accompanied by relaxation of the skull-limbs. In this case neck reflexes are present. In a minority of cases also tonic labyrinthine reflexes have been demonstrated, in which all four limbs reacted in the same sense, and in which, precisely as in animals, a maximum and a minimum position of the head could be determined. If both sets of reflexes are present their cooperation follows the same laws as in animals. It has been shown by Simons and by Walshe that the direction of associated movements of paralysed limbs, evoked by active voluntary movements of non-paralysed parts of the body, can be influenced by the position of the head.

The attitudinal reflexes form a group of tonic reactions, by which the whole body musculature is integrated for a combined and highly adapted

function. The entire body follows the direction assumed by the head, this being very often moved in a certain direction under the influence of the telereceptive higher sense-organs. This provides one of the ways in which the relation of the body to its environment is regulated. It need only briefly be mentioned that the different attitudes, with their different distribution of tone and tension in the numerous muscles of the body, are associated with different distributions of reflex irritability over the central nervous system. Therefore one and the same stimulus may cause quite different reflex reactions according to the different attitudes of the animal at the moment the stimulus is applied.

These short remarks may be sufficient to show to what extent the reflex behaviour of animals may be influenced by attitudinal reflexes. The complexity becomes still greater if besides the bulbar centres with their relatively simple function higher centres come into play. This will be discussed in the next section.

PART II

B. GENERAL STATIC REACTIONS OF THE MID-BRAIN ANIMAL

After cross-section through the *calamus scriptorius* the animal behaves like a spinal preparation without static functions (only the tonic neck reflexes are present); if under the influence of one or other stimulus the muscles get some 'background-tonus,' the change of such tone after turning of the neck can be demonstrated. After a cut just in front of the entrance of the eighth cranial nerves, the animal shows decerebrate rigidity and has active tonic neck and labyrinthine reflexes. The centres which give rise to the rigidity and the labyrinthine reflexes are situated in the caudal part of the medulla oblongata. They are, including their afferent and efferent paths, extracerebellar.

This picture remains in the main unchanged if the cutting of the brain-stem is performed more orally. Then also reflexes on the abducens and trochlearis nerves and neck righting reflexes appear, but the general condition remains the same. The latter does not change fundamentally, until the cut is made through the most oral part of the mid-brain: in rabbits and cats through the foremost half of the anterior colliculi and in front of the origin of the oculomotor nerves. The condition of the animal is then no longer 'decerebrate' but becomes 'normal.' The difference is caused by the absence of rigidity, the appearance of a normal distribution of tone,

and the presence of the righting function. That means that the animal is able from all abnormal positions by its own active movements to right itself into the normal position and to keep this position against all disturbing influences.

If the cuts are made more orally, no *essential* differences in the static behaviour can be observed. It makes no appreciable difference in the static behaviour whether the basal ganglia are present or have been extirpated. If the forebrain is left intact the influence of optic stimuli upon posture in some species of animal can be demonstrated. Extirpation of the cerebellum gives rise to very characteristic symptoms, but all the static reactions which are described in these lectures are present, and can still be evoked with great certainty. Some of these reactions seem to be exaggerated in the decerebellated animals.

The most convenient way to study all static reactions of the mid-brain animal is to prepare a thalamus preparation. Then the heat regulation is undisturbed, the function of the mid-brain centres is not greatly interfered with by operative shock, and in consequence of the absence of the forebrain no voluntary movements disturb the observation. It is clear, however, that control experiments on mid-brain animals should always be made. For this purpose the rabbit, which is very resistant to shock, should be chosen.

1. The Normal Distribution of Tone

The distribution of muscle tone in the whole body musculature in the mid-brain and thalamus animal differs from that in the decerebrate preparation by the absence of the exaggerated enduring contracture of the static muscles. These have only just sufficient tone to carry the weight of the body and to balance it. The result is the 'normal' attitude and posture of the thalamus, as compared with the 'caricature' attitude of the decerebrate preparation.

In the former even slight muscular actions are sufficient to change the position of the body.

While in the decerebrate preparation the flexor muscles are completely deprived of tone, they are in the mid-brain animal just as much under tonic innervation as they are in the normal animal. In consequence of this the flexor muscles participate much more in all sorts of reflexes than they do in decerebrate rigidity. Reflex inhibitions of flexor muscles can, on the basis of their 'background' contraction, easily be demonstrated. The experiments of Girndt have shown how the reflex behaviour of a thalamus animal is influenced by the presence of flexor reflexes.

The attitudinal reactions of the thalamus and mid-brain animal differ also from those of the decerebrate preparation by the presence of flexor responses. Changes in the position of the head, under decerebrate rigidity, give rise to reactions chiefly in the extensor muscles, whereas in the mid-brain and thalamus animal flexors and extensors are influenced simultaneously. The change of tone in the flexors and extensors follows the laws of reciprocal innervation, increased extensor tone being accompanied by flexor inhibition and vice versa. This makes the static reactions more smooth and exact.

After ordinary reflex excitations the extensor muscles do not show the prolonged after-effect of the decerebrate preparation, and this also prevents the appearance of stiff movements. The decerebrate preparation shows no positive supporting reflex and only a very imperfect negative phase. The whole supporting reaction, which changes the limb from the movable and instrumental condition into a static support and vice versa, is only fully developed in the mid-brain or thalamus animal.

All these observations show the fundamental part the mid-brain centres play in the whole static function. It is to be expected that the study of the thalamus animal will disclose many interesting facts, and that, just as the last 20 years have with such great success been devoted to the study of the decerebrate preparation of Sherrington, in the next period the mid-brain animal must be the chief object for further careful analysis.

2. The Righting Reflexes

Analysis has shown that the righting function is carried out by the cooperation of five groups of different reflexes. It is, therefore, intelligible how it should be impossible to study the action of one of these groups by paralysing the sensory nerve-organs, from which this group of reflexes takes its origin. The result of such a procedure would only be that the four other groups of reflexes would compensate for the loss of function so produced, and that probably no disturbance of righting would result. Here, as in other complex functions of the central nervous system, it is not permissible to draw conclusions from the isolated paralysis of one set of reflex centres. A complete understanding of the whole mechanism is only possible if the experiment starts from the 'zero condition' in which *all* centres or mechanism concerned in this complex function have been paralysed, so that it is completely absent in the animal. Then in subsequent experiments one or another centre of sense organ may be spared and the function arising under this new condition compared with the 'zero condition.' It is thus possible to study every single reflex while excluding all others

and, finally, to analyse the cooperation of these several reflexes towards a general function.

a) The 'Zero Condition'

In the case of the righting reflexes the zero condition is fulfilled if a thalamus or mid-brain animal after extirpation of both labyrinths is held freely in the air without touching the ground. Then no attempt will be made by active movements to bring the head or the body into the normal position. If the animal is held by the pelvis in the lateral or supine position the whole body, including the head, remains also in this position. The 'zero condition' of animals with *intact* cerebrum differs according to species. Rabbits and guinea-pigs, in which the eyes are not used for righting purposes, if delabyrinthised and held freely in the air, show no righting reflexes. Cats, dogs, and monkeys, on the other hand, must be also blindfolded.

Under all these conditions the animal is completely disorientated and cannot bring its head or body into the normal position.

b) Labyrinthine Righting Reflexes

If their labyrinths are intact then all thalamus animals as well as normal rabbits and guinea-pigs and blindfolded normal dogs, cats, and monkeys, when investigated freely in the air, show the following reflexes:

If the animal is held by the pelvis in the normal position the head also assumes the normal position. If the pelvis is held in the lateral position the head is by rotation brought into the normal position. It is possible to turn the pelvis from one lateral position into the other, while the head remains in the normal position. In whatever position the pelvis be supported – e.g., supine or vertical with the head above or below – the head itself is always held in the normal position.

These reflexes act primarily on the neck muscles. They are originated in the labyrinths and disappear after labyrinth extirpation. They also disappear after detaching the otoliths by centrifuging. For the discussion as to which otolithic maculae are responsible for the labyrinthine righting reflexes we must divide these reflexes into two groups:

1. The *asymmetrical righting reflexes* bring the head from asymmetrical – e.g., lateral – positions about a vertical plane.
2. The *symmetrical righting reflexes* provide that out of all possible symmetrical positions the normal position is taken.

The asymmetrical righting reflexes are evoked from the maculae sac-

culi. This is proved by the fact that after unilateral labyrinth extirpation the resting position of the head is no longer the normal position, but the lateral position; from which it must be concluded that the maculæ concerned cannot lie in one plane, so that the utricular maculæ cannot be responsible for these reflexes. The asymmetrical righting reflex after unilateral labyrinth extirpation is very strong, if the head is kept in the lateral position with the intact labyrinth below; then the saccular otolith pulls on the macula. The head comes to rest and the reflex therefore reaches its minimum, if the intact saccular macula lies horizontal with the otolith pressing upon it. In this case therefore it can be proved that the maximum of stimulation in the macular epithelium must be evoked by the pulling, and minimum stimulation by the pressing otolith. The utricular maculæ are probably the point of origin of the symmetrical righting reflexes. This has been concluded from experiments, in which the labyrinths of guinea-pigs have been paralysed step by step with cocaine, so that first the saccular and then the utricular reflexes disappeared, while the reflexes from the canals preserved their function for some time longer.

In every case the symmetrical righting reflexes bring the head into such a position that the utricular maculæ lie horizontally, so that the otoliths press upon the sensory epithelium. This reflex then reaches its minimum and the head comes to rest.

The labyrinthine righting reflexes provide for orientation of the head in relation to space, gravity being the controlling influence.

c) Body Righting Reflexes Acting upon the Head

For an isolated demonstration of these reflexes we start again from the 'zero condition,' and hold a labyrinthless thalamus or intact animal (blind-folded or not according to the species) freely in the lateral position in the air. Then the head also will be in the lateral position. We now place the animal upon the table, and notice that immediately after the body of the animal comes into contact with the ground the head is rotated towards the normal position. This reflex is evoked by the asymmetric stimulation of the pressure sense organs on the body surface. This can be proved by compensating for the asymmetry of stimulation – e.g., by placing a weighted board upon the upper side of the animal, so that the pressure upon each side of the animal is the same. The head then falls back into the lateral position. If the board is taken away the head is again righted. If the animal then be lifted from the ground, the head returns to the lateral position. These observations show the importance of tactile stimuli for the orientation of the head. By these influences the head is orientated in

relation to the ground or other surfaces with which the body of the animal comes into contact. Reflexes of this sort can be evoked not only from the surface of the trunk, but also from the soles or palms. In this way the heads of climbing animals, such as monkeys, squirrels, etc., are orientated towards the objects upon which the animal is climbing.

These reflexes also play a rôle in the correction of abnormal positions of the head. After unilateral labyrinthectomy the rotation of the head towards the operated side, which is often very distinct, becomes greatly diminished if the animal be placed on the ground.

In this way two active influences cooperate in righting the head: the one in relation to gravity, the other in relation to the ground.

d) Neck Righting Reflexes

The neck righting reflexes orientate the body in relation to the head. When, by the combined action of the labyrinthine and body righting reflexes, the head is restored to the normal position, while the trunk still remains in the original abnormal position (e.g. the lateral), then the neck is twisted. This evokes a reflex by which the thorax is brought into symmetry with the head. This may give rise to a rotation of the lumbar region, which in turn causes a similar reflex upon the hind part of the body, so that finally the whole body has followed the head into the normal sitting position. In a similar way dorsiflexion of the head gives rise to lordosis of the whole vertebral column. Ventroflexion is followed by a curving of the whole body in the ventral direction. Inclination of the head towards one shoulder evokes curving of the vertebral column with the concavity to this side.

All these influences can be immediately seen if an intact animal be held freely in the air with the pelvis in all different positions. The head is then primarily brought into the normal position, and the forepart of the body follows the head, whereas the pelvis is prevented from doing so by the hind supporting it. Several of these reflexes can easily be demonstrated in the supine position of the animal; movements of the head in different directions evoke in this position very marked reactions upon the hind part of the body. The neck righting reflexes make it possible, by simple movements of the head, to bring the body of even very strong animals on its side.

e) Body Righting Reflexes Acting upon the Body

The neck righting reflexes ensure the orientation of the body in relation to the head; the body righting reflexes right the body in relation to the ground (or any surface with which the body comes into contact – e.g., in

climbing). These reflexes make it possible for the body to be righted, even if the head is not in the normal position.

The easiest way to demonstrate these reflexes is to hold a normal animal in the lateral position in the air, the head also being kept firmly in the lateral position. In this condition the neck righting reflexes tend to keep the body in the lateral position. If now the animal is placed upon the table and the head kept continuously fixed in the lateral position, the body is seen to be righted into the normal position in spite of the tendency of the neck righting reflexes to keep the body on its side. The active stimuli for these reflexes arise in the sensory nerve-endings of the body surface, which are stimulated asymmetrically by the pressure against the ground. If by means of a weighted board the other side of the body is also pressed upon, the symmetry of stimulation is restored and the body therefore remains in the lateral position.

In climbing animals similar strong influences arise from the feet and hands, and cause orientation of the body towards trees, walls, roofs, etc.

f) Optical Righting Reflexes

The four groups of above-described reflexes are the only righting reflexes of the thalamus animal, and also of intact rabbits and guinea-pigs. In higher mammals such as cats, dogs, or monkeys with intact cerebrum the eyes contribute towards the orientation of the head. In order to study these reflexes the delabyrinthised animals must be examined freely in the air. Then it can be seen that the head, if blindfolded, is completely disorientated and shows no correction from any abnormal position. If the eyes are opened, the head is brought into the normal position as soon as the visual attention of the animal is attracted, and it fixes with its eyes something in its environment, such as food, a fly, the assistant, etc. If this visual attention ceases, the head may go back into any abnormal position.

The exact position of the centres for these reflexes has not yet been determined. It may be supposed that they are localised in the optical cortex.

All these reflexes cooperate in the intact animal, and enable the body to attain and to keep a certain position. If the animal is moving on the ground all these reflexes cooperate in the same sense, but if the animal is climbing a vertical surface or beneath a horizontal roof – i.e., of a cage – sometimes conflicting influences come into play and lead to interesting results.

The integrity of every single factor of this complicated function is doubly ensured. The head is righted by labyrinthine, tactile, and optical

stimuli; the body by proprioceptive and tactile stimuli. The tactile stimuli act separately upon the body and upon the head. The orientation of the head and of the body takes place in relation to gravity, sustaining surface (ground, etc.), distant environment (optical), and to parts of the body – a very complex combination of reflexes. It is indeed an interesting task to watch the cooperation and interference of these reflexes during the movements of various animals in their ordinary life.

3. The Centres for the Righting Reflexes

The position and distribution of the centres for the righting reflexes have been determined by Rademaker. In a great number of experiments with cats and rabbits he made transverse sections through the brain-stem at different levels, determined those reflexes which were present after recovery from the shock of the operation and those which were absent, and made in every case a careful histological examination of a complete series of microscopical sections. A synopsis of all experiments showed the most caudal level for each reflex at which a transverse section of the brain-stem did not interfere with its function. The conclusion could then be drawn that the centres of that special reflex must, together with the afferent and efferent paths, be situated caudally from this level. Then cutting across somewhere behind this level led to the disappearance of the reflex. In this case the conclusion that the centre must be situated orally to this level cannot be drawn with absolute certainty, because it is always possible that the centre lies behind the cut, but is thrown out of action by shock or diaschisis. In this way it was found by Rademaker that section through the anterior part of the anterior colliculi and just orally from the points of origin of the third nerves does not interfere with the presence of normal labyrinthine and body righting reflexes, whereas a section carried out some millimetres more caudally – i.e., behind the origin of the third nerves – destroys the above-mentioned righting reflexes. In the latter case the neck righting reflexes are still present. Their centres are arranged more caudally in the pontine region. Extirpation of the dorsal half of the mid-brain does not interfere with the presence of the righting reflexes. Total extirpation of the cerebellum leaves all righting reflexes, including the body righting reflexes, intact. By these experiments it is proved that the centres for the righting reflexes lie in the ventral part of the mid-brain behind a section just in front of the third nerves. The disappearance of the labyrinthine and body righting reflexes after cutting the mid-brain behind the third nerves suggested the possibility that the centres for these reflexes were situated just at the level of the oculomotor nerves. The most remark-

able nucleus here is the red nucleus, the magno-cellular part of which gives origin to the rubro-spinal tract, which crosses at about the same level in the decussation of Forel. As median sagittal splitting of the mid-brain destroys the righting reflexes in question, the probability is increased that the red nuclei are the centres sought for. Therefore Rademaker proceeded to make dorsal or ventral median incisions into the mid-brain, which divided it just deeply enough to leave Forel's decussation undisturbed. Animals with such incisions showed the righting reflexes. But as soon as the cut was made a little deeper, so that the rubro-spinal tracts were severed, the labyrinthine and the body righting reflexes acting upon the body disappeared. Other experiments of Rademaker showed that the righting reflexes were normally present after the destruction on both sides of the substantia nigra and the pyramidal tract. Also lesions lateral to the red nuclei did not prevent the appearance of the righting reflexes. By all these experiments it is proved that in the cat and rabbit the red nuclei are the centres for the labyrinthine righting reflexes and the body righting reflexes which act upon the body. The efferent path for these reflexes is the rubro-spinal tract. The body righting reflexes acting upon the head have their centres at the same level, but not in the red nuclei. The centres for the optical righting reflexes are cortical, the centres for the neck righting reflexes lie more caudally in the pontine or upper bulbar region. The exact course of the afferent paths for all these reflexes is still to be determined. It is only known that they do not pass through the cerebellum.

In the thalamus animal extirpation of the red nuclei or isolated severance of the rubro-spinal tracts causes still another change. It leads to the disappearance of the normal distribution of tone and the appearance of decerebrate rigidity. The presence in the thalamus animal of rubro-spinal impulses counterbalances the influences from the centres in the lower bulbar region, which, if acting alone, cause the extensor tone to be greatly increased with diminution of flexor tone.

The following experiment of Rademaker's was very striking. In a thalamus animal a thread was drawn through the medial plane of the mesencephalon in the dorso-ventral direction just behind Forel's decussation. The animal showed normal distribution of tone, all righting reflexes, and normal sitting and running. Then slight traction was applied to the thread just sufficient to divide the rubro-spinal decussation. The result was maximal decerebrate rigidity, paralysis of the labyrinthine righting reflexes, and the body righting reflexes acting upon the body.

While in the thalamus animal cutting of the rubro-spinal tract causes such marked effect, in the normal animal with intact forebrain the same

operation has much less drastic consequences. The extensor tone is, however, increased, but much less so than in the thalamus preparation. Only if, in addition to the rubro-spinal bundles, the pyramidal tracts are also severed, does there follow a marked increase of extensor tone. The pyramidal tract has the function of partly counterbalancing the influence exerted in the spinal cord by the hind bulbar centres, which tend to increase the extensor tone. We see thus that the tone and excitability of the spinal centres is governed by influences arising in the brain, a part of these tending to shift the mechanism in the direction of increased extensor tone, another part counterbalancing this influence with the result that both groups of muscles get equally their right share.

4. Righting Reflexes in Man

The study of righting reflexes in man is still in its infancy. We know that these reflexes are present here also, but a careful analysis along the lines shown by animal experimentation has not yet been carried out, and not much is known about the way in which they cooperate towards providing the erect posture. Landau, Schaltenbrand and others have begun the study in children during their first developmental stages, in which they acquire the erect posture and learn how to stand and to walk. Only when this pioneer work has been accomplished will an understanding of pathological conditions be possible.

Labyrinthine righting reflexes can be demonstrated in children who are blindfolded and held by the pelvis in different positions in the air. The head can then be seen to be moved towards the normal position (Schaltenbrand).

Neck righting reflexes are very active in man. In children they have been studied by Landau, who showed that babies in the prone position usually bring the head by dorsiflexion into the normal position, and this is followed by strong lordosis of the vertebral column with extension of the limbs. Passive ventroflexion of the head causes disappearance of the lordosis so that the whole body becomes ventrally concave. Schaltenbrand published photographs of babies in which rotation of the head causes the body to roll from the supine into the lateral position, a reflex which, according to Zingerle, can be demonstrated in many patients. Text-book photographs of gymnasts give ample evidence of the presence of similar neck righting reflexes in normal adults.

Our own experience teaches that the optical righting reflexes in man play a very important rôle. Of this many examples could be given. It is sufficient to remember that in aviation the exclusion of visual impressions

when the aeroplane is passing through mist or clouds makes orientation practically impossible. Often when the aviator emerges from the clouds and can once more see the ground, he finds that he has been completely disorientated with respect to the earth.

The 'zero condition,' in which all righting reflexes are suppressed, is realised if labyrinthless deaf-mutes are submerged under water. Then no body righting reflexes can be evoked, optical orientation is absent, and the labyrinths are functionless. As a consequence of this such patients will be drowned if no care is taken to help them out of the water.

Experiments of Garten and his pupils on an inclining chair clearly demonstrated the great influence of the body righting reflexes evoked by the contact with the surface of the seat. Even when labyrinthine impulses were made as ineffective as possible and the eyes were closed, there was a very precise estimation of the smallest deviations from the horizontal plane. It is a pity that his early death prevented Garten from completing this research and from placing his experimental subjects under 'zero conditions.'

As to the relative influence of the different sensory organs for orientation it can be said that optical and tactile influences play a very important rôle in man, whereas the part played by the labyrinths is probably less than in rabbits and guinea-pigs. These observations tend to show that in the mammalian series the rôle of the labyrinths decreases.

FINAL REMARKS

In concluding, I wish to draw your attention to the fact that the whole righting apparatus, with the only exception of the cortical centres for the optical righting reflexes, is arranged subcortically in the brain-stem, and in this way made independent of direct voluntary influences. The attitudinal as well as the righting reactions are involuntary. If under the influence of cortical impulses the normal position of the body be disturbed, the brain-stem apparatus is ready to restore it, so that every new cortical action finds the body in a normal starting position without previous voluntary effort.

By the action of the subcortical mechanisms described in these lectures the different sense organs are always brought into the normal relation with the external world. For the nerve-endings in the skin this is accomplished by the action of the above described attitudinal and righting reflexes. In the case of the eyes a very complicated reflex mechanism has been developed differing in various species of animals, which regulates the position of the eyes in relation to the environment. Here also labyrinthine and

neck reflexes come into play. The result of all these arrangements is that the sense organs are righted in relation to the external world, so that every sensory impression, before being transferred to the cortex cerebri, has already acquired a certain special condition (local sign) depending on the previous righting functions acting upon the whole body or parts of it. In this way the action of involuntary brain-stem centres plays a very important part in conscious activities, especially as regards spatial sensation.

All these things have not yet been worked out in detail, and as these lectures are addressed to an audience of students I am glad to say: There is work enough left for you to do!

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Minor typographical errors have been corrected for this edition.

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