In all of these subjects the blood calcium and phosphorus was normal.

The significance of these findings and their possible relation to parathyroid activity is being further investigated on cases of myxedema, adenoma of the thyroid, parathyroid tetany, and on animals.

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The mechanism of the postural contraction (tonus) of skeletal muscle.

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Those who find inadequate the belief that the sympathetic nervous system controls the tonus of skeletal muscle have been confronted by the difficulty of offering an alternative view satisfactory to themselves and to their opponents. It is the purpose of this communication to suggest a mechanism of tonic contraction compatible with the all-or-none principle of muscular activity. The present conception takes due account of the long-sustained character of postural reactions; it recognizes the lengthening and shortening reactions, and it conforms with the well-recognized cooperative interaction between voluntary and tonic responses. Finally, it takes into account the probable function subserved by the sympathetic nerve supply of skeletal muscle

To examine tonic reactions of skeletal muscle, it is essential to simplify experimental conditions to the greatest possible extent. Consequently, if we utilize the muscles of a decerebrate preparation, which are admittedly tonic, we must exclude all possible extraneous reflex influence. Magnus[1] has found that decerebrate rigidity continues to exist in preparation, the brain-stem of which has been sectioned just above the vestibular nuclei and in

[1] Magnus, R., "Körperstellung," Berlin, Springer, 1924.

which the VIIIth cranial and the I, II, and III cervical nerves on both sides have been severed. The rigidity of a decerebrate preparation continues to exist after complete denervation of the skin in any given limb, and in any given extensor muscle, after section of all nerves except the nerve supplying that muscle. If one examines the vastocrureus muscle of a decerebrate preparation, the skin and all other muscles of both hind extremities of which have been denervated, one finds that so long as the muscle is stretched the rigidity continues to exist. Detach the tendon and allow the muscle to shorten a few millimeters, and the "rigidity" vanishes. Extend the muscle, and postural contraction once more appears, as may be demonstrated readily by application of an ipsilateral inhibitory stimulus to any afferent nerve of the limb for the muscle then reflexes. This response to extension is the stretch reflex, and it is synonymous with muscle tonus. It disappears forever, once appropriate posterior or the anterior roots have been severed.

When the stretch reflex is elicited by a gradual and uniform extending force, it may be impossible, or practically so, to record any action currents from the responding muscle, even though the *active* tension developed may be of the order of several kilos (as shown by subsequent inhibition). When, however, the extending force is applied in abrupt increments, an action current is observable in the muscle after an interval of $\pm$ 7 σ following each irregularity in the stretch stimulus. Since 7 σ is the latency of the knee-jerk, it follows that the observed action current is due to the synchronous character of the stimulus. When elicited by a gradual stretch, on the other hand, the proprioceptive afferent organs are stimulated in sequence, and the resulting temporal dispersion of activity among the constituent reflex arcs renders it impossible to observe action currents in the muscle as a whole. This gives strong *a priori* ground for the belief that the tension of a stretch reflex is maintained by the all-or-none mechanism. Proof that this is the case is provided by the following observation. (Fulton and Liddell.)

When, after a stretch reflex has been elicited, a strong inhibitory stimulus is applied to an appropriate afferent nerve, the *rate* of the ensuing relaxation approximates the rate of relaxation of a motor nerve tetanus. The initial portion of the stretch-reflex relaxation is, however, convex upwards for a short distance, which gives evidence of temporal dispersion in the cessation of fibre activity, thus harmonizing with the observations on the electrical responses. If the tension were maintained by a special "fixing" mechanism it would be inconceivable that it could be caused to relax at the same rate as a motor nerve tetanus.

In 1912 Barbour and Stiles[2] suggested, in referring to certain forms of reflex tetanic response, that "this form of nervous discharge must give rise to alternate movements in neighbouring elements of the muscle, one set of fibres shortening while others relax. The resulting tension may, however, be fairly uniform." Evidence has been given elsewhere to show that a similar form of rotational activity occurs in the stretch reflex, thus accounting for its relative unfatiguability. A stretch reflex may be maintained for hours at a time. Since stretch is the adequate stimulus for the maintenance of this form of response, shifting of the incidence of stretch among the various responding afferent end-organs has been suggested as the probable cause of the rotational activity.

Recent evidence,[3] moreover, has indicated that the stretch reflex is the shortening reaction. At whatever length a tonic muscle may happen to be (within certain limits), extension, if not too severe, causes reflex contraction. The lengthening reaction, on the other hand, is a reflex inhibition resulting from an extension so severe as to stimulate the proprioceptive inhibitory endings.

Voluntary contraction dovetails into tonic contraction, and all available evidence indicates that voluntary activity is interpretable on the basis of the same all-or-none mechanism. There is some justification for Hoffman's[4] view that voluntary contraction is merely myotatic contraction caused by the liberation of the lower spinal centres from cortical inhibition.

The painstaking investigations of Boeke,[5] Dusser de Barenne,[6]

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[2] Barbour, G. F., and Stiles, P. G., *Am. Physiol., Ed. Rev.*, 1912, xvii, 75.

[3] *Cf.*, Ch. xvii of the author's "Muscular contraction and the reflex control in movement." (In press.)

[4] Hoffmann, P., "Sehnenreflexe," Berlin, Springer, 1922.

[5] Boeke, J., "Libro en honor de D. S. Ramon y Cajal," Madrid, 1922, p. 113.

[6] Boeke, J., and Dusser de Barenne, J. G., *Proc. Konin. Akad. Wet.*, 1919, xxi, 927.

Kuntz and Kerper,[7] and others,[8] have provided unimpeachable proof of the existence of sympathetic nerves supplying skeletal muscle fibres. Though the evidence now at hand excludes the interesting possibility that these sympathetic fibres are concerned in the maintenance of tonus, it is nevertheless evident that they must subserve some function, and it is the duty of physiologists to recognize them and to discover what they do. The first positive evidence in this direction has been supplied by L. A. Orbeli[9] of Leningrad. He has demonstrated that stimulation of the sympathetic nerves supplying a skeletal muscle (free from its circulation), accelerates recovery if the muscle is fatigued. In this respect activity of the sympathetic has the same action as adrenalin. Increased susceptibility to fatigue following sympathectomy is the one point upon which all observers who have performed this operation agree. This accordingly lends weight to Orbeli's contention that the sympathetic nervous system increases the "efficiency" of muscular activity. Stimulation of the sympathetic would indeed appear to facilitate the removal of acid metabolites. However, we need to know more about the effect of the sympathetic upon the lactic acid mechanism and upon respiratory exchange before we can define the function of the muscle sympathetics with accuracy.

Full discussion of the questions raised in this communication is given in a forthcoming monograph on "Muscular contraction and the reflex control of movement."

[7] Kuntz, A., and Kerper, A. H., PROC. SOC. EXP. BIOL. AND MED., 1924, xxii, 25.

[8] Agduhr, E. L., *Proc. Konin. Akad. Wet.*, 1919, xxi, 930 and 1231.

[9] Orbeli, L. A., Pavlov Jubilee Volume, Petrograd, 1924, 429. See also *Brit. Med. J.*, 1924, ii, 633.