Reflex Regulation of Posture.[1]

By Dr. F. M. R. WALSHE.

TO those interested in the physiology of the nervous system, the history of our knowledge of the neuro-muscular mechanisms underlying posture must form one of the most fascinating chapters in the records of the science, and it is but fitting that any account of it should be prefaced by an expression of homage to Sir Charles Sherrington, to whose labours we owe the entire foundation of that knowledge.

Sherrington's investigations, in the course of which muscle tonus has been revealed as a purposive reflex reaction and the basis of all postural activity on the part of the musculature, are now thoroughly embodied in physiological thought and do not require detailed reference. It is of interest, however, when we recall the vicissitudes through which the term 'tonus' and our conceptions of muscle tone have passed to refer briefly to the experimental preparation which in the hands of Sherrington, and later in those of Magnus of Utrecht, has provided the key to the elucidation of those intricate neuro-muscular processes which underlie reflex posture. I refer to the decerebrate preparation. Prior to its discovery and description the nature, and even the very existence, of muscle tonus were subjects of conflicting opinion and observation. Numerous investigators had sought for this peculiarly elusive form of muscular activity in the single muscles of cold-blooded animals, and such glimpses of it as had been gained were too restricted in extent and too fugitive for any clue to its nature to be apparent. "To glimpse at the aim of a reflex," as Sherrington has remarked, "is to gain hints for further experimentation on it . . . the larger the muscular field involved in the reflex effect, the plainer usually its purpose."

The decerebrate cat is an animal in which the brain stem has been severed in the region of the tentorium, the section putting out of action all that part of the brain, including the forebrain, which lies anterior to the posterior corpora quadrigemina. Such a preparation may be called a ponto-spinal animal. Following this procedure, there appears an abnormally heightened tonus selectively distributed in those muscles which maintain the animal in its habitual standing posture—in other words, in the group of 'antigravity muscles.' This hypertonus has been called 'decerebrate rigidity,' and its intensity and characteristic incidence throughout the skeletal musculature have made possible a minute analysis not alone of the origin and nature of muscle tone, but also of its significance. Decerebrate rigidity is reflex standing. It will be apparent, therefore, that the discovery of this preparation opened a new and most fruitful era in the physiology of the nervous system.

Briefly, we have in muscle tone an enduring reflex muscular contraction of low intensity, endowed with a quality of plasticity in virtue of which the muscle can maintain a steady tension at varying muscle lengths, and readily overset transiently by intercurrent reflex reactions of phasic or movement type. It is a proprioceptive reaction, the stimulus arising in the muscle engaged in the reflex and consisting of those variations in tension produced by the voluntary motor activities of the animal (Sherrington and Liddell). It is believed that the tonic contraction is of the same nature, and is a function of the same elements in the striated muscle fibre as that seen in the muscle engaged in movement (phasic contraction), its peculiar qualities depending on the fact that now the elements respond in rotation, groups of individual muscles giving asynchronous series of responses.

In that beautiful analysis of reflex reaction which Sherrington has embodied in his book, "The Integrative Action of the Nervous System," he has pointed out that the skeletal musculature is controlled by two great reflex systems, which in the intact animal are in turn controlled by the cerebral cortex. Each system influences its own groups of the musculature, employing them in characteristic fashion. One system, the phasic system, is concerned with short-lived muscular movements and the arcs involved are predominantly spinal. The flexion reflex is a typical example in the group. The other, or tonic, system with which we are now concerned maintains and regulates that steady tonus or tonic contraction which is the basis, the raw material, of posture. Between the two systems there is a close and harmonious relationship, or, in Hughlings Jackson's apt phrase, "a perfect co-operation of antagonism." Every movement starts from and ends in a posture, and even the most superficial observation of some voluntary purposive movement betrays the existence of these two elements. For the effective performance of some movement of a limb it is essential that the organism as a whole should be oriented with reference to gravity and other external forces. The minute experimental analysis of muscular movement confirms this impression and has revealed the activity of the two systems mentioned above.

The tonic reflex system includes the autogenous reaction in the muscle which we call muscle tone, and also a complex series of controlling reactions by means of which tone is adapted to follow up the numerous and diverse movements made by the intact animal.

These regulating tonic reactions arise in the otolith organs of the labyrinths, in proprioceptive nerve endings in the muscles and tendons throughout wide regions of the body, and also in the nerve endings in the body wall which subserve the sense of pressure.

In 1909, as he relates, Magnus chanced to be working with a decerebrate preparation and noticed when he turned the animal from the lateral into the supine position that the extensor hypertonus of its limbs underwent an appreciable increase with the adoption by the limb of an attitude of more complete extension. Further, when the head was so flexed upon the trunk that the line of the mouth made an angle of 45° above the horizontal, an additional increase was seen to set in after a latent period of several seconds. These modifications of tone, and afterwards of limb posture, persisted so long as the new position of the head which had given rise to them was maintained.

[1] Opening paper of a discussion on "Reflex Posture" before Section I (Physiology) of the British Association at Oxford, August 9.

Simultaneously and independently, Sherrington observed that with the animal in a fixed position, rotation of the head to one side caused a similar increase of extensor tonus in the two limbs of the side to which the snout pointed. Extirpation of the labyrinths left the reaction intact, but division of certain cervical posterior roots abolished it. It therefore arose in proprioceptors in the neck musculature.

These observations formed the starting-point of Magnus's great work upon reflex posture, and have resulted in the discovery and classification of an extremely complex series of tonic reactions, which in sum make up the nervous mechanism by which normal postural activity is attained. In addition, Magnus has revealed the existence of a group of phasic reactions arising in the semicircular canals, and these with the tonic reflexes under discussion constitute the whole reflex mechanism of normal co-ordinated muscular activity.

Magnus and de Kleijn found that by imposing variations in the position of the animal's head in relation to the horizontal plane of space certain constant modifications of limb tonus, and therefore limb posture, could be produced. Further, after bilateral labyrinth destruction, variations of head posture in relation to the trunk also elicited certain other constant tonic reactions. These two groups are the so-called tonic labyrinthine and neck reflexes and together make up a group of 'standing reflexes.' By appropriate manipulation of the head by the observer, the animal can be made to take up a wide range of attitudes, corresponding to those habitually adopted by the animal during life. They found, however, that although it could stand, the decerebrate animal, if overturned, lay like a log and had no power of reflex control over the posture of its head. It was clear, therefore, that there must exist in the intact animal other tonic reactions governing head posture. Transection of the brain stem immediately anterior to the mid-brain led to the discovery of these other reactions. The mid-brain animal, for so such a preparation is called, does not exhibit hypertonus, but tone of normal intensity. It can stand, walk, and jump, and if overturned at once actively reassumes the normal sitting posture. If thrown from a height it lands upon its feet. The reactions by which these results are obtained are purely reflex, and the animal is a reflex automaton.

Further analysis of the preparation's activities has revealed the existence of a group of labyrinthine, neck and body 'righting reflexes,' in virtue of which the animal is able to maintain its head right side up in the world. This righting of the head sets in train secondarily all the other reactions by which the trunk and limbs are in turn brought into line with the head. Slow motion kinematograph photographs of the cat falling through space reveal the successive tonic and semicircular canal reflexes described by Magnus and his collaborators. First the head is righted, the anterior and the posterior portions of the trunk follow in turn, and finally, in virtue of phasic semicircular canal reactions, the limbs are outstretched so as adequately to receive the body weight as the animal reaches the ground. The ease and accuracy with which each of the various tonic and phasic reactions separately analysed by Magnus can be followed in such photographs are the most convincing demonstration of the minute accuracy of his observations.

In apes there is added to these labyrinthine and proprioceptive reactions a group of retinal righting reflexes of tonic character.

The reflex arcs of the various reactions we have been considering lie entirely within the limits of spinal cord and brain stem and do not pass through the cerebellum or basal ganglia. There is laid down, then, in the central nervous axis of the animal a mechanism which makes possible all the phasic and postural activities of the intact animal. By an automatic mechanism the animal is kept right side up in the world.

It is to observations made at the bedside by the clinician that we must turn to determine whether or not the laws governing the regulation of posture in a wide range of animal forms—from guinea-pig to ape—hold also for man. The evidence accumulated during the past fifteen years goes conclusively to show that they do.

Warned by the difficulties which the pioneer investigators met with in their animal experiments, the clinician has sought for a form of hypertonus resembling experimentally produced decerebrate rigidity. The student of nervous diseases is familiar with several forms of tonic muscular contraction of considerable intensity, but all except one of these may readily be dismissed as bearing no resemblance to the condition in question. It might be thought that in man a condition of decerebration is not compatible with continued existence, and indeed complete bilateral decerebrate rigidity is one of the rarest observed phenomena. We have, however, in the hypertonus, or spasticity, of the residual hemiplegia left after a cerebral hæmorrhage or softening, a unilateral state of tonic muscular spasm in the limb muscles which is manifestly qualitatively identical with decerebrate rigidity. It arises as a proprioceptive reflex in the muscle concerned, and destruction of the muscle's afferent nerve supply abolishes it. It is plastic, and easily overturned by the same phasic reflexes as have this effect in the animal. It may persist undiminished for years. It has a selective incidence in the limb musculature: in the extensor, or antigravity, muscles of the legs, but in the flexors of the arms. This altered incidence in the upper limbs of man is related to the profoundly altered functions of the fore limbs in this erect animal, and the reasons for so thinking need not now concern us. Further, it has recently been shown that the tonic neck and labyrinthine reflexes of Magnus and de Kleijn may be present in these rigid and paralysed limbs, following the same rules which govern their occurrence and form in the decerebrate animal.

In addition it has been possible to recognise in a very familiar clinical phenomenon the existence of another group of tonic reflexes, arising in the proprioceptors of the normal limb and acting upon the paralysed limbs. It has long been known, and every hemiplegic subject soon discovers the fact for himself, that when with the normal arm the subject makes some forceful, tonically sustained, voluntary movement, the contralateral paralysed limb goes into strong tonic spasm and takes up a new attitude, which is sustained for so long as the voluntary muscular act evoking it. The form, latency, and duration of this so-called 'associated movement' shows it to be a tonic reflex of the same type as those described by Magnus. Further, in favourable cases, a beautiful interaction between labyrinthine, neck and limb reactions may be observed if we combine changes in the position of the subject's head both in relation to space and to his trunk.

It is clear, in short, that the tonic reactions of Sherrington and of Magnus are present in the human subject. In a single personally observed case of complete decerebrate rigidity in the human subject, in which physiological 'decerebration' was performed by a tumour compressing the mid-brain, a perfect decerebrate rigidity with tonic neck reflexes and phasic flexion and crossed extension reflexes were obtainable.

These observations upon the subjects of disease and injury of the nervous system are of a double interest. They serve to correlate the work of the experimental physiologist with that of the clinical observer, they bring the human subject into line with animals lower in the scale. Further, they illustrate the value to the clinician of experimental physiology. For many years the labours of clinical neurologists have accumulated a vast mass of 'physical signs' of disease, which have been used empirically as aids to diagnosis; but so far as possessing other meaning was concerned they remained like the jumbled pieces of a mosaic. Thanks to the light received from the physiological laboratory, it is now possible to piece them together into a coherent and intelligible pattern, and they have become manifestations of a dissolution of nervous function, pregnant with physiological significance. Thus may the clinician not only derive information of inestimable value to him in his analysis of the phenomena of disease, but he may also, in a measure, repay some of his debt to the physiologist by carrying over the latter's animal observations to man.

Some Recent Advances in Astrophysics.[1]

By Prof. E. A. MILNE, F.R.S.

OF late years astronomers have become increasingly despairing as to what the stars are doing—in what direction they are evolving, how they produce the energy they radiate, whether (and if so why) some of them pulsate, how the stars are born and whether they die. At the same time astronomers have become increasingly confident as to what the stars are really like. It is proposed here to deal briefly with one province of this less speculative side of astrophysics, namely, that which is described, broadly speaking, as the subject of stellar temperatures and stellar spectra.

What are called the 'effective temperatures' of the stars have been determined by measurement of their colour, much in the same way as the temperature of a piece of red-hot iron may be estimated from its colour. With the piece of iron, we may measure either the total radiation leaving each square centimetre of its surface, or the ratio of the intensities of radiation for two different constituents of its spectrum. From either of these measurements we may infer the other. Both types of measurement are possible for the sun, and by the work of Abbot, Plaskett, and Fabry and Buisson, they have been shown to be in general agreement. For the stars in general, only the colour type of measurement is possible. It is true that of recent years the heat radiated by the stars has been measured directly, but such measures by themselves yield no more information than a determination of apparent magnitude. Colour-measures, however, by the use of Planck's law, yield the amount of radiation leaving each square centimetre of the star's surface—a quantity expressed parametrically by the effective temperature, or surface brightness.

The importance of this quantity lies in the fact that the total radiation leaving the surface per second is precisely the amount generated in the interior per second, assuming a quasi-steady state. Two examples of its employment in fundamental calculations may be mentioned. The amount of light from a star (a quantity given by the apparent magnitude) reaching the earth is equal to the product of the surface brightness into the solid angle subtended by the star. Hence a determination of surface brightness plus one of apparent magnitude is equivalent to a determination of the angular diameter of the star as seen in the sky from the earth. The confirmation of such estimates by the direct measurement of angular diameters at Mount Wilson by means of the Michelson interferometer affords a useful check on one of the steps in the reasoning, namely, the deduction of radiation per unit area per second from an observation of colour. The second example is that of the estimate of the densities of the components of a double star. The density-ratio of the components may be readily calculated in terms of the ratio of the surface brightnesses, the mass-ratio, and the difference of the apparent magnitudes. In this way it was inferred that the companion of Sirius must have a density some 60,000–70,000 times that of Sirius itself, and the verification of this by Adams at Mount Wilson, by measurements of the Einstein shift in the lines of the spectrum, has been one of the most sensational scientific events of the past year.

The effective temperature, however, is not the temperature of any particular portion of the star. The question arises, Is there any method of determining the actual temperature in the surface regions of a star, which alone we can directly observe? Have we a thermometer? The answer is in the affirmative. We can use the atoms volatilised in the atmosphere of a star as their own thermometer, by observing the absorption spectrum they produce.

The theory depends on the recent progress in atomic physics. It has long been known that the spectra of the great majority of stars fall into a single linear sequence, in which, as we pass by ascending effective temperatures from the red stars to the blue stars, some lines decrease in intensity, others increase, attain a maximum and decrease, others again only appear far on

[1] Substance of a lecture delivered before the Manchester Literary and Philosophical Society on October 19.