MODELLING STUDY OF SPINAL GENERATORS STRUCTURE; THE ROLE OF ALPHA MOTONEURONS, RENSHAW CELLS AND Ia INTERNEURONS IN LOCOMOTION

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Abstract. The properties of a model system composed of nets of motoneurons, Ia interneurons and Renshaw cells corresponding to the set of muscles driving one joint were analyzed from the point of view of their participation in locomotion control, i.e., generation of signals driving individual muscles. The model was constructed of neuron-like analog elements. The relations between the structure of the system, its control by tonic and phasic inputs and the properties of the generated signals were examined. The pattern of activity of motoneuron-like elements was considered to reflect the physiological pattern of muscle activity during locomotion. The network modelled in this way was an adjustable system, i.e., the parameters of the generated pattern could be varied by both tonic and phasic signals. A phasic signal acting on a background of moderate tonic signals seemed to enable a broader adjustment of the parameters of the generated pattern than tonic signals only. The best correspondence between generated and physiological patterns was obtained when the Renshaw cells were additionally and selectively inhibited by tonic signals.

INTRODUCTION

Freusberg (6), Sherrington (23) and other investigators at the end of the nineteenth century found that lumbar spinal cord of the dog which was isolated from supraspinal influences could evoke rhythmic sequences
of limb's flexion and extension movements called "spinal stepping". Van Holst, on the basis of studies of fish locomotion (10), suggested that control signals could be generated in the spinal cord as a result of interaction between the spinal cord nets corresponding to particular executive elements. This idea was then extended to mammalian locomotion. In the period of 1960–1980 there were obtained numerous experimental data (e.g., 8, 16, 24) on the basis of which the hypothesis of spinal generators was formulated. Electrophysiological and behavioral studies (e.g., 8, 12, 13, 25, 26) suggested that the spinal cord had the capacity to generate the control signals for locomotor movements. In addition supraspinal structures were thought to initiate this process by establishing the appropriate level of excitability in spinal circuits and the pattern of their interaction (4, 5). Additional support for this hypothesis was supplied by investigations conducted with the use of mathematical and physical modelling (e.g., 18, 28, 29), which showed the relations between the behavior of the network (in the sense of signal generation), the structure of the network (forms of mutual interactions between elements) and the algorithm of its control.

The control of locomotor movements has been previously modelled in two ways: firstly (18) by investigating networks consisting of model of motoneurons, Renshaw cells and Ia interneurons with the aim of determining what role these elements play in pattern generation. The second approach (29) has been to model the input-output relations of higher order structures in order to discover their role in the overall behavior of the animal.

The purpose of this investigation was to examine some functional properties of a model system composed of model of motoneurons, Renshaw cells and Ia interneurons. We sought to establish the relations between the network structure and the generated pattern; the latter should correspond to the electrical activity of muscles.

The recorded pattern of muscle electrical activity is a constant transformation of motoneurons activity, so we assume that this pattern reflects the features of muscle control signal.

METHODS

Neurophysiological foundations. According to the contemporary opinions, the simplest subsystems of a spinal generator should be the neuronal nets controlling particular muscles. However, it is not established as yet which spinal elements form these nets. It is not known whether the circuits of spinal generator can be composed of neuronal elements coupled with executory elements, i.e., motoneurons (MNs), Renshaw cells
(RCs), Ia inhibitory interneurons (Ia INs). It is a difficult task to solve this problem, because the knowledge of the function of spinal interneurons systems is not sufficient for modelling. It is impossible to answer the question whether the system of spinal interneurons and tracts is a system coupling only particular subsystems of the spinal generator (generators for particular joints and limbs) or forms the generator by itself.

Model investigations showed that even simple networks can generate periodic signals. For instance a network composed of units corresponding to MNs, RCs and Ia INs can generate signals whose period depends on the tonic input control signal and the weight of couplings between units (18).

We decided to model a network composed of MNs, RCs and Ia INs connected according to the electrophysiologicaly established rules of interaction for the following muscles: tibialis anterior (TA), soleus (S) and gastrocnemius lateralis (GL). Such system can be a minimal non-trivial subsystem of spinal generator. "Nontrivial" means that this circuit can generate more complicated patterns than those which are characterized by alternate activity of units only. The scheme of the system with all physiologically possible connections between the elements is shown in Fig. 1.

The subsystems composed of MNs, RCs and Ia INs corresponding to

![Fig. 1. The diagram of the model of the examined net. Triangles represent units which correspond to: motoneurons of gastrocnemius lateralis (GL), soleus (S), tibialis anterior (TA); Ia interneurons (Ia); Renshaw cells (R). Solid lines, physiologically identified connections; broken lines, additionally examined connections; circles, inhibitory inputs; arrows-excitatory inputs; open arrows-tonic excitatory external inputs; arrows with circles-phasic, excitatory external inputs. Note that the weight of given input is denoted by the number of appropriate symbols.](image-url)
the particular muscles were represented in the model by single neuron-like units. Modelling with the structure of the network exactly corresponding to the structure of the modelled system was impossible because of technical reasons (limited number of elements). However, this simplification can be justified, because we were interested in global forms of the system behavior and because the fundamental static and dynamic properties of MNs, RCs and Ia INs nets were still preserved (the units were first order nonlinear elements).

The purpose of investigation was to establish whether, and under what conditions the above system would be able to generate a pattern corresponding to the physiological pattern of muscle activity. We decided to investigate the model with the fundamental system of connections—connections from MN unit to own RC unit, from RC unit to own MN unit and own Ia IN unit, from Ia IN unit to Ia IN and MN antagonistic units as well as the model with various forms of interactions between RC units and between RC and MN units corresponding to different muscles.

The spinal generators are under the influence of tonic and phasic signals coming from supraspinal centers and periphery. It is well known that alternating action of antagonistic muscles can be obtained after deafferentation (8, 14, 19). Moreover, it is known that afferent signals are under phasic control, which means that these signals are not fundamental from the point of view of generation (21, 22). For this reason the feedback loops from the receptors were not included in our model. The phasic influences from supraspinal centers are known from experimental investigations, but the tonic ones may be inferred only from experiments with DOPA (1, 25) and electrophysiological ones (27). We restricted our investigations to subsystems controlling the following muscles: TA, S and GL, because the activity of these muscles did not contain essential components connected with posture and coordination of limb and trunk muscles (20).

On the base of electrophysiological investigations we assumed the following characteristic properties of TA, S, GL muscle activity (control signals) (15,20):
1. For the rat (see Fig. 2a)
   — coactivation of TA and GL before and at the beginning of swing,
   — existence of pause in the activity of all muscles in a short interval during swing.
2. For the cat (see Fig. 2b)
   — coactivation of TA and S, GL at the end of swing and at the beginning of stance,
   — existence of pause in the activity of all muscles in a short interval of stance.
Fig. 2. Patterns of muscle activities during locomotion in rat (a) and cat (b), in relation to the swing. Note that coactivation “C” in “rat type” pattern is at the beginning of swing, while in “cat pattern” at the end of swing. Each row represents muscle activity (shadowed fields). Stance is denoted by the black area in the bottom row, swing by the open one. Other notations as in Fig. 1.

Model of the net. The model described here was constructed as a simple network composed of neuron-like analog electronic units. Input signals were supplied from external sources phasic and/or tonic and from outputs of k units of the network. The neuron-like units (described in detail in (7)) possessed the following properties characteristic for the neuron:

1. The static characteristic of the unit was determined by the following equation:

\[
y_i = \begin{cases} 
0 & \text{for } U_i \leq \theta, \\
\frac{c}{M} & \text{for } U_i \geq M, \\
\frac{a_i}{F_t[U_i - \theta]} & \text{otherwise},
\end{cases}
\]

where: \( y_i \) — frequency of output signal of the \( i \)-th unit, \( u_i \) — frequency of external input signal of the \( i \)-th unit, \( \theta_i \) — threshold of the unit, \( M \) — level of saturation, \( F_t \) — threshold monotonic function with saturation, \( c \) — constant, \( a_i \) — coefficient of amplification, \( w_{ij} \) — weight of the connection between \( i \)-th and \( j \)-th units, \( v_i \) — weight of external input of \( i \)-th unit.

2. Weights of inputs could be adjusted in the range from -10 to +10.

3. Each unit possessed a time constant \( \tau \) which could be adjusted in a range from 0 to \( \infty \).

4. Threshold could be adjusted in the range from 0 to \( \infty \).
5. All signals \( u_t, y_t \) could take on the relative values in the range from 0 to 1; \( y_t = 1 \) corresponded to the maximal excitation of unit obtained when the unit with \( \Theta_t = 0, a_t = 1, \tau_t = 0, v_t = 1 \) was excited with signal \( u_t = 1 \).

**RESULTS**

*Tonic control.* In order to establish the maximal repertoire of functional properties of spinal neuronal nets and to discover to what degree these nets can participate by themselves in the synthesis of control signals, we analyzed six variants of the model.

1. The first variant had the following connections: from MN unit to own RC unit, from RC unit to own MN and Ia IN units, from Ia IN unit to Ia IN and MN antagonistic units. The diagram of connections is shown in Fig. 1 and explained in Table I. Thresholds of all units were

\( \theta_t = 0.5; \) coefficients of amplification \( a_t = 0.5, \) time constants of MN and RC units were equal 0.14 s and that of Ia IN units were equal 0.

The model generated periodic signals after tonic excitation of all units except the RC. An example of generated pattern is given in Fig. 3. After additional tonic excitation of RC units comparable to excitation of other units the system behaved like a monostable one. The cycle duration of generated pattern could be influenced by the tonic signal only, to a small degree.
When synergetic units were given equal levels of excitation the pattern of these units was the same (symmetrical). Unequal excitation of such units, for instance MN units, led to nonsymmetrical patterns. The system generated cyclic pattern for external tonic input excitations $u_t > 0.3$. The critical connection, from the point of view of generation, was the one between RC and Ia units.

![Fig. 3. Patterns of activity of model units corresponding to motoneurons. The network was driven by minimal (a) and maximal (b) tonic excitations only (see Fig. 1), all RC—MN loops were intact. Details of unit connections are explained in the text (variant 3).](image)

To examine the role of RC units we investigated the behavior of 5 variants of the network with additional (in comparison with variant 1) feed-back loops including connections from RC units to synergetic and antagonistic MN and RC units, as shown in Fig. 1 and explained in Table II. The weights of these additional connections were equal — 1 (all other connections as in variant 1).

The influence of the additional connections on the properties of the network was as follows:

2. The network with connections between RC units behaved in a similar manner as in variant 1 (this connection did not change the properties of pattern).

3. The network with connections from RC units to the corresponding antagonistic and synergetic MN units generated a pattern whose period could be adjusted in the range $T_{\text{min}} = 0.6 - T_{\text{max}} = 0.9 \text{ s}$ by tonic signal of MN and Ia IN units equal for all units and varied in the range $u_{\text{min}} = 0.3 - u_{\text{max}} = 1$. 
The matrix of the weights of additional connections between the elements of the network — variants 2, 3, 4, 5, 6. Element \( ij \) in \( k \)-th row of the matrix corresponds to the weight of connection between \( i \)-th and \( j \)-th units for \( k \)-th variant.

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4. The network with connections between RC units and connections from RC units to the corresponding antagonistic and synergetic MN units did not clearly change cycle duration after tonic signal was varied.

Because the connections between RC units and MN and RC units corresponding to the antagonistic pools are not reliably known, we also modelled the following situations:

5. The network with connections from RC units to their synergetic MN units,

6. The network with connections between synergetic RC units and connections from RC units to their synergetic MN units. The behavior of the network in variants 5 and 6 was similar to variants 3 and 4, but the cycle duration was shorter for the same level of tonic excitation.

This means that the pattern cycle duration was only controllable by a tonic signal in the networks which lacked inhibitory connections between RC units. It should be stressed that the influence of the above described connections on the shape of the pattern was negligible.

The behaviour of the network was stable for changes of the weights of connections in the range of at least \( \pm 20\% \) in addition to the stability with regard to the above described changes of the connections and tonic excitations (of course some details of pattern were changed, but the process of generation was preserved). The pattern generated by the
symmetrical network met the fundamental condition, i.e., alternating activity of TA and S, GL, but did not comply with the condition of coactivation.

It appeared that to obtain a pattern with appropriate coactivation of TA and GL units in the rat and TA and S, GL units in the cat it was necessary to introduce some changes in the structure of the network. According to our result in the case of tonic control it was sufficient to break connections between appropriate RC and its MN unit to obtain coactivation. Because it was not possible to disconnect RC and MN units in the situation when there were physical connections of the RC unit with the other units, we modelled a system with inhibited RC units. Inhibition of course decreased the influences of the given RC unit on all MN, RC, Ia IN units with which the contacts were established. In variants 1–4 the inhibition of the RC/GL unit made it possible to obtain patterns with coactivation of the MN/TA and MN/GL units and, moreover, the activity of the MN/TA unit was shortened. Activity of the MN/GL unit lasted longer than that of the MN/S unit. The MN/TA unit was active in the time interval between the end of the MN/S unit activity and the beginning of the MN/S and MN/GL units activity. A pause was observed in the activity of all MN units after the end of the MN/TA unit activity. The system was adjustable: in variant 3 the variation of tonic input excitation of the MN and Ia IN units from $u_{\text{imin}} = 0.3$ to $u_{\text{imax}} = 1$ chan-

Fig. 4. "Rat type" patterns of activity of model units corresponding to motoneurons. The network was driven by minimal (a) and maximal (b) tonic excitation only (see Fig. 1). Details of unit connections are explained in the text. Coactivation is denoted by "C".
ged the period of activity nearly twice. The generated patterns are shown in Fig. 4. These patterns corresponded to the patterns of rat S, TA and GL muscle activity, recorded during walk (15).

Inhibition of the RC/TA unit made it possible to obtain patterns corresponding to patterns of cat S, TA and GL muscles (20). The generated patterns are shown in Fig. 5. Coactivation of the MN/TA and MN/S, MN/GL units was observed at the end of the MN/TA activity—at the end of swing and at the beginning of stance phases. To obtain this pattern it was necessary to decrease the weight of tonic input of the Ia IN/TA unit—from 1.0 to 0.9. These effects could be obtained both in the case of full inhibition of the RC units, as well as when only the weights of the RC unit excitatory inputs were decreased (the units could be still active).

In variants 5 and 6 the conditions of coactivation were a little different. To obtain a model pattern corresponding to the pattern of rat muscle activity it was necessary to decrease only the weight of connection between RC/GL and MN/GL units. The pattern corresponding to the pattern of cat muscles could be obtained either when the weight of connection between the RC/TA and MN/TA units was decreased or when the RC/TA unit was inhibited but not switched off. This means that in variants 5 and 6 some level of the RC units activity was necessary to obtain the required pattern.

Fig. 5. “Cat type” patterns of activity of model units corresponding to motoneurons. The network was driven by minimal (a) and maximal (b) tonic excitation only (see Fig. 1). Details of unit connections are explained in the text. Coactivation is denoted by “C”.
The above results were obtained in the situation when the MN/GL, MN/S and Ia IN units were excited with equal tonic signals. We also investigated the behavior of the network in the case of nonsymmetrical excitation of units. It appeared that after the tonic signal of one MN unit was decreased or increased, the time interval in which the unit was active was also changed in the same direction. Moreover, it was observed that the activity of nonsymmetrically excited synergetic MN units started at different time moments. It appeared that it was possible to obtain coactivation by this method, but the differences between the beginnings of unit activity produced a nonphysiological pattern. In the case when the effective tonic excitatory signal was increased both for the MN/S and MN/GL units by increasing the input weight $v_i$ to 3, the pattern of coactivation similar to the pattern of cat muscles activity was observed, but the pause in the muscle activity was absent. Nonsymmetrical tonic influences on Ia IN units gave a similar effect as in the case of nonsymmetrical influences on MN units. In effect the pattern of "rat type" could be obtained only after the inhibition of RC/GL unit, and the pattern of "cat type" after the inhibition of RC/TA unit.

*Phasic control.* It appeared that phasic excitatory control signals supplied additionally to MN units were an essential in the generation of the network output.

A short phasic signal supplied to MN unit in the basic network (case 1) caused additional bursts of MN unit activity as shown in Fig. 6a. When some threshold value of phasic signal duration had been exceeded, the synchronization of the network with the source of this signal was observed and the burst originating from phasic control "stuck" to the

*Fig. 6* "Rat type" patterns of activity of model units corresponding to motoneurons. The network was driven by short phasic signal (a) and phasic signal of suprathreshold duration (b) (see Fig. 1). Details of unit connections are explained in the text.
one generated by the network itself as shown in Fig. 6b. It appeared that it was possible to prolong the MN unit activity to such a degree that coactivation of antagonistic units was observed. If both MN/S and MN/GL units had been excited with an additional phasic signal, it was possible to obtain the pattern of “cat type” with appropriate coactivation. It should be stressed that in the case of the network controlled with phasic signal on the background of tonic signal, the period of generated pattern could be adjusted in a broader range by way of synchronization with phasic signal than in the case of tonic signal alone.

As mentioned above, the network could generate only if at least two loops from RC to Ia' IN units were intact. Therefore, the analysis of the network behavior when RC units were switched off was possible only in the case of phasic control. It appeared that with RC units switched off, it was possible to obtain the alternate pattern of MN units activity with phases of coactivation after the excitation of these units with tonic as well as phasic signals.

It should be mentioned that when all units (also Ia IN) had been excited with phasic signals only, the network repeated this signal and did not form any characteristic pattern. In the case of phasic and tonic signals the period of the network pattern was equal to the period of phasic signal, but the phasic signal as a pattern was not repeated simply by the network, but was transformed into a specific pattern with coactivation. Moreover, the duration of MN units activity was also a specific property of the network and was correlated but not equal to the duration of phasic excitatory impulses.

These results can be summarized in the following way:

1. The network with a fundamental system of connections (variant 1-RC units influenced only own MN and Ia IN units) generated a symmetrical pattern, whose cycle duration could be controlled by the tonic signal only to a small degree.

2. Feed-back loops between RC units (variant 2) did not change the network controllability.

3. Feed-back loops from RC units to synergetic MN units or synergetic and antagonistic MN units (variant 3) made it possible to control the cycle duration by tonic signal.

4. Feed-back loops between RC units in the network with feed-back loops from RC units to synergetic MN units or synergetic and antagonistic MN units (variant 4) cancelled the possibility to control the cycle duration by tonic signal.

5. To obtain appropriate coactivation of MN units it was necessary to supply either additional inhibitory signals to RC units or phasic excitatory signals to MN units.
DISCUSSION

We can conclude that the system shown in Fig. 1, modelling the neuronal system of motoneurons, Renshaw cells and Ia interneurons, is able to generate patterns corresponding to the pattern of muscle activity observed in locomotor movement. The discussed system is a nontrivial one in the sense that corresponds to the main set of muscles acting in one joint, and not to a simple pair of two antagonistic muscles. The obtained results supply arguments in favour of the hypothesis that the lowest circuit of spinal locomotor generator can be composed of motoneurons, Renshaw cells and Ia interneurons. These elements can work as a generator in result of their appropriate excitation and coupling. The appropriate pattern could be generated when only tonic signals were used. It was not necessary to supply phasic supraspinal or afferent signals.

The system can be adjusted in the sense of period duration by both tonic and phasic signals. It appears that the phasic signal acting on the background of tonic signal is more effective than tonic or phasic alone; the network with phasic excitation alone is not able to generate the appropriate pattern. These findings correspond to the observed excitatory role of DOPA or nonspecific influences on spinal elements in a spinal animal (Afelt, personal communication).

The obtained results bring also some data on the base of which more detailed conclusions regarding the role of Renshaw cells are possible.

The analysis of behavior of the net made it possible to conclude that feed-back loops among RC units corresponding to different muscles almost cancel the influence of the intensity of the tonic signal on the period of generated pattern. On the other hand, the feed-back loops from RC units on MN units corresponding to synergetic and antagonistic muscles create a relationship between the intensity of the tonic signal and the period. The singular loops: RC—MN and RC—Ia IN can be selectively inhibited without loss of generation and what is more the inhibition of loops made it possible to obtain patterns which corresponded to patterns of muscle activity observed during walk in the rat and the cat.

It is not possible to discuss in details the obtained results in terms of physiological data because anatomical data concerning the connections of Renshaw cells are not yet available. Anatomical investigations do not exclude the possibility of connections between the Renshaw cells and motoneurons corresponding to synergetic and antagonistic muscles.

The observed influence of selective inhibition of Renshaw cells on the generated pattern is consistant with physiological data on the inhi-
bition of Renshaw cells during locomotion (3). Hultborn's (11) investigations show that the Renshaw cells also obtain synaptic inputs from sources other than motoneuron axon collaterals. That means that Renshaw cells can be controlled independently of motoneuron control. During controlled locomotion in high decerebrate cats, Ia inhibitory interneurons exhibit activity modulated in phase with that in motoneurons belonging to the same muscles which give Ia input to the motoneurons. Phasic entrainment of Ia interneuron discharge during the step cycle persists after complete de-efferentation of the hindlimbs, thus removing movement as a source of fluctuating Ia input. This result indicates phasic control of Ia interneurons by the intraspinal mechanism that generates the step cycle, since the effect is also unmodified by the removal of the cerebellum, which in turn removes the projection in descending pathways known to project to Ia interneurons (2). This fact suggests that some subsystems of the spinal generators may be formed of the net composed of Ia interneurons and neuronal cells connected to them. Jankowska et al. (13), postulated that motoneurons receive phasic postsynaptic excitatory signals from an unknown source during locomotor movements. They also proposed that this source rather than the disinhibition of motoneurons in the loop MN—RC—Ia IN—MN caused alternating activity of the neuronal system and that Renshaw cells were not important for motoneuron timing. Our results are not contradictory and show that the system MN—RC—Ia IN is controllable by means of phasic and tonic signals and that the cooperation of both signals is necessary to obtain the final pattern. The same applies to the Renshaw cells, which are not the only element to contribute to the timing of motoneuron firing. Renshaw cells may also participate in the way that influences from higher centers control spinal circuits. We are concerned here with one of the most common principles of the nervous system operation: a given function is not realized by a single mechanism but by a specific cooperation of many. However, each of them can assure the realization of this function to some degree. There are also some physiological data (9, 17) showing that locomotion is still possible after pharmacological disruption of the interactions between Renshaw cells and other elements of the described net. Our modelling suggests that a much greater degree of control of motoneuron firing is possible when Renshaw cells are also subject to phasic and tonic inputs originating from extrinsic centers. We therefore propose that effects of extrinsic tonic and phasic inputs on the final pattern of motor output may be partially mediated by Renshaw cells.

In summary, the subsystem MN—RS—Ia IN is an important element of the whole spinal generator system. Ultimately it forms muscle
levels of the system as well as from other MN — RC — Ia IN subsystems. The basic alternating pattern can be obtained for various methods of coupling of RC and MN units. To obtain patterns with coactivation, additional influences on connections between RC and MN units should be introduced. The system can generate alternating signals if excited only with tonic signals or alternatively by a specific pattern of unspecific phasic signals acting on a background of tonic signals.

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