The Physiology of Posture

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(Abstracted by Dr J. S. Fraser, F.R.C.S.E.)

THE study of the physiology of posture is of relatively recent date and is largely due to the work of Sherrington. Posture is an active process resulting from the co-operation of a great number of reflexes, many of which have a tonic character. Magnus groups postural activities under the following headings: (1) Local static reactions: (2) Segmental static reactions: (3) General static reactions. He also distinguishes (*a*) static reactions of the oblongata animal (decerebrate preparation) in which the spinal cord is in connection 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 co-operate.

1. Local Static Reactions—A limb may be used for different purposes, *e.g.* fighting, in which it is moved freely at all joints, or it may be transformed into a stiff *pillar*, to carry the weight of the body; this is accomplished by a series of local static reflexes. The whole process is known as the *supporting reaction.* The passage 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.*

The Positive Supporting Reaction.—The effective stimulus for this reflex is (in the case of the fore-limbs of the cat) stretching of the flexor muscles of the fingers and hands; stimuli from the pads of the toes co-operate to the same effect. In standing, the ligaments of the leg are only of secondary importance. The muscles support each part of the limb and the body as a whole, and are brought into tonic contraction by impulses from the central nervous system. In deep narcosis it is impossible, by changing the position of its most distal part, to transform the limb into a supporting pillar.

The *myotatic reflexes* of Liddell and Sherrington are of great importance. These authors found, in decerebrate preparations, tonic reflex contractions caused especially in the extensor muscles by even slight stretch of the muscle. The contraction is just sufficient to counterbalance the stretch. This myotatic reflex comes into play in the flexor muscles of the hand and fingers of the cat, which are stretched during standing. Further, 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 forearm, so that we have to deal with synergistic reinforcement of tonic contraction. Sherrington has shown that in ordinary *movements* antagonistic muscles obey the law of reciprocal innervation, *e.g.* flexion of the hand is accomplished by contraction of the flexors and simultaneous relaxation of the extensors; but, in the supporting reflex, the antagonistic muscles exert a synergistic function (simultaneous contraction of both flexors and extensors) and the result is *fixation of the joint.* The elbow also becomes

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fixed. Fixation against flexion is accomplished because the flexors of fingers and hand take origin from the epicondylus medialis humeri, and will therefore, if stretched during standing, cause fixation of the elbow directly by myotatic reflexes. Further dorsiflexion of the hand and fingers gives rise to reflex contraction of the triceps. Fixation against extension is secured by a reflex contraction of the biceps caused by the dorsiflexion of the hand and fingers, reinforced by a reflex from the stretched triceps. In much the same way the shoulder-joint is fixed and the scapula kept in contact with the thorax.

2. Segmental Static Reactions.—These need not be considered.

3. General Static Reactions.—In the "decerebrate" preparation the hind part of the bulb has been left in functional connection with the spinal cord. The "decerebrate rigidity" now develops and is characterised by a strong tonic contraction of the "antigravity" muscles, viz., the extensors of the limbs and back, the elevators of the neck and tail, and the closing muscles of the jaw. Their antagonists, the flexors, have either a very slight tone or even none at all. If placed on its feet the decerebrate preparation will stand, but the posture of the animal becomes abnormal. "Decerebrate rigidity" is a reflex phenomenon. The chief stimuli arise in the proprioceptive sense organs of the contracted muscles themselves.

A. General Static Reactions of the Decerebrate Preparation.

Tonic Labyrinthine Reflexes.—The neck reflexes must be excluded by cutting on both sides the three first cervical posterior roots or by immobilising head, neck and thorax by a strong plaster-jacket. The fore-limbs are left unrestrained. The extensor tone becomes maximal in the supine position, with snout about 45° above the horizontal plane. The minimum and maximum positions differ by 180°. In all other positions the extensor tone is intermediate. These reflexes last as long as a certain position is maintained. They disappear after bilateral labyrinth extirpation. A delabyrinthised decerebrated cat, in which the neck has been immobilised by a plaster bandage, can be brought into all possible positions without any change in the tone of the limb muscles.

The tonic labyrinthine reflexes arise from the otolithic organs. When guinea-pigs under ether are centrifuged at high speed, the otolithic membranes are detached by centrifugal force, whereas the canals remain intact. 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 two maculæ utriculi are situated in the same plane, which is nearly horizontal, when the animal carries its head in the normal position. The two maculæ sacculi form an angle of rather less than 90° with the utricular maculæ and face towards the lateral side. 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 of the utricle. The centres of the tonic labyrinthine reflexes upon the limb muscles have their position in the hind part of the bulb, behind the entrance of the 8th nerves. The utricular macula sends impulses to the limbs of both sides,

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but to the neck muscles of the crossed side only. Unilateral labyrinth extirpation is therefore followed by turning of the neck. 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.

In the intact animal the flexor muscles also have tone and react to the tonic neck and labyrinthine reflexes. Increase of extensor tone is associated with diminished flexor tone and vice versâ. In this way the attitudinal reflexes of intact animals are much smoother than the stiff and always exaggerated attitudes of the decerebrate preparation. In man the presence of attitudinal reflexes in ordinary life is not striking, but in a certain percentage of babies the influence of head rotation upon arms and legs can be seen. In pathological conditions attitudinal reactions in man may become evident, especially when disease has interfered with the function of the higher parts of the brain, *e.g.* head rotation may cause extension of the jaw-limbs, accompanied by relaxation of the skull limbs.

B. General Static Reactions of the Mid-Brain Animal.

(1) After cross-section through the calamus scriptorius the animal behaves like a spinal preparation without static functions (only the tonic neck reflexes are present). (2) After section just in front of the entrance of the 8th nerves, the animal shows decerebrate rigidity and has active tonic neck and labyrinthine reflexes. (3) This picture remains in the main unchanged if the cutting of the brain-stem is performed more orally, though reflexes on the abducens and trochlearis nerves appear. (4) The general condition does not change fundamentally, until the section is made through the most oral part of the mid-brain in front of the origin of the oculo-motor 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. (5) If the sections are made more orally, no *essential* differences in the static behaviour can be observed. It makes no appreciable difference whether the basal ganglia are present or have been extirpated. (6) If the fore-brain is left intact the influence of optic stimuli upon posture in some species of animal can be demonstrated.

The most convenient way to study all static reactions of the mid-brain animal is to make a thalamus preparation, in which voluntary movements are eliminated.

The Righting Reflexes.—The righting function is carried out by the co-operation of five groups of different reflexes. 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.

(*a*) *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. No attempt is now made by active movements to bring the head or the body into the normal position. (The "zero condition" of animals with *intact* cerebrum differs according to species. Rabbits and

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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.)

(*b*) *Labyrinthine Righting Reflexes.*—If the 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 pelvis is held in all possible positions the head is always brought into 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.

(1) The *asymmetrical righting reflexes* bring the head from asymmetrical, *e.g.* lateral, positions into symmetrical positions about the vertical plane and 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, which do lie in one plane, cannot be responsible for these reflexes.

(2) The *symmetrical righting reflexes* provide that out of all possible symmetrical positions the normal position is taken. The maximum of stimulation in the macular epithelium is 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. 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.*—We start 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. The reflex is evoked by the asymmetrical 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. The head then falls back into the lateral position. If the board is taken away the head is again righted. If the animal be lifted from the ground, the head returns to the lateral position. These reflexes can also be evoked from the soles or palms, and in this way the heads of climbing animals, such as monkeys, squirrels, etc., are orientated. After unilateral labyrinthectomy the rotation of the head becomes greatly diminished if the animal be placed on the ground.

(*d*) *The Neck Righting Reflexes* orientate the body in relation to the head. When, by the labyrinthine and body righting reflexes, the head is restored to the normal position, while the trunk still remains in the lateral position, the neck is twisted. This evokes a reflex by which the

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thorax is brought into asymmetry with the head. Rotation of the lumbar region in turn causes a similar reflex upon the hind part of the body, so that finally the whole body assumes the normal sitting position. These reflexes can also be demonstrated in the supine position; movements of the head then evoke marked reactions upon the hind part of the body. Simple movements of the head bring the body of even very strong animals on its side (sitting on a horse's head, Abs.).

(*e*) *The Body Righting Reflexes acting on the body* right the body in relation to the ground, even if the head is not in the normal position. We first hold a normal animal in the lateral position in the air, the head also being kept lateral. If now the animal is placed upon the table and the head kept lateral, 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 sensory nerve-endings of the body are stimulated asymmetrically by the pressure against the ground.

(*f*) *Optical Righting Reflexes.*—The four groups of reflexes described above are the only righting reflexes of the thalamus animal, and also of intact rabbits and guinea-pigs. In higher mammals, such as cats or monkeys, with intact cerebrum, the eyes contribute towards the orientation of the head. If the delabyrinthised cats are examined freely in the air, the head, if blind-folded, shows no correction from any abnormal position. If the eyes are opened, the head is brought into the normal position as soon as the animal fixes its eyes on something in its environment, such as food. The position of the centres for these reflexes are probably localised in the optical cortex.

All these reflexes co-operate in the intact animal, and enable the body to attain and keep a certain position. 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 Centres for the Righting Reflexes.

The centres for the righting reflexes have been determined by Rademaker, by transverse sections through the brain-stem at different levels. In the cat and rabbit the red nuclei are the centres for the labyrinthine and also for the body righting reflexes acting on the body. The efferent path for these reflexes is the rubro-spinal tract. 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, as total extirpation of the cerebellum leaves all righting reflexes, including the body righting reflexes, intact. In the thalamus animal extirpation of the red nuclei or isolated severance of the rubro-spinal tracts 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. If, in addition to the rubro-spinal bundles, the pyramidal tracts are also severed, there follows a marked increase

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of extensor tone. The pyramidal tract has therefore 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 are 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 their right share.

Righting Reflexes in Man.

Labyrinthine righting reflexes can be demonstrated in children who are blind-folded and held by the pelvis in different positions in the air. Neck righting reflexes are very active in man. Babies in the prone position usually bring the head by dorsiflexion into the normal position; this is followed by lordosis of the vertebral column with extension of the limbs. Passive ventroflexion of the head causes disappearance of the lordosis. Rotation of the baby's head causes the body to roll from the supine into the lateral position. The optical righting reflexes in man play a very important rôle. In aviation the exclusion of visual impressions when the aeroplane is passing through clouds makes orientation practically impossible. 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. Such patients will be drowned if no care is taken to help them out of the water. In the mammalian series the rôle of the labyrinths decreases; in man it is less than in rabbits and guinea-pigs.

The whole righting apparatus, with the 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. If under the influence of cortical impulses the normal position of the body is disturbed, the brain-stem apparatus is ready to restore it.

REVIEW OF BOOK

Pathology and Treatment of the Inflammatory Diseases of the Nasal Accessory Sinuses. By Professor Dr M. Hajek, Chief of the Laryngo-Rhino-Otological Clinic, University of Vienna. Translated and edited by Joseph D. Heitgar, B.A., M.D., Louisville, Kentucky, and French K. Hansel, M.D., M.S., St Louis, Missouri. Fifth Edition, completely revised and enlarged, in 2 volumes, 702 pages, with 7 plates and 185 figures in the text. London: Henry Kimpton. 1926. Price 75s. net.

THE publication of this work in English forms a landmark in the history of British rhinology. The book was originally published in 1898, and four editions appeared prior to the war. We have had to wait nearly thirty years before having in our language the views of

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