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Excitatory and inhibitory Pathways involved in lower Reflex Integration

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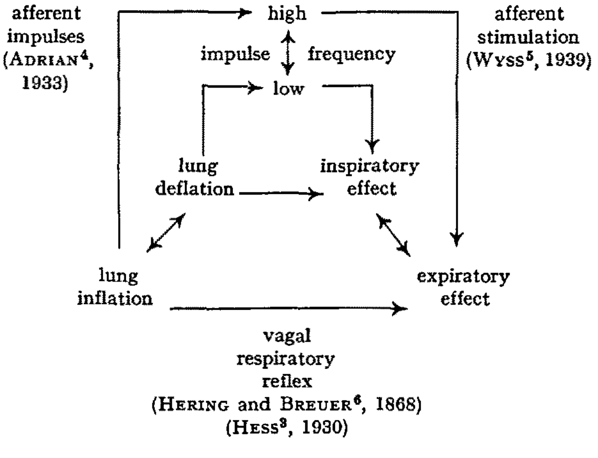
Recent investigations have brought more detailed information as to Sherrington's fundamental concept of the neuronic structure of elementary reflexes (Sherrington[2], 1906; Creed[3] *et al.*, 1932). Thus the work of Eccles[4] (1936), Gasser[5] (1937), Barron and Matthews[6] (1938), Lorente de Nó[7] (1939), Gesell[8] (1940), Bremer[9] and co-workers (1942), Lloyd[10] (1944) and of many others provides the basis for a better understanding of the intimate mechanisms concerned in reflex excitation and inhibition.

The object of the present contribution is to suggest a possible mechanism of simultaneous excitatory and inhibitory action in one and the same reflex. The neuronic arrangement herein referred to as the basic functional structure of an elementary reflex derives from experimental data obtained by systematic analysis of vagal respiratory reflexes (Wyss[11], 1939–1944). Its general significance for spinal reflexes and its bearing upon characteristic features of reflex action, such as summation, after-discharge and rebound, have also been pointed out by Wyss[12] (1944). This attempts to explain the central distribution of reflex facilitation and inhibition resulting from the stimulation of a particular afferent fibre system.

Schulgin[1] (1910) and Rice[2] (1938) were the first to show that the nature of the respiratory effect produced by afferent stimulation of the cut vagus nerve in the neck of the rabbit depends on stimulus frequency. Unaware of these earlier findings, Wyss made the same observations in 1939 and related them closely to the pulmonary inflation and deflation reflexes as described by Hess[3] (1930) and to the frequency of impulses discharged by the pulmonary stretch receptors on gradually increasing lung inflation (Adrian[4], 1933). Stimulation at low frequencies, like deflation of the lungs, gives rise to a characteristic inspiratory effect, whereas with higher frequencies or lung inflation, a typical expiratory effect is obtained. The essential mechanism of expiration being inhibition of inspiration, this result means that, on the central inspiratory activity, afferent impulses with low frequencies have an excitatory effect and, with higher frequencies, an inhibitory one. By interfering stimulation of both vagus nerves, some evidence has also been provided in support of the



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[1] Institut de Physiologie, University of Geneva, Switzerland.

[2] C. S. Sherrington, The integrative action of the nervous system. London: Constable 1906.

[3] R. S. Creed, D. Denny-Brown, J. C. Eccles, E. G. T. Liddell and C. S. Sherrington, Reflex activity of the spinal cord. London: Oxford Univ. Press 1932.

[4] J. C. Eccles, Erg. Physiol. *38*, 339 (1936); Physiol. Rev. *17*, 538 (1937); Ann. Rev. Physiol. *1*, 363 (1939); J. Neurophysiol. *9*, 87 (1946).

[5] H. S. Gasser, Harvey Lectures *32*, 169 (1937).

[6] D. H. Barron and B. H. C. Matthews, J. Physiol. *92*, 316 (1938).

[7] R. Lorente de Nó, J. Neurophysiol. *2*, 402 (1939).

[8] R. Gesell, Erg. Physiol. *43*, 477 (1940); Schweiz. med. Wschr. *71*, 398 (1941).

[9] F. Bremer, V. Bonnet and J. Moldaver, Arch. int. Physiol. *52*, 1, 215 (1942); F. Bremer and V. Bonnet, Arch. int. Physiol. *52*, 153 (1942).

[10] D. P. C. Lloyd, Physiol. Rev. *24*, 1 (1944).

[11] O. A. M. Wyss, Pflügers Arch. *242*, 215 (1939); *243*, 457 (1940); Schweiz. med. Wschr. *71*, 290 (1941); *73*, 961 (1943); Helv. physiol. acta *1*, 301 (1943); C. r. Soc. Phys. Hist. nat. Genève *61*, 63 (1944).

[12] The author's scheme of a dual internuncial neurone connection accounting for excitation and inhibition in vagal as well as in simple spinal reflexes (Wyss, 1944) has been taken up by Marcel Monnier (Schweiz. med. Wschr. *75*, 296 [1945]; Schweiz. Arch. Neurol. *56*, 313 [1946]) in order to apply this new conception to neurological problems. It must however be emphasized that, thus to transpose this particular neuronic arrangement on the transverse section of the gray matter of the spinal cord, does not tally any more with the scheme's original meaning, and must have been done for reasons not mentioned in the two papers.

[1] S. Schulgin, Z. allg. Physiol. *10*, 367 (1910).

[2] H. V. Rice, Amer. J. Physiol. *124*, 535 (1938).

[3] W. R. Hess, Pflügers Arch. *226*, 198 (1930).

[4] E. D. Adrian, J. Physiol. *79*, 332 (1933).

[5] O. A. M. Wyss, Pflügers Arch. *242*, 215 (1939).

[6] E. Hering and J. Breuer, Sitzber. Akad. Wiss. Wien, Math.-naturwiss. Kl. Abt. 2, *58*, 909 (1868).

view that only one set of afferent fibres is involved in this inspiratory-excitatory and inspiratory-inhibitory reflex. The two antagonistic responses, then, are due to different summation phenomena, occurring at the level of the respiratory centre. It has been suggested that the expiratory effect, i. e., the inspiratory inhibition, is brought about by the opening, due to the increasing frequency of afferent impulses, of a new central path, which exerts a direct inhibition either on the central inspiratory activity, or on the spinal inspiratory motoneurones (Wyss[1], 1940).

Separate mechanical destruction in the floor of the fourth ventricle of either an inspiratory or an expiratory reflex centre with the ensuing elimination of only the inspiratory or only the expiratory component of the vagal respiratory reflex (Bartorelli and Wyss[2], 1941) gave further strong support to the assumption of a dual reflex pathway with two distinct "centres" for the inspiratory and the expiratory effect. These two primary reflex centres have recently been localized in the nucleus of the tractus solitarius and the adjacent part of the lateral reticular formation, at a more cranial level for the "expiratory centre" (Andereggen, Oberholzer and Wyss[3], 1946), a more caudal level for the "inspiratory centre" (Wyss and Croisier[4], 1943; Oberholzer, Andereggen and Wyss[5], 1946). They are distinctly, but not more than two millimeters, apart from each other and correspond to the entrance of the vagal root fibres.

A simple neurophysiological interpretation of these experimental facts is given by the schematic representation of Figure 1, illustrating the central disposition of vagal inspiratory and expiratory reflexes. It is assumed that the afferent impulses in the vagal pulmonary fibres reach the inspiratory as well as the expiratory centre, either by means of fibre bifurcation or in wholly separate fibres. Further histological studies will have to decide between these two alternatives. However this may be, at low impulse frequencies, such as those coming from lung deflation, only the inspiratory centre will be excited, for the expiratory centre is believed to have a much lesser "summation power" than the inspiratory one. But with higher frequencies, as elicited in the same afferent fibres by lung distension, the expiratory centre will also be excited and now its inhibitory action on the inspiratory activity will predominate. Thus by gradually increasing lung volume or afferent stimulation frequency, the initial inspiratory facilitation will be converted into an inhibition of inspiratory tendency, i. e., the inspiratory effect will subside and be replaced by an expiratory one (see Wyss[1], 1939, Fig. 3).

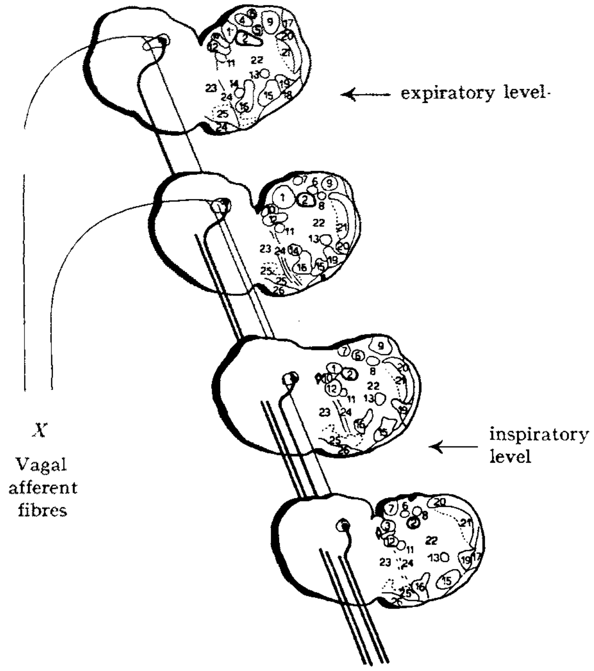

Fig. 1. Location of vagal respiratory reflex centres in the nucleus of the Tractus solitarius. Transverse sections of the rabbit's Medulla oblongata at one millimeter distance from each other, and corresponding to plates XXXIV—XXXVII of the Atlas of Winkler and Potter[2] (1911). *X:* afferent pulmonary fibres of the vagus nerve. *1* Nucleus dorsalis nervi X – *2* Fasciculus solitarius et nucleus fasciculi solitarii – *3* Nucleus dorsalis nervi XI – *4* Nucleus descendens nervi VIII – *5* Radix descendens nervi VIII – *6* Nucleus Burdach – *7* Nucleus Goll – *8* Nucleus Monakow – *9* Nucleus proprius corporis restiformis – *10* Nucleus intercalatus Staderini – *11* Nucleus Roller – *12* Nucleus nervi XII – *13* Nucleus ambiguus – *14* Nucleus salivarius inferior – *15* Nucleus funiculi lateralis – *16* Tractus Deiters descendens – *17* et *18* Tractus spino-cerebellares dorsalis et ventralis – *19* Tractus rubro-spinalis – *20* Radix spinalis nervi V – *21* Substantia gelatinosa – *22* et *23* Formationes reticulares lateralis et medialis – *24* Nervus XII – *25* Oliva inferior – *26* Pyramis.

The most likely neuronic arrangement of the described reflex integration is shown in its simplest form by Figure 2. The afferent fibres or fibre collaterals (*a*) enter into synaptic connection with the neurones of both the inspiratory and the expiratory reflex centres. These two sets of central neurones lie in the same anatomical structure, but at a lower and a higher level respectively. They are to be considered as internuncial neurones acting in an opposite manner, i. e., excitatory and inhibitory, on the inspiratory motoneurones (*M*) of the spinal level. For the sake of a general application on reflex mechanisms, and supposing that expiration is primarily an inhibition of inspiratory activity, the inspiratory interneurone is indicated as excitatory (*E*), while the expiratory interneurone is described as in-

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[1] O. A. M. Wyss, Pflügers Arch. *243*, 457 (1940).

[2] C. Bartorelli and O. A. M. Wyss, Boll. Soc. ital. Biol. sper. *16*, 219 (1941).

[3] P. Andereggen, R. J. H. Oberholzer and O. A. M. Wyss, Helv. physiol. acta *4*, 213 (1946).

[4] O. A. M. Wyss and M. Croisier, Helv. physiol. acta *1*, 89 (1943).

[5] R. J. H. Oberholzer, P. Andereggen and O. A. M. Wyss, Helv. physiol. acta *4*, fasc. 4 (1946).

[1] O. A. M. Wyss, Pflügers Arch. *242*, 215 (1939).

[2] C. Winkler and A. Potter, An anatomical guide to experimental researches on the rabbit's brain. Amsterdam: W. Versluys 1911.

hibitory (*J*). The excitatory interneurone (*E*), with its descending fibre entering into ordinary synaptic contact with the motoneurone (*M*) provides facilitation for the latter. The inhibitory interneurone (*J*) on the other hand, is believed to exert a direct inhibition on the motoneurone.

The possibility that the inhibitory influence of the interneurone *J* should appear not on the motoneurone, but at the level of the interneurone *E*, seems excluded by several experimental facts: (1) In the vagal respiratory reflex, the expiratory, i. e., inspiratory-inhibitory effect is by no means abolished after the removal of the inspiratory, i. e., excitatory centre (BARTORELLI and WYSS[1], 1941; OBERHOLZER, ANDEREGGEN and WYSS[2], 1946). (2) Inhibition of inspiratory motoneurones has been obtained by electrical stimulation of descending spinal paths (RIJLANT[3], 1940). (3) Direct inhibition of motoneurones has also been observed in the spinal two-neurone reflex system (LLOYD[4], 1941). A hitherto unknown mechanism must be at the bottom of this direct inhibitory action on neurones (LLOYD[5], 1944). Special inhibitory synapses lying on the axon hillock side of the soma may be involved as indicated in the scheme of Figure 2 (WYSS[1], 1942).

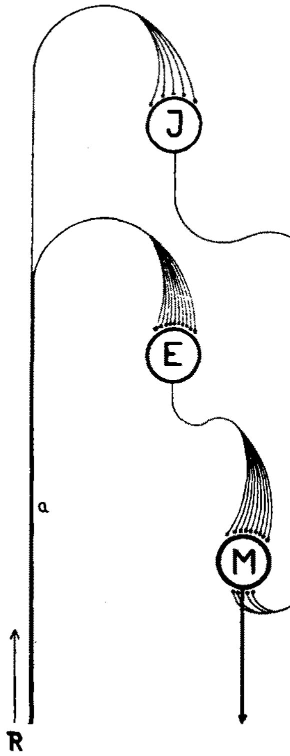

Fig. 2. Neuronic arrangement of excitatory and inhibitory reflex pathways.
R—a: afferent fibres from peripheral receptors.
E = excitatory, *J* = inhibitory internuncial neurone.
M = motoneurone.

The intact reflex system presented in Figure 2 acts in the following manner. By weak or moderate stimulation of the peripheral receptors *R*, low-frequency trains of afferent impulses are arriving at, and impinging on, the interneurones *E* and *J*. But only the excitatory interneurone *E* is able to respond to those infrequent impulses, its "summation power" being high enough, and far higher than that of the inhibitory interneurone *J*. Thus, a weak or moderately intense stimulation will strongly activate the motoneurone *M* and will therefore give rise to an excitatory reflex response. With stronger afferent stimulation however, the increasing frequency of the centripetal impulses will also succeed in exciting the inhibitory interneurone *J*, which will now exert its inhibitory effect on the motoneurone *M*. This direct inhibition is supposed to supersede any activation through excitatory synapses and by its intervention, the discharge of the motoneurone *M* will be stopped at once, this in spite of a heavy synaptic bombardment continuously arising from the excitatory interneurone *E*. For there is no reason to believe that higher afferent frequencies should lose their excitatory influence on the interneurone *E*. On the contrary, some experimental evidence points to the fact that, during a period of reflex inhibition due to more frequent afferent impulses, the excitatory centre *E* must pursue its activity in the same, or even in a higher, state of excitation. Thus a reflex inhibition may be elicited by increasing afferent stimulation, but the excitatory component is ready to reassert its influence at any sudden release of the inhibitory activity (see below: rebound).

In the neuronic arrangement of Figure 2, the central distribution of excitation and inhibition is considered as depending upon different functional properties between the interneurones *E* and *J*. The former is regarded as having a higher "summation power" than the latter. Assuming temporal summation at afferent synapses, the greater facilitating ability may be explained by a more enduring local excitatory process at the cell surface of the interneurone *E*. But spatial summation could also account for this functional difference, provided that the only number of the afferent synapses be supposed to be greater at the surface of the interneurone *E* than at that of the interneurone *J*. A spatial summation would hold especially for physiological (asynchronous) excitation of the individual afferent fibres. In this case, the functional properties of the receiving cell surface may even be looked upon as identical in the two groups of internuncial neurones, though situated at different levels within the same anatomical structure. The descending fibre connec-

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[1] C. BARTORELLI and O. A. M. WYSS, Boll. Soc. ital. Biol. sper. *16*, 219 (1941).

[2] R. J. H. OBERHOLZER, P. ANDEREGGEN and O. A. M. WYSS, Helv. physiol. acta *4*, fasc. 4 (1946).

[3] P. RIJLANT, C. r. Soc. Biol. *134*, 253 (1940); Mém. Acad. roy. Méd. Belgique *1*, fasc. 10 (1942).

[4] D. P. C. LLOYD, J. Neurophysiol. *4*, 184 (1941).

[5] D. P. C. LLOYD, Physiol. Rev. *24*, 1 (1944).

[1] O. A. M. WYSS, Rev. méd. Suisse romande *62*, 797 (1942).

tions, however, must be essentially different for these two internuncial neurones, their synapses at the site of the motoneurone being excitatory for the one, and inhibitory for the other. Nevertheless, a structural as well as functional similarity of the excitatory and inhibitory interneurones must not be overlooked and it might be logical to consider them both as derived from a common internuncial neurone type. The cells forming a higher level of the interneurone pool may be regarded as receiving a smaller number of afferent synapses and sending relatively more inhibitory efferents to the motoneurones, whereas the lower level interneurones would be covered with a greater number of afferent synapses, and connected with the motoneurones by much more, or even exclusively, excitatory synapses. It would thus be possible to explain this dual reflex integration on the basis of a most simple neuronic arrangement, for which however, no anatomical support has as yet been given. The vagal respiratory reflex centres may perhaps prove the very example for studying possible morphological differences in the afferent and efferent synaptic connections of functionally different internuncial neurones.

Several experimental findings point to a general application of the presented principle of neuronic arrangement on simple spinal reflexes. A likewise inhibitory action of higher frequencies upon the reflex contraction elicited by lower rates of stimulation has been observed in the spinal preparation of Batrachians (FRÖHLICH[1], 1909, VÉSZI[2], 1910, MATTHAEI[3], 1920, CROISIER[4], 1944) and mammals (BERITOV and BAKURADZE[5], 1940, BERNHARD and SKOGLUND[6], 1942). Corresponding summation phenomena have been described for single shock stimulation by BREMER[7] (1930), ECCLES and SHERRINGTON[8] (1931) and BERNSTEIN[9] (1937), and for inhibition and facilitation of the knee-jerk, by MALING[10] (1946). The rebound contraction is even more evident, and appears more frequently, in spinal than in the vagal respiratory reflexes, where it occurs only occasionally and takes the form of an inspiratory after-effect succeeding the expiratory response of a high rate stimulation of rather high intensity. It is worth noting that the spinal reflex rebound depends also upon the frequency of stimulation, i. e., it develops as soon as the reflex contraction becomes more and more inhibited, while the rate of afferent impulses increases (CROISIER[4], 1944). In order to explain the rebound by a post-inhibitory release phenomenon as originally put forward by SHERRINGTON and SOWTON[1] (1911), it may be assumed that the two internuncial neurones E and J of Figure 2 differ functionally in so far as the neuronic after-discharge is rather highly developed in the excitatory neurone E, whereas it scarcely exists in the inhibitory neurone J. Hence direct inhibition shows little or no after-effect and at the break of a high rate stimulation, the motoneurone M will continue to be stimulated for some time by the after-discharge of the interneurone E and will therefore respond to the withdrawal of the stimulus by a post-stimulative outburst of contraction. With lower frequency stimulation, where no inhibition occurs, a similar motor discharge follows the end of the stimulus like an ordinary "positive after-effect", i. e., the after-discharge of the interneurone E simply delays the subsidence of the excitatory motor reaction. Accordingly, in vagal respiratory reflexes, post-stimulative after-effects are usually inspiratory and this applies to lower (inspiratory) as well as to higher (expiratory) rates of stimulation. Moreover, the immediate effect of a non-stimulating vagotomy is, as far as it occurs, always an inspiratory one, and is particularly enhanced by lung distension (WYSS and OBERHOLZER[2], 1946). It is therefore a special kind of rebound contraction, elicited by the withdrawal of the normal afferent stimulation which, in the different phases of breathing, contains both lower and higher impulse frequencies.

In spinal reflexes, the anatomical distribution of excitatory and inhibitory internuncial neurones is certainly much less accurate than in the respiratory centre. Assuming that both types of interneurones lie at different levels within the same anatomical structure, as indicated by the localization of the vagal respiratory reflex pathways, some segmental distribution, with the inhibitory interneurones at a relatively higher level than the excitatory ones, may equally exist in the spinal reflex centres. The experimental fact that a direct inhibition of spinal motoneurones can be obtained by stimulating the next but one higher ipsilateral dorsal root, whereas closer related afferents produce facilitation (LLOYD[3], 1941), may also support this view (See also: RENSHAW[4], 1946). But in spinal reflexes the single shock activation or inhibition of motoneurones proves to be a more important physiological mechanism than in vagal respiratory reflexes and it would even account for a somewhat different behaviour of the spinal reflex act, when elicited by afferent stimuli of various frequencies. Thus the initial phasic contraction, as observed by FRÖHLICH[5]

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[1] F. W. FRÖHLICH, Z. allg. Physiol. *9*, 55 (1909).

[2] J. VÉSZI, Z. allg. Physiol. *11*, 168 (1910).

[3] R. MATTHAEI, Z. allg. Physiol. *18*, 281 (1920).

[4] M. CROISIER, Helv. physiol. acta *2*, 97 (1944).

[5] I. BERITOV and A. BAKURADZE, C. r. Acad. Sci. U.R.S.S. *26*, 961, 965 (1940).

[6] C. G. BERNHARD and C. R. SKOGLUND, Acta physiol. Scand. *4*, 125 (1942).

[7] F. BREMER, C. r. Soc. Biol. *103*, 509 (1930).

[8] J. C. ECCLES and C. S. SHERRINGTON, Proc. roy. Soc. London B *107*, 535 (1931).

[9] S. BERNSTEIN, Amer. J. Physiol. *120*, 798 (1937).

[10] H. M. MALING, J. Neurophysiol. *9*, 317 (1946).

[1] C. S. SHERRINGTON and S. C. M. SOWTON, Proc. Roy. Soc. London B *83*, 435 (1911).

[2] O. A. M. WYSS and R. J. H. OBERHOLZER, forthcoming (1947).

[3] D. P. C. LLOYD, J. Neurophysiol. *4*, 184 (1941).

[4] B. RENSHAW, Amer. J. Physiol. *146*, 443 (1946).

[5] F. W. FRÖHLICH, Z. allg. Physiol. *9*, 55 (1909).

(1909) for higher rates of stimulation and described by this author as "Anfangstetanus" in opposition to the "Dauertetanus" of low frequency stimulation, finds its functional equivalent in vagal respiratory reflexes only under those rather exceptional conditions, where a single shock applied to the afferent vagus nerve is liable to produce a single twitch in the inspiratory muscles (Vagus-Zwerchfell-Reflex; HOFFMANN, SCHNEIDER and KELLER[1], 1931). It may happen then that a high-rate stimulation of vagal afferents gives rise to an early inspiratory contraction before the normal expiratory effect is fully developed. Such single twitch reactions, however, may not be regarded as the common physiological basis of reflex function. They must be considered, in the respiratory as well as in simple spinal reflexes, as special phasic manifestations of a more general tonic mechanism, i. e., they are brought about by a strong and synchronized stimulus operating on a neuronic system, which allows a more immediate and even monosynaptic reflex transmission.

It may follow from these considerations that the basic functional structure of reflex integration lies in a double-path interneurone connection as indicated in Figure 2, and that the two-neurone reflex arc ("réflexe circonscrit" of CAJAL[2], 1909; RENSHAW[3], 1940) supervenes as a secondary short-circuiting reflex mechanism, subserving some instantaneous motor reactions, such as the phasic form of the stretch reflex (LLOYD[4], 1943). But in sustained proprioceptive or myotatic reflexes, internuncial neurones are also involved, and they may be responsible for the tonic character of these more enduring motor reactions. There is reason to believe that the internuncial neurones described for the vagal respiratory reflexes behave like the interneurones of a proprioceptive reflex system, in which the two-neurone reflex arc is of but little importance. Moreover, the mediation of the flexor reflex contains an internuncial neurone even for the single twitch type, as has recently been shown by LLOYD[1] (1943). This also confirms the statement that a three-neurone connection ist the most common neuronic arrangement for lower reflex integration.

Zusammenfassung

Auf Grund der Frequenzabhängigkeit des respiratorischen Effektes der afferenten Vagusreizung und des lokalisatorischen Nachweises von zwei getrennten zentralen Schaltstellen für den inspiratorischen und den exspiratorischen Effekt läßt sich ein funktionelles Schema der vagalen Atmungsreflexe aufstellen. Die afferenten Lungenfasern des Vagus treten in synaptische Verbindung mit Schaltneuronen im Nucleus tractus solitarii und in der angrenzenden Zone der Formatio reticularis lateralis. Auf einem mehr kaudalen Niveau sind diese Schaltneurone inspiratorisch wirksam; ihre Neuriten bilden erregende Synapsen an den inspiratorischen Motoneuronen. Auf einem etwas mehr kranialen Niveau sind sie exspiratorisch wirksam; es wird angenommen, daß sie über besondere Synapsen eine direkte Hemmung auf die inspiratorischen Motoneurone ausüben. Diese exspiratorischen bzw. inspiratorisch-hemmenden Schaltneurone haben ein geringeres «Summationsvermögen» als die inspiratorischen und werden daher erst durch höhere afferente Erregungsfrequenzen in Aktion versetzt. Ihr hemmender Einfluß ist aber imstande, die motorische Auswirkung der gleichzeitig immer vorhandenen inspiratorischen Aktivierung gänzlich zu verhindern. Dieses Prinzip des doppelten zentralen Schaltweges für Erregung und Hemmung läßt sich in verallgemeinerter Form auf spinale Reflexe anwenden, wo ein hemmender Einfluß steigender afferenter Erregungsfrequenzen ebenfalls besteht. Ein in ähnlicher Weise antagonistisch wirkendes Schaltneuronsystem ist für Reflexe mit tonischem Charakter als grundlegend anzunehmen, während der direkte monosynaptische Schaltweg als sekundär vereinfachter Mechanismus für gewisse phasische Reaktionen zu betrachten ist.

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[1] P. HOFFMANN, M. SCHNEIDER and C. J. KELLER, Z. Biol. *91*, 196 (1931).

[2] S. R. CAJAL, Les nouvelles idées sur la structure du système nerveux chez l'homme et chez les vertébrés, Paris: Reinwald 1894. Histologie du système nerveux de l'homme et des vertébrés, Vol. 1, Paris: Maloine 1909.

[3] B. RENSHAW, J. Neurophysiol. *3*, 373 (1940).

[4] D. P. C. LLOYD, J. Neurophysiol. *6*, 293, 316 (1943).

[1] D. P. C. LLOYD, J. Neurophysiol. *6*, 293, 316 (1943).

Substances thioloprives

Par Z. M. BACQ, Liége

IV. *(Suite)*

Actions physiologiques similaires des oxydants, métaux lourds, toxiques de guerre et acides acétiques monohalogénés

a) *L'effet Lundsgaard*

Nous appelons «effet Lundsgaard» la contracture particulière du muscle strié décrite par LUNDSGAARD[1] après empoisonnement par les acides acétiques monohalogénés. Ces acides neutralisés ne sont pas contracturants par eux-mêmes, mais si on excite le muscle soit par le courant électrique (LUNDSGAARD) soit par les ions potassium (BACQ et GOFFART[1]) (fig. 4*a*), on voit se développer rapidement une contracture persistante qu'accompagne une excitation progressive. Le muscle contracturé ne contient pas plus d'acide lactique qu'un muscle au repos; la glycolyse est en fait inhibée par

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[1] E. LUNDSGAARD, Biochem. Z. *217*, 162 (1930) et *227*, 51 (1930).

[1] Z. M. BACQ et M. GOFFART, C. r. Soc. Biol. *133*, 694 et 696 (1940).