

Opening Lecture

Some Comments on “Tone”

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The relation of posture to movement was a subject of great actuality to physiologists working within the first half of this century. The outcome of it all was that tone became defined as postural reflexes adjusting body to ground and parts of the body to one another. Familiar to all are the postural adjustments so thoroughly elucidated by Magnus and De Kleijn. Their findings tended to clench the notion of tone as postural reflexes, one to which Sherrington also adhered.

From the declining interest in reflexes such tonus problems have suffered without being revived and systematically pursued as studies of motor control and its organization. The work on gamma-spindle problems in the early fifties drew attention to another and, indeed, much older way of thinking of “tone”, not necessarily as reflex but as a kind of state of light excitation, the opposite to “slackness”. Thus, for instance, the transition from sleep to arousal is reflected on the motor side by a mobilization of the gamma-spindle apparatus. This, in the cat, is another state, one of preparedness and proprioceptive awakening with subliminal or liminal activation of the motoneurons. We shall probably hear of recent contributions to this concept of “tone” by Grillner, present at this Symposium; I mean the monoaminergic mobilization of a new state of motor preparedness in the spinal cord of the spinalized cat.

This particular aspect of “tone” has been much studied in the cat with its prominent “red” muscles loaded with spindles and run by small alpha motoneurons which are easily excited to long-lasting discharges outlasting the stimulus. If I have understood Henneman correctly, he would think of this faculty merely as a matter of neuron size. My own view has always been, and still is, that behind such observations there is a specific neural organization. This may well be represented at different levels, not only in the spinal cord. However, it is not my intention today to place before you the arguments for a specific tonic neural organization in the cat. I merely wanted to refer briefly to the kind of work that in the present time has sustained a concept of “tone” as a state, naturally also reflected in reflex excitability.

I have taken up this subject in order, firstly, to draw attention to man and some clinical work of interest in this context and, secondly to make a final suggestion. In trying to understand how “the body has, as it were, an uncanny knowledge of all the relevant laws of mechanics” Martin (1967, 1977), has been led to the concept of a specific tonic organization. From his clinical experience he mentions a number of cases in which the voluntary activity is intact while tone is lost; for instance, a girl

whose head fell down if she closed her eyes but who was capable of raising her head promptly when asked to do so, still with closed eyes. Though vestibularis may be regarded as a specifically postural receptor, it can be functionally normal in a patient incapable of standing, rising from a chair or holding up his head without a voluntary effort. The upright position of man seems to have made proprioceptive information relatively more important. A patient incapable of walking may be induced to do so when forced to imitate the rocking sideways movements that the centre of gravity executes in walking. These follow from the shift of the weight from one leg to the other. These examples are given by Martin.

Apparently, Denny-Brown (1962) does not agree with this idea of a tonic governor or organization, single or hierarchically organized. He states: "In disagreement with earlier views, we find that the motor disorder of extrapyramidal disease points clearly to identity of the mechanisms of posture and movement, for the more completely the projected type of movement disintegrates the more obviously there is abnormality of posture. Movement in its most simple form is change of posture" (p. 124).

In spite of these opposite views the two authorities are in essential agreement about the leading role in tone of that great output organization, the globus pallidus. One therefore wonders whether their difference of opinion does not chiefly concern the degree of independence that is allotted to the globus pallidus. After bilateral destruction of this structure in the monkey, Denny-Brown found the animal unable to stand, its hand and feet quite useless, no righting reflexes. Brooks (1975) has recently applied his technique of local cooling to the globus pallidus of the monkey. He found that, provided vision was excluded, there was a breakdown of alternating movements, suggesting, indeed, a regulatory role in posture for this structure in agreement with the ideas of Martin.

In thinking, as I do, about hierarchically organized tonic centres the question arises as to how the two aspects of tone, that of a "state" discussed above, and the control of postural reflexes are related. To be at all relevant for its purpose a postural response must enter into any movement from its very beginning and participate in it all the time, unless interrupted or suppressed by a ballistic motor act in which the contractile energy, released by a brief burst of spikes, is transferred into the mass of the moving parts. Therefore, the required postural organization should be specially directed towards neurons capable of an easy and early mobilization and capable also of supporting maintained activity. Different channels must have access to the same postural governor.

When Hagbarth and Eklund (1966) demonstrated the slow rise of the motor response elicited by vibration at the tendon of tibialis anterior in man, they seemed to me to have described activity of a tonic organization, now known to be spinal (Gillies et al., 1971; Burke et al., 1976). Their access to it was largely if not wholly proprioceptive, unphysiological though it be to mobilize spindles bypassing the link between alpha and gamma motoneurons. This organization would seem to be spinal in the same way as stepping is spinally organized. Supraspinal control is known to be present in both cases. It seems likely that the same spinal organization is mobilized by the basal ganglia to produce *both* manifestations of "tone", the state of preparedness and the postural reflexes.

My comments on "tone" have served the purpose of preparing the ground for their final aim which is to suggest that neurophysiology should return to the types of experiment carried out by Magnus and De Kleijn and cease to regard them as a

finished chapter. There are available in them precise tests that can be related to the issues that I have discussed here. And it is a curious fact that the Dutch workers never took to the stereotactic technique of Horsley and Clarke, invented about fifteen years before their time.

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