ON STRUCTURES OF THE MUSCLE CONTROL SYSTEM

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Summary

On the basis of many neurophysiological data and some results of modelling, several diagrams are given which illustrate some principles and structural properties which are found in the motor system of the nervous system. These principles are considered taking into account the possibilities of occuring of optimal or suboptimal systems in the muscle control system. An approximate partition of the hierarchic motor system on several levels performing different functions is presented. Particular attention is paid to the lowest level of the hierarchy which contains peripherico-spinal loops of muscle control. It is stressed that all feedback loops in the muscle control system as well as all couplings among circuits controlling different cooperating muscles may have variable amplification. Depending on the values of the amplifications which are set up, the system may be adopted to different movement which must be performed. It is emphasized that it is very purposeful to use similar solutions in control systems of artificial limbs and manipulators.

Introduction

Despite a great number of studies, particularly neurophysiological, concerning the structure and function of the muscle control system it is very difficult to set forth even a very general schematic of that system. However we do have some more information about the lowest part of that complex system, which permits us to draw some connections and circuits and to pick up some structural properties of the lowest levels of the motor system hierarchy. The importance of the knowledge of these structures is appreciated not only by physiologists and physicians but also by investigators and developers of artaficial limbs. Moreover the subject is very interesting from the control engineer's point of view, especially when considered as an optimal system. Such a point of view seems to be necessary for an understanding of the many properties of motor systems as well as for an application of their principles not only for designing the control circuits of artificial limbs and manipulators but also for designing the complex automatic control systems for other purposes.

The investigation of a control system as an optimal system requires the establishment of the general aim of the arrangement taking into account the existing constraints as well as optimality criteria. It is well known that the general aim of the motor system is to cause a movement of a limb, a part of the body, or the whole body, or to sustain a position against external forces. The selection of appropriate values formation or resistance must be made taking into account the following additional factors:

1. Mechanical constraints among different parts of the body.
2. Mutual position and velocity at the beginning of the movement.
3. The influence of inertia of the body and supported objects.
4. The influence of external forces (i.e. gravity).

From the midst of different dynamic tasks which are performed by the motor system it is reasonable to select two kinds of movements:

1. Precise, usually voluntary movements which are performed with maximal time and space accuracy.
2. Stereotype, usually fast and rhythmic movements with considerable contribution of reflexes and small contribution at higher control level.

The conversion from the first to the second kind of movements involves considerable changes in structure and properties of the circuit involved in the control, and sometimes with changes of optimality criterion.

There exist different views concerning optimality factors which may be taken into account in movement control but with enough evidence it may be stated that the following criteria may be involved:

1. Accuracy in space as well as in time of the trajetory or final point of the movement.
2. Velocity in the meaning of the minimal time which is needed to achieve the final point.
3. Effort in the meaning of minimal energy consumption.
4. Size of the structures involved in movement control.

The last criterion is less obvious but is very important for general behavior of the organism especially under difficult conditions. That criterion is of importance in the application of extremely complicated control circuits in large systems.

There exist many reasons for the statement that particular muscle control circuits are approximate to optimal systems since they accomplish their task efficiently.

General Structure of the Motor Control System

In the various levels of the motor system so many different centers are involved that every introduction of general classification causes many controversies. In Figure 1 the most important centers and connections of the motor system are presented and the following levels of hierarchy are introduced:

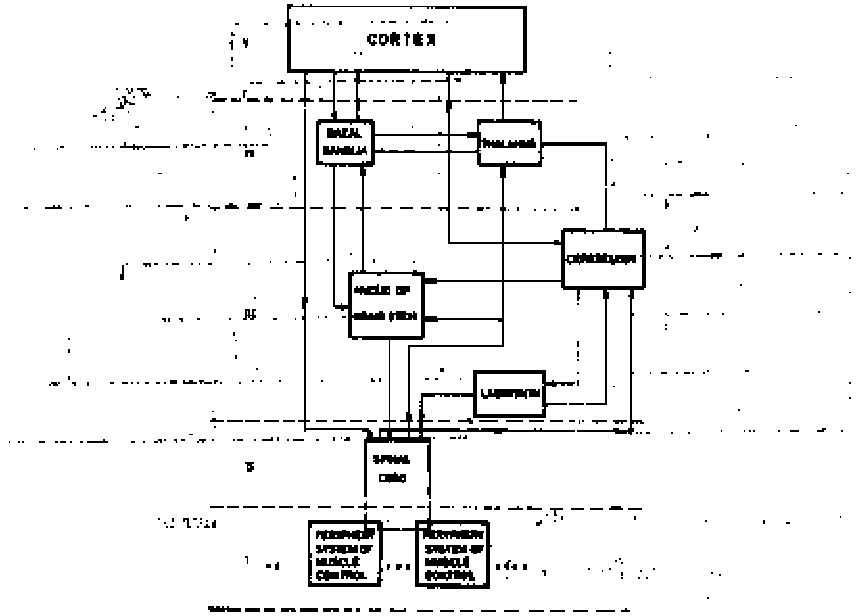

Fig. 1. Principal centers and connections in the motor control system.

1. A set of feedback loops involving an actuator namely the muscle with appropriate sensing elements. That level we shall call periphérico-spinal level.
2. A segment of spinal cord participating in coordination of collaborating muscles.
3. A set of supraspinal centers involving reticular formation, vestibular system, and cerebellum. It is accepted usually that that assembly forms a coordinating and corrective system.
4. A set of subcortical nuclei forming basal ganglia including thalamus. That set participates in programming, coordination and creating of stereotypes.
5. Cerebral cortex— the highest coordination and decision center.

In general two kinds of connection rules of particular levels in hierarchic system are possible (Fig. 2 a and b). In the first kind every level is connected only with neighbouring levels and in the second one there exist connections among every level. Comparing these schemes with that one given in Figure 1 it is easy to see that in motor systems the second kind of connections exists. It is of great importance for speed and precision of information and decision transmission, and also for separation of functions among different levels, especially for the possibility of change of autonomy at the lower levels.

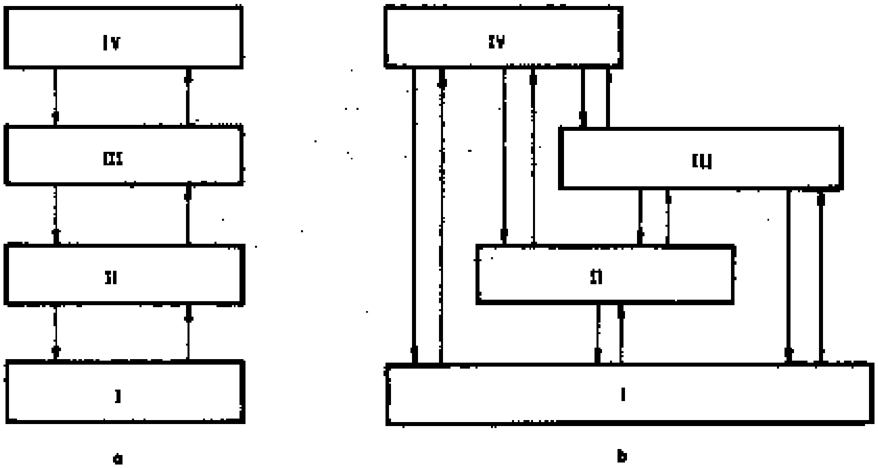

Fig. 2. Principal possibilities of interconnections in hierarchical systems.

Some Properties of the Peripherico-Spinal Level of the Muscle Control System

A complete diagram of all known feedback loops embodying muscle function would be very complicated, and would contain at least eight different circuits. In Figure 3 only four of the most important feedback loops are shown:

(I) — Spindle primary loop giving information to the motoneuron about changes of the length of the muscle — in effect about the difference among length of the muscle and length of the spindle.

(II) — Golgi-organ loop giving the information about the strength developed by the muscle.

(III) — Renshaw cells loop which has some stabilising function.

(IV) — A loop containing tactile receptors which plays an important role in limb movement.

Similar diagrams have been described in [1], [2], and [3] but it is reasonable to complete these descriptions with some remarks which are important from the point of view of optimal control. First of all in many papers (see [5] and [6]) it is emphasized that the excitability of every loop i.e. the resultant amplification in the loop may be controlled by supraspinal signals as well as by loops controlling other muscles. As it results from Grufinkel's work [7] it is possible that at the first phase of the movement control the amplification factor in the loop (I) is very close to unity. Therefore the system is very close to self-oscillation and the process of contraction is very fast. In the next phase of the movement, the contraction of the muscle causes a decrease of spindle excitation and the amplification factor in that loop decreases. From control theory we know that a decrease of amplification reduces the overshoot.

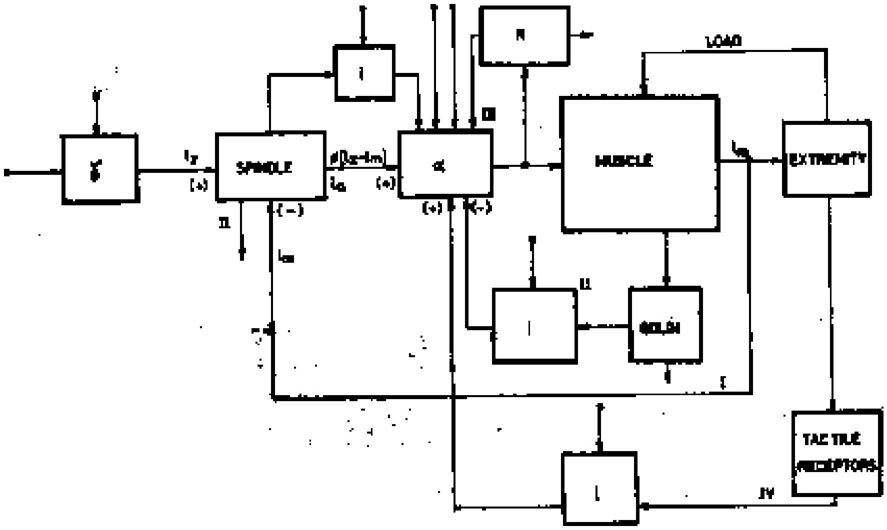

Fig. 3. Control loops for a single muscle.

From many investigations of spindles and their afferents we know that the feedback signal in the loop (I) is proportional not only to the measured value (being the difference of the length of the spindle and of the extra-fusal fibers), but mainly to the first derivative. As a result, we deal here with PD (proportional-derivative) control which is well known in control theory. Such control surpasses the proportional control from the point of view of time optimality. Besides, as we know from many experiments (see for ex. [8]) there exist two sorts of afferent fibers controlling spindle contraction namely static γ— fibers and dynamic γ— fibers. Static fibers control in principle generation of afferent signals which are proportional to input signal (difference of the length). On the other hand the dynamic fibers affect the signals which in the first approximation are proportional to the first derivative of length. Then there exists the possibility of independent influence on P-control and D-control.

The opinion which is sometimes delivered that the Golgi loop protects only muscle against overload seems to be oversimplified. It is worthwhile to emphasize that that loop plays an important role in muscle coordination owing to many interneuronal connections. Much interest is evoked by the role of Renshaw-cells loop.

The fact that the Renshaw loop forms negative feedback indicates stabilising functions performed by that loop. Some neurological data suggests that the Renshaw cells play an important role in desynchronization of α-cells, excitation of which increases the smoothness of muscle contraction. To verify that opinion some investigations on neural net model (Fig. 4) were done in the laboratory of Bionics in the Institute of Automatic Control in Warsaw. The investigations were done with the help of four neuron models and four Renshaw cell models. The appropriate connections are shown in Figure 5. It appeared that that kind of connection assures proper desynchronization of α-cells. An individual pulse (with the duration of five to ten miliseconds) applied to all α-cells does not excite all cells simultaneously but causes individual, slightly delayed firing of cells. Moreover it was stated that the effect of desynchronization is smaller not only after exclusion of a Renshaw cell but also after reduction of the number of α-cells in the net. The situation is similar to the situation in the first phase of poliomyelitis when some cells in ventral horn of spinal cord are damaged. As we shall see a little further, Renshaw cells played an important role in collaboration of two antagonistic muscles.

Fig. 4. Neural net model.

In conclusion we may say that the peripherico-spinal system of muscle control containing some different feedback-loops with nonlinear elements with controlled properties (excitability) and many inputs is well adapted for optimisation.

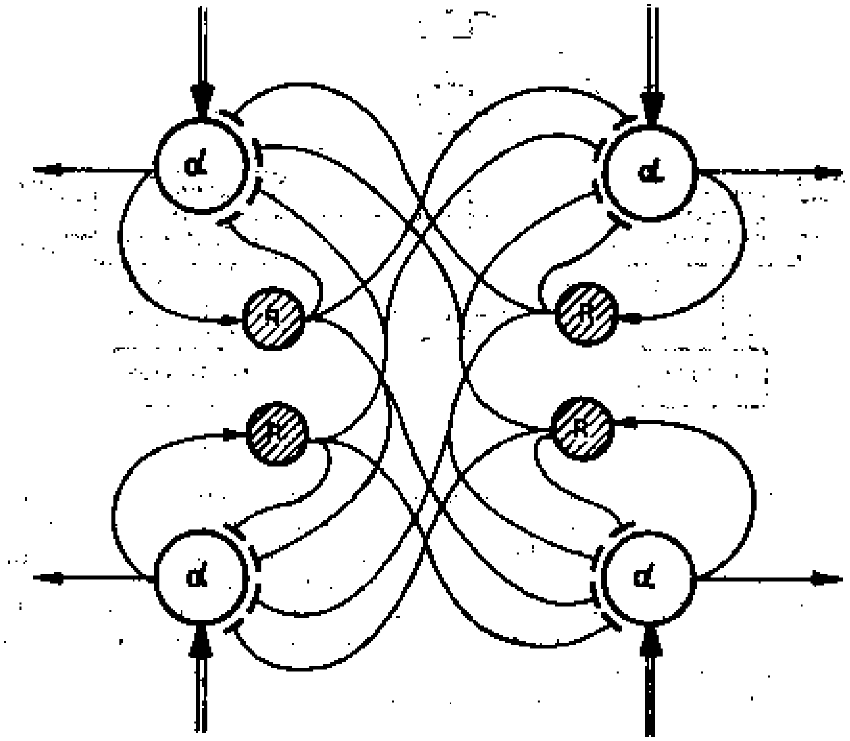

Fig. 5. Modelling of desynchronization.

Remarks Concerning Coordination of the Antagonistic Muscle Control

In the classical work of Sherrington it is stated that there exists mutual coordination among antagonistic muscles. The well known rule of reciprocal innervation shows that there exists an antagonistic action in control of flexion and extension. In many further works it was shown that among control systems of two antagonistic muscles there exists a full assembly of positive as well as negative connections. These connetions are shown roughly in Figure 6. As we see in every connection there exist some intermediary elements (interneurons). Excitability (i.e. amplification factor) of these elements may be varied through broad range, with help of some additional multiplying inputs which are influenced by supraspinal signals.

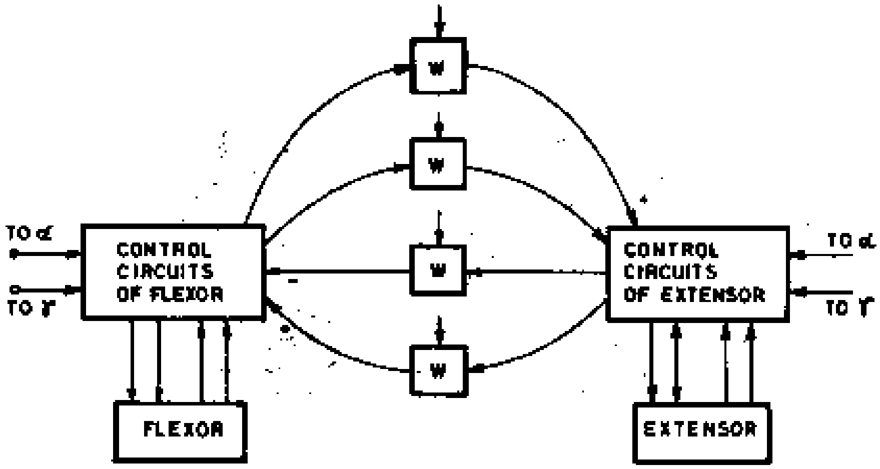

Fig. 6. Diagram of collaboration of antagonistic muscles.

Taking into account well known results from electronic circuit theory, especially multivibrators, and also some results from simple neuron circuit modelling, we may notice that two kinds of operation of such antagonistic control circuits are possible:

1. Operation with strong mutual couplings when the whole system works similarly to a bistable multivibrator or a self oscilating multivibrator (depending on the degree of inhibition of every part of the system).
2. Operation with weak mutual couplings but with strong upper control of every muscle.

The first kind of operation we may observe when the subject performs rhythmic, stereotypic movements and when one can discover physiologycally a strong antagonistic action among opposing muscles (for example during a scratching reflex). The supraspinal influence is then limited only to setting up proper couplings. The second kind of operation appears during slow but precise movements which are controlled by higher centers.

In general the system with the structure shown in Figure 6, i.e. containing many inputs which affect the dynamics of controlled objects is, from the automatic control point of view, a well controlled system. It is very easy to set up optimal condition in such system.

The very simplified picture of mutual connections may be completed thanks to many up-to-date works concerning properties of spinal connections particularly that of Lundberg [5], [6], E. Jankowska [10], [11] and others. However the results do not give a complete image of cooperative structure even among a single pair of antagonistic muscles. The first question which appears here is whether the influence of one control system (for flexion for example) on the second one (for extension for example) has a multiplicative or additive character, i.e. whether the signals from the antagonistic muscle are added or change the excitability of the appropriate neuron only. Besides it is very important to establish which signals are exciting and which are inhibiting ones, and also in what manner one gets stable performance of the whole system in spite of the existence of so many feedback loops. An idea about the character of couplings is given in the diagrams which are presented by Lundberg (Fig. 7). We shall not go into details of these diagrams

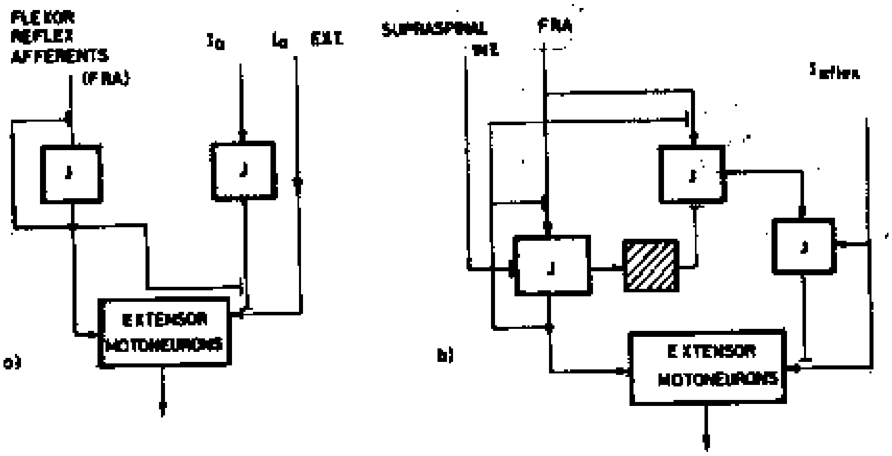

Fig. 7. Examples of interconnections in the spinal cord.

which may be found in Lundberg's paper [6] but it is worthy to notice that in such structures some controlled connections exist. The value of the coupling through such connections (frequency of transmitted signals) is that the system may be controlled through additional inputs which may be influenced from supraspinal centers as well as from the peripheral ones. We may select often two sorts of connections. The operation of the connection of the first sort has a very short duration, but the others operate much longer after the excitation and may solve static tasks [6].

The structure of the connections from Renshaw cells proposed by E. Jankowska may serve as good example of mutual influences in control loops (Fig. 8). The internuntial neuron "I" transmitting inhibition from primary spindle fibres to the antagonists may be excited by supraspinal influences. Excitation of internuntial neurons causes, of course, an enhancement of mutual reciprocity. At the same time the firing of α-cells of the antagonist, which may affect not only the static state but first of all the dynamics of the processes in that pair of antagonistic muscles.

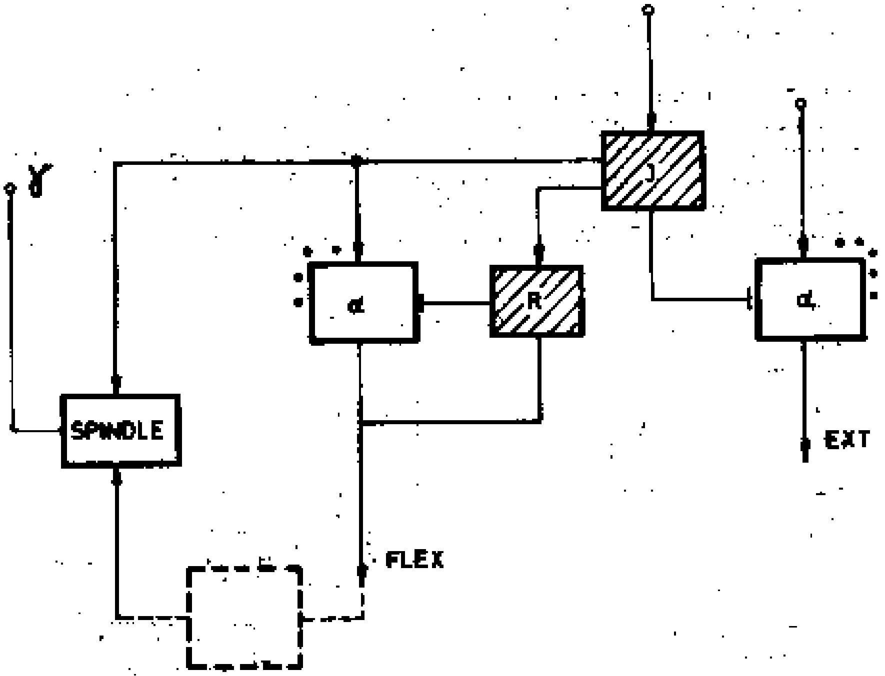

Fig. 8. Connections of Renshaw cells.

In Figure 9a general structure containing most important connections among antagonists is presented. As we see there exists a complete set of connections; namely, mutual excitation, mutual inhibition as well as "inhibition of inhibition", and the value of every connection may be controlled Such a structure in spite of the simplifications introduced, has so many inputs that the possibility of setting up the optimal conditions, as well as generation of stereotypic movements is much greater than in conventional automatic control systems. Particularly, one may say that a muscle control system gets current information about the processes in control loops of antagonistic muscles.

It is striking that in muscle control circuits there are so many inhibiting signals which have crucial influence on the stability of the whole system, but these problems need much more investigations. Moreover the cognition of general properties, especially the dynamic properties of such a complicated control system needs particular investigation including modelling and general analysis of the described structures. The problem becomes complicated also because the properties of particular elements, especially dynamic elements are known to a minimal degree. For example the existence of inputs with presynaptic inhibition which have presumably multiplicative character and also the existence of short feedback loops have fundamental significance in fast, dynamic processes.

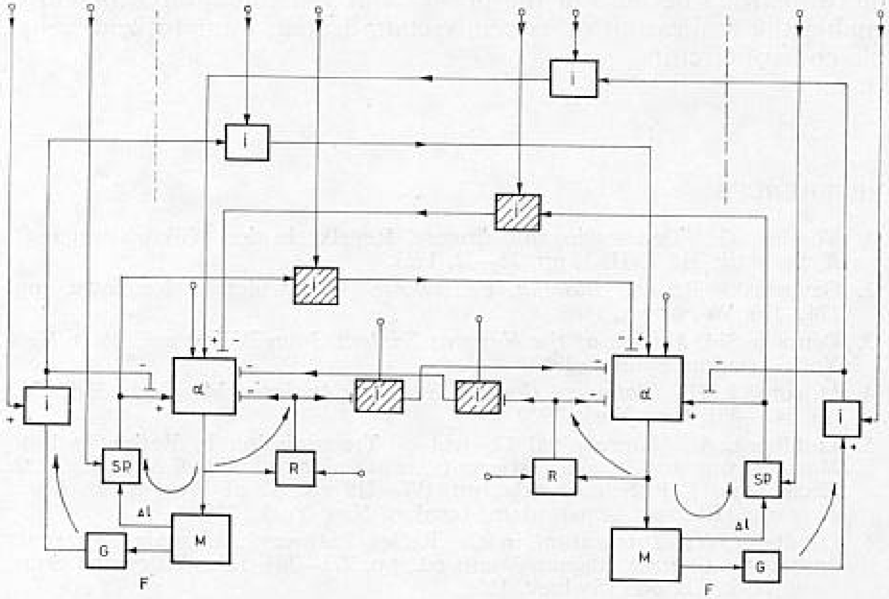

Fig. 9. Coordination between two antagonistic muscles.

Concerning the often formulated hypothesis about statistical connection rules in neural nets, we must emphasize that just the motor system and particularly its lower level has in general well identified structure. We do not speak here about detailed separation of particular synaptic connections which may be unidentified but rather about rules of connection which are identified in general.

It is easy to guess that a symmetrical situation of two antagonistic musles leads to symmetry in corresponding control circuits but when two antagonistic muscles are not in symmetrical situation, due to the influence of the force of gravity for example, then the corresponding control circuits are also asymetric [2], [12]. We have then an additional indication that control systems are in some way adapted to the performed task and to existing constraints mentioned in the introduction.

Considering the performace of some up-to-date solutions of artificial limb, it is easy to notice that the designers avoid use of complicated automatic control systems. This of course has negative influence on artificial limb performance. It is evident that the reasons for this are difficulties in selection of proper control circuits and reliability of control circuits applied and additional requirements concerning power sources. It seems obvious that existing muscle control systems can suggest many reasonable solutions and many of the properties of the circuits presented here may be implemented in control circuits of artificial limbs. This is now even more justified because of the presence of integrated circuits which enable the realization of extremly complicated, miniaturized, reliable control circuits.

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