

Abb. 4. *a* Besonders regelmässige spontane Aktivität einer Querknospenreihe (von links nach rechts zu lesen). *b* Dasselbe Präparat bei Hin- und Herschwanken der gesamten Wassermasse (ebenfalls von links nach rechts zu lesen); kopfwärts gerichtete Wasserbewegung wirkt frequenzbeschleunigend, schwanzwärts gerichtete hemmt die spontanen Impulse.

fläche einmal in Längsrichtung der Knospenreihe, dann quer zu ihr anzuströmen, ergaben eine etwas grössere Wirksamkeit im letzteren Fall. Das galt aber nur, wenn die Strömung dabei von hinten nach vorn lief; Anströmen in Richtung von vorne nach hinten bewirkte im Gegenteil, wie gesagt, Hemmung der Impulse.

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#### Summary

Electrophysiological recording of the spontaneous activity from a single group of lateral sense organs on the abdomen of *Xenopus laevis* results in a more or less regular series of large spikes, either all of the same height or of two different sizes (each group is innervated by two "large" lateralis fibres). Mechanical stimulation of such a group may cause a rise or a fall of spontaneous impulse frequency. There is evidence for a two-directional sensitivity of the same unit (nerve fibre) from a single group, out of the middle as well as out of the dorsal lateral line.

### The Relation Between Gamma Motor Activity and the Electroencephalogram

The gamma motor fibres of LEKSELL<sup>1</sup>, innervating the intrafusal fibres of the muscle spindles, have a wide range of connections and are controlled not only by spinal reflexes but also to a great extent from supra spinal levels. Diffuse connections between the gamma motor system and most parts of the brain have been demonstrated, and the physiological significance of the muscle spindle activity has recently been elucidated by GRANIT and his collaborators<sup>2</sup>. In all this work, attention has been drawn to the close relation between the

gamma motor system and the reticular activating system<sup>3</sup> on the one hand, and the bulbo-reticular inhibitory system<sup>4</sup> on the other. One might therefore expect to find correlations between the activity of cerebral cortex and of muscle spindles under conditions in which the influence of spinal reflexes on muscle spindles was minimized and kept constant. By recording electroencephalogram and the activity of single muscle spindles simultaneously under various conditions in cats and rabbits, this was verified, and sometimes extremely good correlation was obtained.

Electroencephalograms from motor, temporal and occipital areas of the cortex were recorded in lightly anesthetized cats and rabbits, simultaneously with the activity of single muscle spindles led from fine filaments of dorsal roots. Needle electrodes for subcortical stimulation and heating electrodes for the thermosensitive structures of the anterior hypothalamus were inserted stereotaxically. As a rule "arousing" stimuli such as nociceptive procedures, lowering the body temperature, twisting the pinna or electrical stimulation of the mesencephalic reticular formation were found to "activate" (desynchronize) the cortical activity and at the same time to cause increased muscle spindle activity. On the other hand, procedures which were found to inhibit muscle spindle activity, such as raising the body temperature, local heating of the hypothalamus, and elicitation of some skin reflexes from the upper thoracic and neck region, were usually accompanied by synchronization of cortical activity. "Spontaneous" fluctuations in cortical activity were several times found to be synchronous with those seen in the muscle spindle record, *c.f.* Figure. The anesthetic level had, however, to be critically balanced. Doses of anaesthetics just large enough to give slow wave activity in the electroencephalogram, did not abolish gamma motor activity. In such cases, hypothalamic heating could influence muscle spindle discharge without any noticeable effects on the electroencephalogram. Unimpaired cortical activity was thus not necessary for hypothalamic effects on gamma motor activity. Neither were the changes in cortical activity secondary to fluctuations in muscle spindle discharge, since they were readily obtained in *encéphale isolé* preparations. Thermosensitive structures in the anterior part of the hypothalamus may thus influence

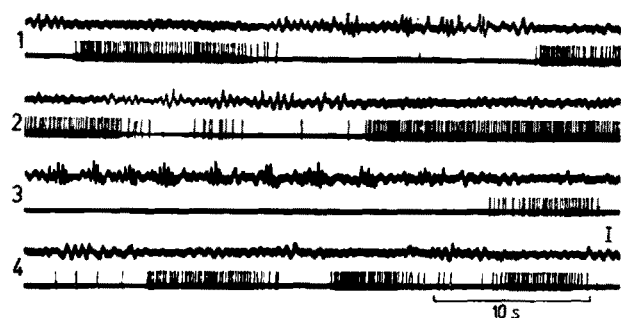
<sup>1</sup> L. LEKSELL, *Acta physiol. scand.* 10 [Suppl. 31], 84 (1955).

<sup>2</sup> R. GRANIT, *Receptors and Sensory Perception* (Yale Univ. Press, New Haven 1955).

<sup>3</sup> G. MORUZZI and H. W. MAGOUN, *Electroenceph. clin. Neurophysiol.* 1, 455 (1949).

<sup>4</sup> H. W. MAGOUN, *Science* 100, 549 (1941).

cerebral cortex and gamma motor system by a common relay system within the reticular formation of the brain stem.



Rabbit. Chloralose-urethane. EEG from left motor area. Muscle spindle afferent from left gastrocnemius. Note high frequency irregular spindle discharge simultaneously with periods of desynchronized EEG. Muscle spindle silent when slow waves appear in EEG.

Occasionally a muscle spindle was inhibited synchronously with cortical "arousal" when stimulating the midbrain tegmentum, indicating that the activating relay system of the brain stem may be functionally subdivided, or may be less functionally uniform than is often believed. Another consideration that has to be borne in mind is that the single spindle afferent sampled in such an experiment may not be typical of the gamma system as a whole. Electroencephalogram gives statistical information of the activity in a great number of neurones. The muscle spindle test might, on the contrary, tell us about the situation in a restricted part of the motor system only. Considering this the good correlation generally obtained is still more impressive.

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### Zusammenfassung

Es wurde gezeigt, dass die Weckreaktion im EEG meist mit Erregung der Muskelspindeln verknüpft war. In tieferer Narkose konnten die Muskelspindeln bei Erwärmung des Hypothalamus noch beeinflusst werden, ohne dass im EEG nennenswerte Veränderungen auftraten. Thermische Reizung im Hypothalamus konnte aber auch bei der «*encéphale isolé*»-Katze langsame, grosse Wellen in Grosshirnrinden-Ableitungen hervorrufen. Wahrscheinlich werden die Muskelspindeln und die Aktivität der Grosshirnrinde dabei über dasselbe System vom Hirnstamm beeinflusst.

rate of muscle atrophy. A disturbance of the trophic influence of the nervous system is generally assumed, but the term "trophic influence" lacks a physiological definition.

A number of papers published by GUTMANN and his collaborators show that the basis of nervous trophic influence is in the activation of metabolic recovery processes following muscle stimulation (GUTMANN, VODIČKA and VRBOVÁ<sup>1</sup>; BASS, GUTMANN and VODIČKA<sup>2</sup> and others). These recovery processes differ in rate and extent in normal innervated and denervated muscles. They have been found to be influenced by the functional state of nerve centres. For example, coffee activates these recovery processes, while bromides depress them. Myelotomy (GUTMANN, VODIČKA and VRBOVÁ<sup>1</sup>), as well as reflex nociceptive stimulation (GUTMANN and VODIČKA<sup>3</sup>) have a similar depressing effect on these metabolic recovery processes.

After section of the dorsal roots in the cat and the rat, a tendency to extension develops, which is in accordance with observations described in literature (HERING<sup>4</sup>, RANSON<sup>5</sup> *et al.*). We have had ample opportunity of observing exaggerated reflex activity of the de-afferented hind limb, e.g. crossed extensor reflex etc. (see also TRENDLENBURG<sup>6</sup>, BREMER<sup>7</sup>, RANSON<sup>5</sup> *et al.*). From our observations, we have been able to conclude that tendency to extension after de-afferentation does not develop immediately after the operation but by the 7th-10th day, and is not dependant on the presence of spinal ganglia. It seems probable, therefore, that these changes of excitability are of central (spinal) origin and that tendency to extension is not mediated by the spinal ganglia as RANSON<sup>5</sup> postulated. Extirpation of spinal ganglia leads to a similar tendency to extension of section of the dorsal roots proximal to the ganglion.

It is possible to interpret these findings in terms of Cannon's Law of Denervation (CANNON and ROSENBLUETH<sup>8</sup>) and consider them to be the result of afferent denervation of spinal neurones. DRAKE and STAVRAKY<sup>9</sup> have postulated this extension of the Law of Denervation to de-afferentation. We have offered the following explanation. Antigravity muscles are mostly connected to the myotatic 2-neurone reflex arc, so that degeneration of the central stump of the dorsal roots leads to the destruction of synaptic endings on extensor motoneurones, while flexor motoneurones are, most probably, to a great extent protected by their interneurone pool.

We have further evidence for the increased excitability of extensor motoneurones after de-afferentation. Changes of chronaxy in cats before and after de-afferentation were studied. Chronaximetric difference between flexor and extensor muscle groups is well marked under normal conditions in cats, similar to man (LAPICQUE<sup>10</sup>), and is present until about the 10th day after the operation. By this time we noted a gradual decrease in chronaximetric

<sup>1</sup> E. GUTMANN, Z. VODIČKA, and G. VRBOVÁ, *Physiol. Bohemoslov.* 3, 182 (1954).

<sup>2</sup> A. BASS, E. GUTMANN, and Z. VODIČKA, *Physiol. Bohemoslov.* 4, 267 (1955).

<sup>3</sup> E. GUTMANN and Z. VODIČKA, *Physiol. Bohemoslov.* 2, 389 (1953).

<sup>4</sup> H. E. HERING, *Neurol. Zbl.* 17, 1077 (1897).

<sup>5</sup> S. W. RANSON, *Arch. Neurol. Psychiat.* 19, 201 (1928).

<sup>6</sup> W. TRENDLENBURG, *Arch. Physiol.* 1906, 1.

<sup>7</sup> F. BREMER, *Ann. Physiol. Physicochim. Biol.* 4, 750 (1928).

<sup>8</sup> W. B. CANNON and A. ROSENBLUETH, *The Supersensitivity of denervated Structures. A Law of Denervation* (New York, 1949).

<sup>9</sup> C. G. DRAKE and G. W. STAVRAKY, *J. Neurophysiol.* 11, 229 (1948).

<sup>10</sup> L. LAPICQUE, *L'excitabilité en fonction du temps* (Paris 1926).

### Excitability Changes and Muscle Atrophy After De-afferentation

The problem of muscle atrophy has absorbed the interest of a large number of experimental and clinical workers. In spite of many new facts in this field it is not possible, at the present time, to state precisely, which factors are most important in determining the onset and