

Animal Posture

Croonian Lecture

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Every movement starts from and ends in some posture, so that I think a discussion of ‘animal posture’ falls well within the scope of the intention of Dr William Croone, when he founded these annual Lectures to promote the study of ‘muscular motion.’ Before beginning I wish to emphasise how greatly I appreciate the honour of delivering before you this Lecture, and how I especially enjoy the pleasure of doing so with Sir Charles Sherrington in the Chair, who long ago took the trouble to introduce me to his beautiful methods of investigating the central nervous system, and to allow me an insight into his fruitful views on the function of nervous centres.

As it is impossible to consider the whole problem of posture in one short lecture, I propose to speak to you today on four partial problems, which are closely connected with each other, and which provided the starting points for investigations which have been carried out in my laboratory at Utrecht, with the aid of a great number of able collaborators. These partial problems are:

1. *Reflex standing.* In order to carry the weight of the body against the action of gravity, it is necessary that a certain set of muscles, the ‘standing muscles,’ should have by reflex action a certain degree of enduring tone, to prevent the body from falling down on the ground.
2. *Normal distribution of tone.* In the living animal not only do these standing muscles possess tone, but also the other muscles of the

body, especially their antagonists, *i. e.*, the flexors. Between these two sets of muscles a certain balance of tone exists, so that neither set of muscles gets too much or too little tone.

3. *Attitude.* The position of the different parts of the body must harmonise with each other; if one part of the body be displaced, the other parts also change in posture, so that different well-adapted attitudes, evoked by the first displacement, will result.
4. *Righting function.* If by its own active movements or by some outside force the body of an animal is brought out of the normal resting posture, then a series of reflexes are evoked, by which the normal position is reached again.

The main *centres* for all these four functions are situated in close neighbourhood subcortically in the brain-stem. Their function is to compound the activity of the whole body musculature to what we call '*posture.*' The lower centres for the muscles of the different parts of the body are arranged segmentally in the spinal cord; the higher centres in the brain-stem put them into combined action, and in this way govern the posture of the animal as a whole. We have here a very good example of what Sherrington has called the 'integrative action of the nervous system.' And integration is especially necessary in the case of posture, because nervous excitations arising from very different sense organs are flowing towards the postural centres in the brain-stem, and must be combined so that a harmonising effect will result.

Nervous impulses, which can influence posture, arise:

1. From the labyrinths, a double sense-organ: the otoliths reacting to changes in position, the ampullæ of the semicircular canals to accelerations;
2. from the proprioceptive sense-organs in muscles, joints and tendons;
3. from exteroceptive nerve endings of the body surface, chiefly from the pressure sense-organs, which are stimulated, if the body touches the ground;
4. from teleceptors, reacting to distance stimuli, such as the eye, the ear, the nose. In fact a very finely elaborated central apparatus is needed to combine and distribute all these afferent impulses, depending on and adapted to the always changing circumstances of environment.

After these introductory remarks we can turn to our subject itself and first discuss '*reflex standing*.' It is not necessary to go into any details about that problem before this Society, as we owe to your President the fundamental investigations which form the solid basis for all work on this question. So a few remarks will be sufficient.

If we try to put the body of a dead animal upon its feet, the carcass immediately falls down to the ground, because the relaxed muscles cannot carry the weight of the body against the action of gravity. The same happens with a living animal after total extirpation of the brain, so that only the spinal cord is in functional connection with the muscles. Such a 'spinal animal' can, of course, perform movements with a high degree of perfection. After pinching one foot, we see the limb retracted away from the stimulus; a spinal preparation, suspended in the air, will perform with its hind legs regular alternating movements resembling closely the running movements of the intact animal; by rubbing the skin gently a scratch reflex of apparently normal shape and frequency is evoked; distension of the lowest parts of the bowel causes all the complicated movements which accompany normal defecation. The centres of the spinal cord can indeed cause and regulate very complicated combinations of movements, but they are unable to give to the muscles that steady and enduring tone which is necessary for simple standing.

It has been shown by Sherrington that this state of affairs is fundamentally changed, if the spinal cord be in functional connection with the hind part of the bulb. By cutting across the brain-stem somewhere between the posterior half of the medulla oblongata and the foremost part of the mid-brain, the 'decerebrate rigidity' arises, in which the standing muscles acquire an abnormally high degree of tone. These anti-gravity muscles are the extensors of the limbs, the extensors of the back, the elevators of neck and tail, and the closing muscles of the jaw. The antagonists of these muscles, *i.e.*, the flexors, have, on the contrary, either no tone at all or an abnormally low degree of tone. The consequence is, that the decerebrate preparation will *stand*, if it has been put upon its feet, but stands *in an abnormal posture*, with exaggerated extension of limbs, neck and tail. The distribution of tone is an abnormal one. The stimuli inducing the enduring tone of the standing muscles in decerebrate rigidity arise from different sources, the proprioceptive sense-organs in the contracted muscles themselves laying the most prominent rôle.

In order to get a *normal distribution of tone* the presence of the foremost part of the mid-brain is necessary. By cutting the brain-stem somewhere in front of the mid-brain or by extirpation of the forebrain, so that

a 'mid-brain animal' or a 'thalamus animal' results, one gets preparations in which the standing muscles still have tone, but not an exaggerated one, as after decerebration, but a normal one as in intact animals. On the other hand, the flexors are no longer toneless, but have as much tone as a normal animal usually has.

A thalamus animal therefore will stand in a 'normal' posture and not in the hyperextended posture of the decerebrated preparation.

It has been found in careful experiments by Dr Rademaker in Utrecht, that the presence of the 'red nucleus' is essential for the change from decerebrate rigidity to normal distribution of tone, and that the rubro-spinal tract carries the impulses down to the spinal cord, by which this difference is called forth. In the thalamus animal the extensors of the limbs just have sufficient tension to balance the weight of the body against gravity, so that every force tending to raise or to lower the body can easily move it in one or the other direction.

The motor centres of the cortex cerebri have a similar but by no means so strong an influence, which is exerted by way of the pyramidal tract. They also tend to diminish decerebrate rigidity, but are much less important for this function than the system of the red nucleus.

I have discussed the problem of standing hitherto in a more general way, speaking of the body as a whole. Still more interesting is the investigation of the rôle which the different parts of the body, each for itself, play in the joint function of standing. The relation in position of all the parts of the body to each other forms the basis of *attitude*. In normal animals and man the positions of the different segments and parts are always in harmony, and it is easy even for a layman to detect what is a 'normal,' a 'pathological' or a 'caricature' posture. As soon as the position of one part changes, the other parts of the body also acquire a new position; the result is a new attitude, which in a normal individual is again harmonious.

The most fundamental attitudinal reflexes can best be studied in the decerebrate preparation. We put such an animal on its feet and pinch one hind foot; the stimulated limb is retracted from the ground and the hind part of the body is no longer carried by two, but only by one limb. Nevertheless, it does not fall, because together with the homolateral flexion reflex a crossed extension reflex of the opposite limb is evoked, by which the limb is strongly stretched and is able to carry the weight quite alone. This is what one could call a 'segmental' attitudinal reflex, in which only one segment of the body is concerned. Several segmental reflexes of that kind have been studied. But more important are the general attitudinal reflexes, by which the whole body is influenced.

It is noteworthy that these reflexes are most easily evoked from the foremost part of the body, from the head, in which the teleceptive sense organs are situated, so that distance stimuli influencing the position of the head can in this way also impress different attitudes upon the whole body. One can, in fact, in the decerebrate animal, by simply changing the position of the head, give to the body a great number of attitudes, resembling closely the normal harmonious attitudes of the intact animal. The analysis of these reactions, which I had the opportunity of effecting in cooperation with Dr A. de Kleyn, showed that they are the result of the combined action of two sets of reflexes, *tonic labyrinthine and tonic neck reflexes acting on the body muscles*. That is what one would expect, as in changing the position of the head one performs two separate things: 1) changing the position of the head *in space*, and therefore stimulating the otolithic apparatus; 2) changing the position of the head *in relation to the body*, therefore flexing or twisting the neck and stimulating the proprioceptors of the deep structures of the neck.

In order to study the tonic labyrinthine reflexes, one has to exclude the neck reflexes, either by cutting the first three posterior sensory roots or by bandaging head, neck and thorax, so that no neck movements are possible. If one brings such an animal into different positions in space, only one position of the head is found in which the tone of the standing muscles is maximal – supine position of the head, with the snout a little above the horizontal plane. There is another position of the head, differing from the first one by 180°, in which the tone of the standing muscles reaches a relative minimum, so that some tone is still present, but less than with the head in any other position. In all other positions of the head in space the tone of the standing muscles assumes values between those extremes. Under the influence of the tonic labyrinthine reflexes the tone of all the standing muscles always changes in the same direction. The flexors are influenced in the opposite direction. With maximal tone of the extensors the flexors are (in the decerebrate preparation) relaxed; with minimal tone of the extensors they may acquire some tension.

In order to study the tonic neck reflexes alone, one has to exclude labyrinthine reflexes by labyrinth extirpation. Under these conditions flexing, bending, twisting of the neck evokes tonic reflexes, in which usually one-half of the body reacts in an opposite way to the other, *e.g.*, the forelimbs being extended, the hind-limbs relaxed, and *vice versa*. But there are also neck reflexes, with which all four limbs react in the same sense.

If both sets of reflexes are present, the result is a very complicated one, because the same movement of the head in relation to the body will, with

different positions of the body in space, give rise to different labyrinthine reflexes; therefore one has to study the effects of all different movements of the head in all different positions of the body. It has been possible to refer all attitudinal reactions, observed in very numerous experiments, to the cooperation of labyrinthine and neck reflexes. The general rule is, that every group of muscles reacts to the algebraic sum of stimuli arising from the labyrinth and neck receptors, so that if the extensors of one forelimb, for example, get increased tone from both the labyrinths and the neck, the limb will be strongly stretched, whereas if it gets increased tone from the labyrinths and decreased tone from the neck, it may remain unchanged altogether.

The centres for these attitudinal reflexes are the most caudally situated ones of all postural centres: those for the tonic neck reflexes in the two highest cervical segments, those for the tonic labyrinthine reflexes in the hind part of the bulb, behind the plane of entrance of the VIII. cranial nerves. These reflexes are called tonic, because they last as long as the head keeps a certain position; and that not only for minutes and hours, but for days, months and even years. After unilateral labyrinth extirpation in the rabbit turning of the neck results, which evokes the normal tonic neck reflex, one forelimb being extended, the other flexed. If the other labyrinth is not extirpated in a second operation, in order to put the head right again, the turning of the head will last as long as the animal lives, and the tonic neck reflex at least several months. We are accustomed to believe that muscular action is liable to fatigue, and this, of course, is true for movements, and especially for movements performed against resistance. But muscular action concerned in keeping some part of the body in constant and unchanging position gives rise to much less fatigue, and the attitudinal tonic reflexes evoked from the head appear to be practically indefatigable.

Now the question arises, what use the normal, not decerebrated animal makes of these reflexes. A normal rabbit sits usually in a squatting posture with head down, forelimbs flexed and back curved. By taking the head and flexing it dorsally, so that the snout is raised, a combined labyrinthine and neck reflex is evoked, by which both forelimbs are strongly stretched, the fore part of the body raised and the back extended. It is not even necessary to initiate this reaction by a passive movement of the head. The latter can be made to move actively by means of the distance receptors. If a cat is sitting in a cage and a piece of meat is held low down near the ground, the animal fixes the food with its eyes, bends the head in the ventral direction, evokes labyrinthine and neck reflexes, which tend to

flex the forelimbs, and the whole body of the animal is in this way directed towards the food. By moving the meat upwards, one makes the animal follow the food with its eyes, flex the neck dorsally and give rise to labyrinthine and neck reflexes, by which the forelimbs are strongly extended, the fore part of the body raised; whereas in the hind limbs, neck and labyrinthine reflexes just compensate each other, so that no change in their posture occurs. The result is a somewhat 'monumental' attitude, by which the body of the animal is again directed towards the meat and at the same time brought into a posture which enables it to jump and to catch its prey.

Suppose a cat is standing in the middle of the room, and a mouse is running on its right side along the wall. The optic and acoustic stimuli act on the telereceptors of the cat's head, and make it turn the heavy head to the right. By this the centre of gravity of the fore part of the body is displaced to the right. At the same time tonic neck reflexes are evoked, by which the vertebral column is curved and the right forelimb strongly extended, so that it carries the weight of the body alone and prevents it from falling. The left forelimb has nothing to carry, and in harmony therewith this limb relaxes under the influence of the tonic neck reflex. At the same time the distribution of excitability in the motor centres of the spinal cord is rearranged by the turning of the neck, so that, if for some reason running movements begin, the limb which has no static function will always make the first step. In this way the moving mouse impresses on the cat through the mediation of tonic neck reflexes an attitude, by which the cat is focussed towards the mouse and made ready for movement. The only thing the cat has to do is to decide: to jump or not to jump; all other things have been prepared beforehand reflexly [reflexively] under the influence of the mouse, which will be the object of the resulting jump.

These examples may give an impression of the different ways in which the tonic labyrinthine and neck reflexes are used during the normal life of intact animals. They can easily be extended by watching various kinds of animals. Only in the monkey they cannot easily be detected, because with the higher development of the forebrain and the greater complication of movements these lower postural reflexes are partly suppressed. It is necessary to decerebrate or narcotise a monkey in order to show that he has the same attitudinal reflexes, obeying the same laws, as are shown by other animals.

Also, in man during ordinary life the attitudinal reflexes cannot easily be detected. In the infant child several of them are present. In adults instantaneous photographs show sometimes postures in agreement with the laws of attitudinal activity of the brain-stem centres. I owe to Dr Wolf

the acquaintance with fast cinema photos of golf players, showing that at the top of the swing the shoulders are turned by 180° in relation to the head, which is kept fixed in space as firmly as possible. In this way a tendency is evoked to extend the left arm and to twist the body to the left – movements which appear to be performed, indeed, by the subsequent photographs, and which seem to be facilitated and strengthened by the preliminary starting posture of the head and body. It is this fixing of the head in the line of sight of the ball which is insisted upon as essential to the performance of a correct shot.

Many masterpieces of painting or sculpture representing human beings are consistent with the laws of attitudinal reflexes. But under pathological conditions, especially if the function of parts of the cerebrum is disturbed, they are released, and are now used frequently by neurologists for diagnostic purposes. Thus, in some cases of chronic hydrocephalus, turning of the head causes the arm (or leg) towards which the face is turned, to be extended as long as the head keeps this position, but to relax as soon as the head turns to the other side. There are not so many cases in which tonic labyrinthine reflexes have been demonstrated with certainty; one of these was a patient with amaurotic idiocy, who exhibited in one position of the head in space flaccidity, in another strong tonic extension of both arms and legs, neck reflexes being excluded by firmly bandaging head, neck and thorax, so that no neck movements were possible.

Every change of attitude, with its different positions of all the parts of the body, changes the reflex excitability of these parts, and in some cases changes also the sense of the reflex evoked, excitations being converted into inhibitions, reflex extensions into flexions, and so on. One and the same stimulus applied to one and the same place on the body may give rise to very different reactions, in consequence of different attitudes which have been imposed to the body before the stimulus is applied. The laws governing such changes of reaction have been greatly elucidated, but the results are somewhat complicated, so that they cannot be summarized in a short lecture. Only one case may be mentioned. It sometimes happens that in consequence of shock or inhibition a certain movement of the head will not evoke the tonic neck reflex we should expect. In this case an indifferent stimulus, which under ordinary conditions would never evoke postural reactions, can induce the tonic reflex which the movement of the head was not able to provoke.

It is interesting that the same phenomenon has been found in human patients by two independent observers – Dr Simons of Berlin, and Dr Walshe of London. After shot-wounds of the brain, with consequent uni-

lateral paralysis, strong movements of the hand on the normal non-paralysed side evoke involuntary associated movements of the paralysed arm and leg. Turning of the head in many of these patients fails to give rise to direct tonic neck reflexes affecting the paralysed limbs, but influences the direction of the associated movements. If the face is turned towards the paralysed side the associated movement will be extension, whereas flexion results if the face is turned towards the sound side. In this way the position of the head determines the sense of movements caused by indifferent stimuli.

The foregoing examples are sufficient to give an impression of the importance of attitudinal reflexes in animals and human beings under normal and pathological conditions.

The decerebrate animal has no *righting function*. Put on its feet it stands, but if it receives a blow, it falls on its side and is unable to return to the normal standing position. The mid-brain animal behaves in a very different manner. Not only is the distribution of tone a normal one, but also the righting function is fully developed, and the animal is able, from all abnormal positions, to come back reflexly into the normal position. The reflexes which cooperate in attaining this result are the 'righting reflexes.' They can best be studied in the mid-brain animal, or thalamus animal, in which the forebrain has been removed, so that no voluntary corrections of abnormal sensations are possible. We have to deal with a pure reflex machinery of a very high degree of perfection.

The first group to be described are the *labyrinthine righting reflexes*, evoked from the otolithic apparatus and tending to bring the head into and to keep it in the normal position. In order to give an isolated demonstration, one has to hold the body of a thalamus animal (*e.g.* a rabbit) freely in the air, so that it does not touch the ground. Suppose the animal is held by the pelvis, one can turn the latter from one lateral position to the other and still the head is kept in normal position. The same holds good if the animal is hanging with head down, or if the pelvis is turned into [to] the supine position, and so on. What ever situation one gives to the hind part of the body, the head is kept, as by a magic force, in its normal position in space. This magic force is provided by the stimuli arising from the otolithic apparatus. By labyrinth extirpation, or by centrifuging away the otolithic membranes from their maculæ, these righting reflexes are abolished, the head is now absolutely disorientated in the air, and will remain in any position (lateral, supine position, and so on) according to the position of the hind part of the body.

Suppose I hold the pelvis of a delabyrinthized thalamus animal in the

lateral position in the air, then the head will remain also in the lateral position. The body is now placed (always in lateral position) on the floor. At the moment the body touches the ground, one sees the head righted into the normal position. This reaction is evoked by the asymmetric stimulation of the exteroceptive pressure sense organs of the body surface, as is proved by the fact that the head immediately goes back into the lateral position if a weighted board is put on the uppermost side of the body and the asymmetric stimulation by the ground thus compensated. After the board has been removed, the head is righted again; if the animal is taken away from the floor and held freely in the air, the head falls back into the lateral position. In this way contact with the ground rights the head (*body-righting reflexes acting on the head*).

Labyrinthine and exteroceptive stimuli cooperate in bringing the head into the normal position relative to space and environment. If the head has been righted by both or one of these influences, whereas the body remains in an abnormal (e.g. lateral) position, then the neck is twisted. This gives rise to excitation of the proprioceptive sense organs of the muscles (joints, tendons) in the neck, so that '*neck righting reflexes*' are evoked, which first make the thorax follow the head and right it into the normal position. Now the lumbar region of the trunk will be twisted, a new reflex caused, and finally the whole body will stand in normal position, following the head.

Our own experience and observations on animals show us, that these neck righting reflexes cannot be the only ones which guarantee the normal position of the body. The latter can stand and can right itself, even when the head is *not* kept in the normal position. So there must be some reflexes capable of righting the body if the head has not been righted beforehand. These reflexes exist and can easily be demonstrated. Hold an animal freely in the air and fix the head firmly in the lateral position. Then without resistance the body may easily be kept in lateral position. If the body now be put on the table, it is righted as soon as it touches the surface, in spite of the head being kept in lateral situation, and in spite of the neck righting reflexes tending to hold the body in the lateral position. The active stimulus is again the asymmetric pressure on the exteroceptors of the body surface, as can easily be proved by the use of a weighted board (*body righting reflexes acting on the body*).

In the case of this very important function everything is doubly secured. The head is righted by labyrinthine and exteroceptive reflexes; the body by proprioceptive and exteroceptive reflexes; exteroceptive stimuli control the normal position of head and body; so that, if one of these apparatuses

becomes paralysed, others will still be in function.

These four groups of righting reflexes are the only ones which can be demonstrated in the thalamus animal. Normal rabbits and guinea-pigs have no other righting reflexes. But the higher mammals such as cats, dogs and monkeys are, with intact cerebrum, in the possession of a fifth set of reflexes: the *optical righting reflexes*. To demonstrate them, one has to hold a delabyrinthized dog or monkey freely in the air; if the attention of the animal is attracted by something in its environment, and it therefore fixes the latter with its eyes, the head is immediately brought to the normal position and kept so as long as the optical attention is focussed on the subject. So a telereceptor has gained influence upon the righting apparatus. This is the only righting reflex having its centres not in the brain-stem but higher up in the cortex cerebri.

The multiplicity of reflexes, causing and maintaining the erect position, makes it intelligible how labyrinthless deaf-mutes can stand and walk without apparent disturbance. Only if brought under water, where the optical impressions cannot be used and no body righting reflexes can be evoked, they are completely disorientated and will be drowned if they are not helped out of the water.

It seems to be of the greatest importance, that the whole central apparatus for the righting function (with the only exception of that for the optical righting reflexes) is placed subcortically in the brain-stem and by this means withdrawn from all voluntary action. The cortex cerebri evokes during ordinary life a succession of phasic movements, which tend over and over again to disturb the normal resting posture. The brain-stem centres will in the meantime restore the disturbance and bring the body back into the normal posture, so that the next cortical impulse will find the body prepared to start again. It is also an essential condition for the right interpretation of all *sensory* impressions reaching the cortex, that the body be always brought into the normal position by a purely automatic subcortical arrangement, which controls the spacial relation of the body to its environment. In his last anniversary address your President called attention to the importance this arrangement possesses from a psychological point of view.

The knowledge of the righting reflexes permits a better understanding of many pathological and pharmacological conditions. A good example is presented by the asphyxial convulsions. Asphyxia stimulates motor centres in the spinal cord and the bulb. The effect of excitation of these centres varies, however, according to the state of excitability of the righting centres. If the latter are in good functional condition, then the animal will

run and jump; if they are semi-paralysed, the animal will roll over, turning over its back or its belly; if they are completely paralysed, it will lie on its side and show tonic and clonic convulsive fits. We have here the pharmacological parallel to the above-mentioned fact, that postural activities can modify the reactions of the body to subsequent indifferent stimuli.

Mr Versteegh of Utrecht, has studied the disturbance of motor coordination following the ingestion of alcohol in rabbits. At the time the first signs of intoxication appear, the righting reflexes acting on the head are normal, and also the body righting reflexes acting on the body. So the head is kept in normal position and the body is able to right itself. But the neck righting reflexes are paralysed, so that, if the head turns in the one or the other direction, the body does not follow, but goes its own way. The result is the characteristic unsteady gait of the intoxicated.

The time available does not allow me to go into details about the working of another extremely well-adjusted central apparatus which governs the positions of the eyes.

The resting position of the eyes is not a fixed one, but changes according to the different positions of the head. Therefore a fine regulation by means of the eye muscles becomes necessary, which have to be controlled by sensory impulses. In man and in animals with frontally arranged eyes, the two visual fields overlap, and one eye can therefore control the position of the other by means of optical impulses. This is impossible in animals with lateral eyes, whose visual fields are separate or overlap only slightly. Here a special non-optical reflex arrangement has been developed, which ensures that in the different position of the head the optical world is not displaced in an irregular way, but keeps a certain relation to the animal, and that the right and left halves of the visual world do not diverge.

This is accomplished, as has been shown by de Kleyn, by combined action of otolithic and neck reflexes, influencing the eye muscles. If a rabbit sits in the normal position, and then by movements not exceeding the normal range brings its head into another position, then the eyes move in the orbit so that the movement of the head is entirely compensated, and the eyes keep their position relative to space. So, in spite of head movements, the visual world does not move and the two halves of the visual environment of the animal do not diverge. This reaction is initiated by another reflex. If the animal brings the head into a new *position*, it makes a *movement*, and, in doing this, stimulates the ampullae of the semicircular canals, which gives rise to short-lasting motor reflexes acting on the eye muscles. If the animal is in the normal position the movements of the eye-balls, evoked by these reflexes, are always carried out in such a direc-

tion that the *bulbus oculi* is brought into just that position in which it will then be fixed by the compensatory static reflexes which have just been described. The canals begin, the otoliths and neck receptors complete and steady the reaction: a very finely adapted mechanism indeed. The same connection between motor and static activities has been found also in many other postural reactions, as recently in the myotactic reflexes of Liddell and Sherrington.

In this case also as in the case of the righting reflexes an unconscious subcortical mechanism brings the eyes into the right position, so that the optical impressions to be transmitted to the cortical centres carry with themselves the correct spacial basis, prepared for them in advance and – in the case of the rabbit – almost independent of optical stimuli.

The centres regulating the postural functions described are arranged in the brain-stem in three functional groups:

1. the centres of the attitudinal reflexes behind the plane of entrance of the VIII. nerves;
2. the centres of the eye-reactions between the entrance of the sensory nerves concerned and the eye-muscle nuclei;
3. the centres of the righting reflexes (with the sole exception of the optical righting centres in the cortex) in the mid-brain.

Of the latter, the neck righting centres extend as far down as to the pons and upper part of the bulb, whereas the other righting centres lie at the level of the red nucleus. As Rademaker has shown, the nucleus ruber is indeed the centre for the labyrinth righting reflexes and for the body righting reflexes acting on the body, but not for the body righting reflexes acting on the head. The efferent path of the two first named reflexes is the rubro-spinal bundle, the afferent tracts have still to be found. Thus a first beginning has been made towards translating the physiological facts into anatomical language, and we hope that still further progress will be possible in this direction.

With the exception of the optical righting reflexes, all the reactions described in this lecture have been found to be present in all species of mammals investigated (guinea-pig, rabbit, cat, dog, monkey) and many of them in other vertebrates too. But the use which the different sorts of animals make of these reflexes is very different, and the relative importance of one or the other group of postural reflexes for various species also varies widely. This seems self-evident, if one compares, *e.g.* the simple shape and limited movements of a guinea-pig with the very complicated movements

of such an elegant springing and climbing animal as the monkey. Generally speaking, the relative importance of labyrinthine reflexes decreases with increasing development, so that guinea-pigs and rabbits have very strong, monkeys and men much less preponderant labyrinthine reactions, while in the monkey the reactions evoked by means of the eyes and by touch and pressure to the exteroceptive nerves play a very prominent role.

The short review which I have been able to give you of the present status of some parts of postural physiology shows that the action of the bulbar and midbrain centres can now be understood in their principal lines, and that the points are known at which still further investigation of detail is wanted. But this picture would be faulty, if it gave you the impression that the whole problem of animal posture had been solved. That is by no means the case. Besides the medulla oblongata and the mid-brain there are other parts of the brain, which have probably also an influence on body posture. Their physiology is unfortunately more or less unexplored. In the first place the *striatum* and *pallidum* may be mentioned in this connection. Neurologists are at the present time greatly interested in these parts of the brain-stem, because in several diseases, such as Parkinson's and Wilson's disease and in certain forms of encephalitis, severe lesions are usually found post-mortem in the basal ganglia. In these diseases postural disturbances play a prominent role. Consequently in neurological literature one encounters a general belief in the postural functions of these centres. Unfortunately in most cases also other parts of the brain are found to be involved. Besides that, neither extirpation nor stimulation of the basal ganglia has given any evidence of postural influences arising in the striatum and pallidum. Our knowledge therefore of the role which these centres may perhaps play in the maintenance of posture is at most very restricted.

Still worse perhaps is the situation with regard to another very important part of the brain, the *cerebellum*. Experiments have proved that all postural reflexes discussed in this lecture are present and perfectly undisturbed after total extirpation of the cerebellum. Therefore their centres as well as their afferent and efferent tracts are extracerebellar. Through the brilliant investigations of Luciani and others we know that loss of the cerebellum is followed by severe motor and postural disturbances. These symptoms, however, cannot depend on the cerebellum, which has been removed, but are evoked by the rest of the central nervous system, which has been spared. Unfortunately we know not a single function or reflex positively connected with the cerebellum, in such way that it is absent after cerebellar extirpation, and present after ablation of other parts of the

brain, as long as the cerebellum remains uninjured. Our evidence of the postural activity of the cerebellum is purely negative. The great advantage during the investigation of the postural functions of bulb and mid-brain was, that we could there deal with positive reflexes (righting and attitudinal) which are present as long as the hind part of the brain-stem is intact. I am convinced that as soon as we succeed in finding positive reflexes connected with the cerebellum, it will be possible to elucidate the mystery of this undoubtedly very important part of the central nervous system. Only then can the question of the importance of the different *cortical* centres for posture be raised.

In the study of posture therefore it is the same as in other parts of science. Every step of progress makes it possible in formulate new questions and to delimit anew the bounds of the unknown. In proceeding, one reaches summits which do but open new prospects over vast fields yet to be explored.

Minor typographical errors have been corrected for this edition.

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