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Cameron Prize Lectures

ON

SOME RESULTS OF STUDIES IN THE PHYSIOLOGY OF POSTURE.

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BY RUDOLPH MAGNUS,

PROFESSOR OF PHARMACOLOGY, UNIVERSITY OF UTRECHT.

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 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 fore-brain 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 fore-brain 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 coöperation 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 mechanisms 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 coöperation 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

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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 maculæ 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 into symmetrical 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 maculæ sacculi. 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 the 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 (blindfolded 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, &c., 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 coöperate 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 fore-part of the body follows the head, whereas the pelvis is prevented from doing so by the hand 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, &c.

(*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, &c. 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 coöperate 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 coöperate 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, &c.), distant environment (optical), and to parts of the body—a very complex combination of reflexes. It is indeed an interesting task to watch the coöperation 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 remarkable 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 fore-brain 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 coöperate 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 sensations.

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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