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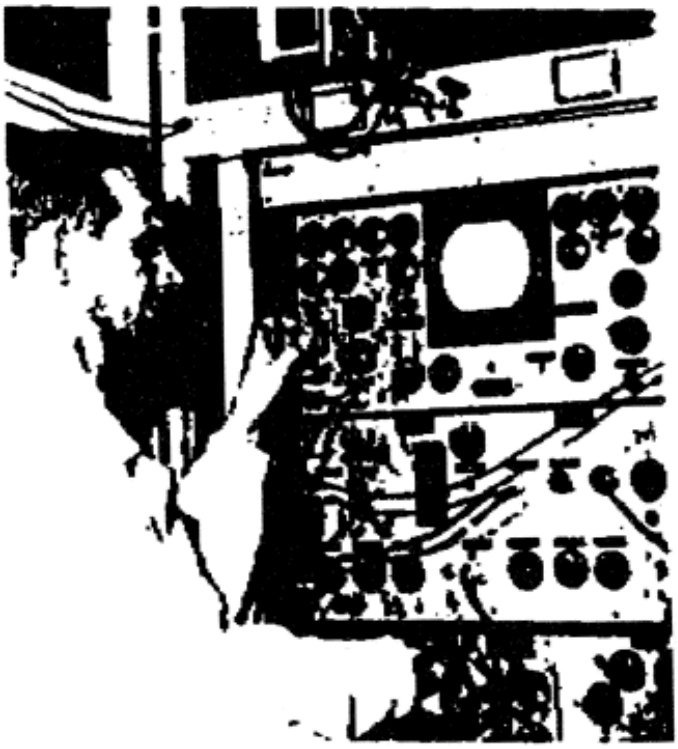

Kaada and the Mauro stimulator (1950)

The discovery of motor control by brain centers operating the gamma-spindle-loop

by

Ragnar Granit

How did Birger Kaada and I come together? I had been invited to Oslo to be Faculty opponent for the public examination of Kaada's thesis (1951). This dealt with movements elicited by electrical stimulation of "rhinencephalic" centers in the brains of primates, dogs and cats. Obliged to be critical I also raised the question of whether the motor impulses from these sites went straightaway to the large ventral horn cells or did so across (what later became known as) the gamma-spindle loop? The question postulated the existence of an unknown x, the supposition that the brain could handle the gamma-spindle loop.

My thinking in this matter proceeded along such lines because of Leksell's Thesis (1945) from our laboratory in Stockholm. The late Sir Bryan Matthews (1933) had shown that strong motor nerve stimulation contracted spindles but Leksell went further and proved up to the hilt that stimulus strength capable of eliciting an action potential-wavelet in ventral root of gamma conduction velocity raised a discharge in muscular afferents. Since only muscle spindles had a motor supply Leksell concluded that slowly conducting gamma fibres were the motor fibres for the spindle's so-called intrafusal muscles.

I thought that Kaada paled a little at this extravagant hypothesis -- indirect control of a muscular sensor from the brain! So I invited him on the spot to come over to Stockholm to find out by experimentation whether or not my question had any background of facts. Kaada had far more experience than I of stereotactic stimulation in the brain. I, on my side, had set up the complete technical arrangements for the experiments required to answer this and other questions pertaining to the role of muscle spindles in motor control. So, when Kaada arrived early in the

New Year 1952, we could start straightaway.

We began and continued the experiments in an atmosphere of great excitement because success was immediate. Silent spindle afferents fired and spontaneously active ones increased their discharge rate in response to stimulation of known motor sites in the brain and this effect was seen at a very much lower threshold than that needed for contracting the muscle harboring the isolated spindle-fibre recorded in the dorsal root. A myograph sensitivity of a mm excursion for one gram was normally used but in the end similar experiments were conducted by recording directly from isolated gamma fibres.

I quote from the summary of our 1952 paper (Kaada no. 20): "muscle spindles could be accelerated or decelerated by stimulation of various central structures known to influence motor activity". An example: "A highly efficient facilitatory mechanism for the muscle spindles was found in the brain stem and diencephalic reticular system." Deceleration of spindle activity down to complete inhibition was obtained from the bulbo-reticular inhibitory system and from the anterior lobe of the cerebellum. I vividly remember how excited we were when the loudspeaker recording from an afferent root filament or from an efferent gamma fibre became dead silent upon weak stimulation of the anterior lobe.

Struck by the strong effects on the gamma-spindle loop we nevertheless did "not propose the hypothesis that all tonic changes of the muscles consist in changes of a spindle activity that indirectly, over the postural reflexes, determine the level of excitability of the spinal cord and other centers. But our results make it necessary to ascribe to this particular mechanism a most important role... All concepts involving motor activity will have to be experimentally revised from this point of view", we wrote.

There is no point in pursuing the further development of these ideas. It is well known that our results stimulated much research in

several places. Our laboratory was filled with young people from many countries, all of them eager to study brain control of movement in relation to muscular sensory endings, in particular the spindle endings. The term "motor control" got some substance to its bones and I used it in naming the First Nobel Symposium in Stockholm "Muscular Afferents and Motor Control" (1965).

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Numbers refer to Kaada's publication list.

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