

A MODEL FOR THE SPINAL CONTROL OF ANTAGONISTIC MUSCLES

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Abstract

A model is developed and analysed for two antagonistic muscles working against a common load and controlled by spinal circuitry. The connections of α - and γ -motoneurons, as well as IA inhibitory interneurons and Renshaw Cells are included, together with descending inputs onto these spinal neurons. Special cases are considered in which control is carried out solely by α -motoneurons, γ -motoneurons, IA interneurons or Renshaw Cells, as well as the case when feedback from the muscles is eliminated. The roles of muscles and loads, feedback pathways, spinal circuitry and descending inputs in the production of oscillatory movements are discussed.

1. Introduction

Muscles are normally arrayed in antagonistic groups to produce movements in two directions about a joint. The spinal cord has a variety of options in controlling these antagonistic groups. One or the other may be activated selectively to varying degrees or they can be coactivated to increase the stiffness about a joint (reviewed by Stein, 1982). To produce a single, rapid movement a characteristic pattern is often observed in which one group (the so-called agonist muscles) are activated to get the movement going, then the antagonist muscles are activated to brake the movement and finally the agonist muscles are activated again to stabilize the limb at the intended, final position (Hallett *et al.*, 1975). While such patterns of activation seem to “make sense” qualitatively, there have been few attempts to analyse such movements quantitatively (but see Hatze, 1980). In producing a particular pattern, is the nervous system attempting to minimize the energy consumed by the muscles, the time to reach the end point, the oscillation about the end point or some combination of these goals?

In order to examine such questions we have considered a simple model (see Fig. 1) consisting of two muscles (muscles 1 and 2 enclosed by dotted lines) working in opposite directions against a common load, consisting in general of a mass M , an external spring of stiffness K_e and a dashpot of viscosity D (Oğuztörel and Stein, 1982). To permit as many analytic results to be derived as possible, we have assumed initially that each muscle behaves linearly, although important nonlinearities can easily be added (Hatze, 1977; Stein and Oğuztörel, 1982). Muscles will clearly only behave linearly over a restricted range of positions, and over a small range the differences between the body's angular coordinates and the linear movements in Fig. 1 can be ignored.

A particular pattern of activity in muscles can also be produced in a variety of ways by the spinal cord (Fig. 2). In principle, descending inputs could activate

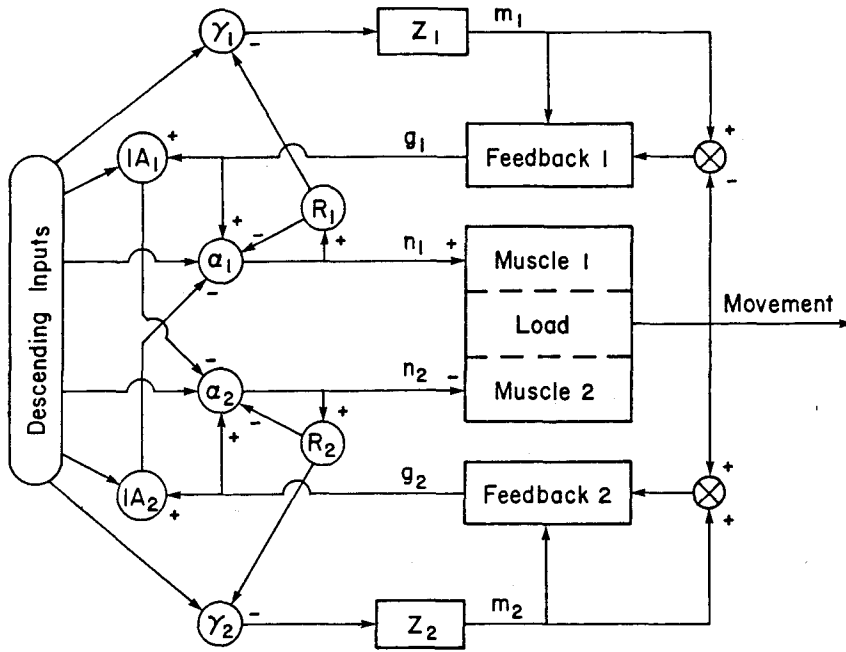


Fig. 1. Pattern of connections of descending inputs to spinal neurons, antagonistic muscles and their load. Details of the nomenclature are given in the text.

α -motoneurons with a preprogrammed pattern to generate the desired movement. In practice, the smaller γ -motoneurons are also activated to varying degrees (Matthews, 1972). These motoneurons do not exert enough force to produce measurable movements of the whole muscle, but they do produce contractions of intrafusal muscle fibres (whose properties are indicated by the boxes labelled Z_1 and Z_2), which in turn modify the feedback coming from the muscle spindle receptors. This is done through a simple summation of the desired movements m_1 and m_2 produced by the intrafusal muscle fibres and the actual movement, as well as more complex effects on the gain of the feedback (Matthews, 1972; Stein and Ögüztörel, 1981).

The feedback, particularly from the primary muscle spindle afferents (IA fibres), directly excites their own α -motoneurons and through the action of particular interneurons (IA₁ and IA₂ in Fig. 2) inhibits the antagonist motoneurons. Interestingly, these interneurons receive many of the same descending inputs as the α -motoneurons and may be involved in determining the extent to which the different muscle groups are activated alternatively or together (Hultborn, 1977). One other well-known type of inhibitory interneuron, the Renshaw cell (R_1 and R_2) has also been included in Fig. 2. These interneurons are excited by activity in α -motoneurons and in turn inhibit the same group of α -motoneurons (Renshaw, 1941; Cleveland and

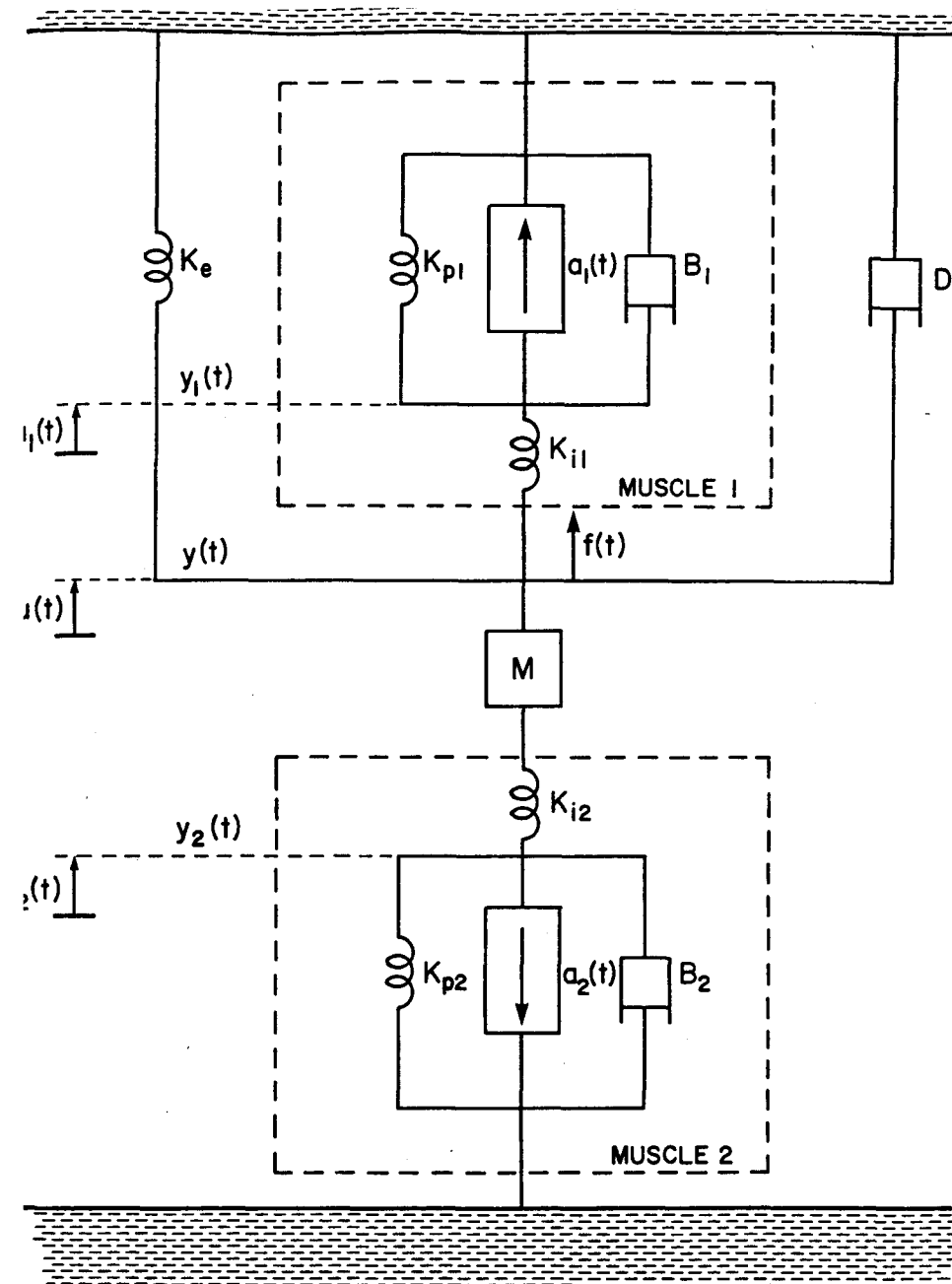


Fig. 2. The simple viscoelastic model of the muscles, including active force generating elements ($a_j(t)$) and a generalized load consisting of a mass, a dashpot and a spring. The $y(t)$ measure positions with respect to a fixed point, whereas the $u(t)$ are deviations from the steady-state position. Further details in the text and Ögüztörel and Stein (1982).

Ross, 1977). However, the Renshaw cells have also been shown to inhibit γ -motoneurons to almost the same extent as α -motoneurons (Ellaway and Murphy, 1981).

One reason for including the well-known connections from IA inhibitory interneurons and Renshaw cells, is that Miller and Scott (1977) have shown that these connections alone, in the absence of connections to the muscles or feedback from the muscles, are sufficient to produce the rhythmic alternating patterns normally observed during locomotion. However, by experimentally blocking these inhibitory connections (Menzies *et al.*, 1978) and eliminating phasic feedback (Jordan *et al.*, 1979), the locomotory patterns could still be produced by stimulating descending inputs. Thus, these interconnections are not necessary for producing locomotion.

In the next section we describe the model mathematically and then in successive sections analyse the simplifications that result if descending inputs excite α -motoneurons alone, γ -motoneurons alone, IA interneurons alone or Renshaw cells alone. Experimentally, there is little evidence for descending inputs onto Renshaw cells, so this section is included mainly for mathematical completeness. A final section deals with the important simplifications that result in the absence of feedback, in which movements are produced "open loop". The strengths of the spinal connections shown (and other connections which might have been added to Fig. 2) are not known accurately, so it is not our purpose here to present detailed simulations. Rather, we are interested in the general form of the solutions. To the extent that the connections can be specified, simulations may be presented in a subsequent publication.

2. Modelling and mathematical description of the system

The basic models for the antagonistic muscular and neuromuscular systems considered in the previous section are shown in Fig. 1 and Fig. 2, respectively. Some of the notation is indicated in the figure, and further details are listed below (with some minor changes in the nomenclature from the earlier ones (cv. Oğuztöreli and Stein, 1975-77, 1979-80, Stein and Oğuztöreli, 1976a,b, 1981).

LIST OF SYMBOLS

- j : index for the muscles, $j = 1, 2$;
- r : index for the reflex pathways, $r = 1, 2, 3$;
- B_j : viscosity of the active state element of the j -th muscle;
- β_j : rate constant for the decay of the active state of the j -th muscle;
- D : viscosity or external damping of the load;
- K_e : stiffness of the external elastic elements in the load;
- K_{ij} : stiffness of elastic elements internal to the j -th muscle, but in series with the j -th active state element;
- K_{pj} : stiffness of elastic elements in parallel with active state element of the j -th muscle;
- M : mass;

- $F_{0j}H_{jr}$: the sensitivity (or in general the gain) of the j -th muscle receptors in the r -th feedback pathway: $F_{0j} \geq 0$, $H_{jr} \geq 0$, $H_{j1} + H_{j2} + H_{j3} = 1$;
- F_{1j} : the gain in the γ_j -motoneuron pathway;
- t_{rj} : pure time delays in the r -th feedback pathway for the j -th muscle which in general will arise in nervous conduction, sensory transmission and excitation-contraction coupling: $t_{j1} < t_{j2} < t_{j3}$;
- τ_{1rj} : the time constant which indicates the velocity sensitivity of the r -th reflex pathway of the j -th muscle;
- τ_{2rj} : the time constant which indicates the acceleration sensitivity of the r -th reflex pathway of the j -th muscle;
- t : time (s);
- s : Laplace variable;
- $\delta(t)$: the Dirac delta function;
- $a_j(t)$: active state of the j -th muscle at time t ;
- $f(t)$: external force at time t ;
- $n_j(t)$: neural input to the active state of the j -th muscle at time t ;
- $i_{\alpha_j}(t)$: input on α_j -motoneuron to the j -th muscle at time t ;
- $i_{\gamma_j}(t)$: input on γ_j -motoneuron to the j -th muscle at time t ;
- $IA_j(t)$: inhibitory activities from IA_j interneuron at time t ;
- $R_j(t)$: inhibitory activities from R_j Renshaw interneuron at time t ;
- $u(t), u_1(t)$: deviations from the equilibrium positions at time t ;
- $V(s)$: Laplace transform of a time function $v(t)$;

$$(2.1) \quad V(s) = \int_0^t v(t)e^{-st} dt \quad (v(t) \leftrightarrow V(s));$$

- $z_j(t)$: the shortening generated by the j -th muscle in response to the γ_j -motoneuron impulses, which is the inverse Laplace transform of the γ_j -motoneuron pathway transfer function

$$(2.2) \quad Z_j(s) = \frac{F_{1j}}{(s + \zeta_{1j})(s + \zeta_{2j})},$$

where ζ_{1j} and ζ_{2j} are nonnegative constants, $F_{1j} \geq 0$, $\zeta_{1j} \approx 10$ and $\zeta_{2j} \approx 30$;

- $h_{rj}(t)$: the sensory feedback in the r -th pathway for the j -th muscle,
- $$(2.3) \quad h_{rj}(t) = F_{0j}H_{rj}[u_j(t - t_{rj}) + (\tau_{1rj} + \tau_{2rj})\dot{u}_j(t - t_{rj}) + \tau_{1rj}\tau_{2rj}\ddot{u}_j(t - t_{rj})];$$
- $h_j(t)$: the total sensory feedback for the j -th muscle,

$$(2.4) \quad h_j(t) = \sum_{r=1}^3 h_{rj}(t) \\ = F_{0j} \sum_{r=1}^3 H_{rj}[u_j(t - t_{rj}) + (\tau_{1rj} + \tau_{2rj})\dot{u}_j(t - t_{rj}) + \tau_{1rj}\tau_{2rj}\ddot{u}_j(t - t_{rj})]$$

Note that the functions $u(t)$, $u_1(t)$, and $u_2(t)$ are determined by the convolution integrals

$$(2.5) \quad u(t) = \int_0^t [\tilde{p}(t-\tau)n_1(\tau) + \tilde{q}(t-\tau)n_2(\tau) + r(t-\tau)f(\tau)]d\tau,$$

$$u_j(t) = \int_0^t [\tilde{p}_j(t-\tau)n_1(\tau) + \tilde{q}_j(t-\tau)n_2(\tau) + r_j(t-\tau)f(\tau)]d\tau,$$

$j=1,2$, where $\tilde{p}(t)$, $\tilde{q}(t)$, $\tilde{p}_j(t)$, $\tilde{q}_j(t)$, $r(t)$, and $r_j(t)$ are the inverse Laplace transforms of $\tilde{P}(s)$, $\tilde{Q}(s)$, $\tilde{P}_j(s)$, $\tilde{Q}_j(s)$, $R(s)$ and $R_j(s)$, respectively (cf. Oğuztöreli and Stein, 1982a):

$$(2.6) \quad \begin{aligned} \tilde{P}(s) &= P(s)/(s + \beta_1), & \tilde{P}_j(s) &= P_j(s)/(s + \beta_1) \\ \tilde{Q}(s) &= Q(s)/(s + \beta_2), & \tilde{Q}_j(s) &= Q_j(s)/(s + \beta_2) \end{aligned}$$

and

$$(2.7) \quad \begin{aligned} P(s) &= K_{i1}(B_2s + K_{i2} + K_{p2})/W(s) \\ Q(s) &= -K_{i2}(B_1s + K_{i1} + K_{p1})/W(s) \\ R(s) &= (B_1s + K_{i1} + K_{p1})(B_2s + K_{i2} + K_{p2})/W(s) \\ P_1(s) &= [(Ms^2 + Ds + K_e + K_{i1} + K_{i2})(B_2s + K_{i2} + K_{p2}) - K_{i2}^2]/W(s) \\ Q_1(s) &= -K_{i1}K_{i2}/W(s) \\ R_1(s) &= P(s) \\ P_2(s) &= -Q_1(s) \\ Q_2(s) &= [K_{i1}^2 - (Ms^2 + Ds + K_e + K_{i1} + K_{i2})(B_1s + K_{i1} + K_{p1})]/W(s) \\ R_2(s) &= -Q(s), \end{aligned}$$

where

$$(2.8) \quad \begin{aligned} W(s) &= (Ms^2 + Ds + K_e + K_{i1} + K_{i2})(B_1s + K_{i1} + K_{p1})(B_2s + K_{i2} + K_{p2}) \\ &\quad - K_{i1}^2(B_2s + K_{i2} + K_{p2}) - K_{i2}^2(B_1s + K_{i1} + K_{p1}) \\ &= \alpha^{-1}(s^4 + c_3s^3 + c_2s^2 + c_1s + c_0) \end{aligned}$$

with

$$(2.9) \quad \begin{aligned} \alpha &= (B_1B_2M)^{-1} \\ c_0 &= \alpha\{K_e(K_{i1} + K_{p1})(K_{i2} + K_{p2}) + K_{i1}K_{p1}(K_{i2} + K_{p2}) + K_{i2}K_{p2}(K_{i1} + K_{p1})\} \\ c_1 &= \alpha\{D(K_{i1} + K_{p1})(K_{i2} + K_{p2}) + K_e[B_1(K_{i2} + K_{p2}) + B_2(K_{i1} + K_{p1})] \\ &\quad + K_{i1}[B_1(K_{i2} + K_{p2}) + B_2K_{p1}] + K_{i2}[B_2(K_{i1} + K_{p1}) + B_1K_{p2}]\} \\ c_2 &= \alpha\{M(K_{i1} + K_{p1})(K_{i2} + K_{p2}) + D[B_1(K_{i2} + K_{p2}) + B_2(K_{i1} + K_{p1})] \\ &\quad + B_1B_2(K_e + K_{i1} + K_{i2})\} \\ c_3 &= \alpha\{M[B_1(K_{i2} + K_{p2}) + B_2(K_{i1} + K_{p1})] + B_1B_2D\} \end{aligned}$$

Considering the signal flow in the block diagram in Fig. 2, we successively find the following relationships:

$$(2.10) \quad \begin{aligned} U(s) &= \tilde{P}(s)N_1(s) + \tilde{Q}(s)N_2(s) + R(s)F(s) \\ \tilde{U}_j(s) &= \tilde{P}_j(s)N_1(s) + \tilde{Q}_j(s)N_2(s) + R_j(s)F(s) \\ N_1(s) &= I_{\alpha_1}(s) + G_1(s) - \theta_1R_1(s) - \theta_2LA_2(s) \\ N_2(s) &= I_{\alpha_2}(s) + G_2(s) - \theta_3R_2(s) - \theta_4LA_1(s) \\ LA_1(s) &= I_{1A_1}(s) + G_1(s) & (IA_j(t) \leftrightarrow LA_j(s)) \\ LA_2(s) &= I_{1A_2}(s) + G_2(s) \\ R_j(s) &= N_1(s)/(s + \delta_j) & (R_j(t) \leftrightarrow R_j(s)) \\ G_1(s) &= H_1(s)[-U_1(s) + M_1(s)] \\ G_2(s) &= H_2(s)[U_2(s) + M_2(s)] \\ M_1(s) &= [I_{\gamma_1}(s) - \theta_5R_1(s)]Z_1(s) \\ M_2(s) &= [I_{\gamma_2}(s) - \theta_6R_2(s)]Z_2(s), \end{aligned}$$

$$H_j(s) = F_{0j} \sum_{r=1}^3 H_{rj} [1 + (\tau_{1rj} + \tau_{2rj})s + \tau_{1rj}\tau_{2rj}s^2] e^{-st_{rj}}$$

where $\delta_1, \delta_2, \theta_1, \dots, \theta_6$ are certain nonnegative numbers. As defined in Eq. (2.10), δ_1, δ_2 are rate constants determining the period over which inputs from α -motoneurons are integrated by Renshaw cells.

θ_1, θ_3 are the strengths of connections from Renshaw Cells to α -motoneurons. θ_2, θ_4 are the strengths of connections from IA inhibitory interneurons to α -motoneurons and

θ_5, θ_6 are the strengths of connections from Renshaw Cells to γ -motoneurons.

In the following we shall omit the argument of a Laplace transform $V(s)$ and denote it simply by V . By successive back substitutions we find

$$(2.11) \quad \begin{aligned} M_1 &= I_{\gamma_1}Z_1 - \frac{\theta_5}{s + \delta_1}Z_1N_1 \\ M_2 &= I_{\gamma_2}Z_2 - \frac{\theta_6}{s + \delta_2}Z_2N_2 \\ G_1 &= -H_1U_1 + I_{\gamma_1}H_1Z_1 - \frac{\theta_5}{s + \delta_1}H_1Z_1N_1 \\ G_2 &= H_2U_2 + I_{\gamma_2}H_2Z_2 - \frac{\theta_6}{s + \delta_2}H_2Z_2N_2 \\ LA_1 &= -H_1U_1 + I_{1A_1} + I_{\gamma_1}H_1Z_1 - \frac{\theta_5}{s + \delta_1}H_1Z_1N_1 \\ LA_2 &= -H_2U_2 + I_{1A_2} + I_{\gamma_2}H_2Z_2 - \frac{\theta_6}{s + \delta_2}H_2Z_2N_2 \end{aligned}$$

and

$$(2.12) \quad \begin{aligned} \left(1 + \frac{\theta_1 + \theta_5 H_1 Z_1}{s + \delta_1}\right) N_1 - \frac{\theta_2 \theta_6 H_2 Z_2}{s + \delta_2} N_2 &= C_1 - [H_1 U_1 + \theta_2 H_2 U_2] \\ - \frac{\theta_4 \theta_5 H_1 Z_1}{s + \delta_1} N_1 + \left(1 + \frac{\theta_3 + \theta_6 H_2 Z_2}{s + \delta_2}\right) N_2 &= C_2 + [\theta_4 H_1 U_1 + H_2 U_2] \end{aligned}$$

where

$$(2.13) \quad \begin{aligned} C_1 &\equiv C_1(s) = [I_{\alpha_1} - \theta_2 I_{1A_2}] + [I_{\gamma_1} H_1 Z_1 - \theta_2 I_{\gamma_2} H_2 Z_2], \\ C_2 &\equiv C_2(s) = [I_{\alpha_2} - \theta_4 I_{1A_1}] + [I_{\gamma_2} H_2 Z_2 - \theta_4 I_{\gamma_1} H_1 Z_1]. \end{aligned}$$

Put

$$(2.14) \quad C \equiv C(s) = (s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1)(s + \delta_2 + \theta_3 + \theta_6 H_2 Z_2) - \theta_2 \theta_4 \theta_5 \theta_6 H_1 H_2 Z_1 Z_2.$$

Then, by solving the system (2.12), we obtain

$$(2.15) \quad \begin{aligned} N_1 &= \frac{s + \delta}{C} \{ -[s + \delta_2 + \theta_3 + \theta_6(1 - \theta_2 \theta_4) H_2 Z_2] H_1 U_1 \\ &\quad - \theta_2 (s + \delta_2 + \theta_3) H_2 U_2 \\ &\quad + (s + \delta_2 + \theta_3 + \theta_6 H_2 Z_2) C_1 + \theta_2 \theta_6 H_2 Z_2 C_2 \} \\ N_2 &= \frac{s + \delta_2}{C} \{ \theta_4 (s + \delta_1 + \theta_1) H_1 U_1 \\ &\quad + [s + \delta_1 + \theta_1 + \theta_5(1 - \theta_2 \theta_4) H_1 Z_1] H_2 U_2 \\ &\quad + \theta_4 \theta_5 H_1 Z_1 C_1 + (s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1) C_2 \} \end{aligned}$$

Further, put $V_{jk} = V_{jk}(s)$, $X = X(s)$, $X_j = X_j(s)$, and

$$(2.16) \quad \begin{aligned} V_{j0} &= (s + \delta_1) \{ (s + \delta_2 + \theta_3 + \theta_6 H_2 Z_2) C_1 + \theta_2 \theta_6 H_2 Z_2 C_2 \} \tilde{P}_j \\ &\quad + (s + \delta_2) \{ \theta_4 \theta_5 H_1 Z_1 C_1 + (s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1) C_2 \} \tilde{Q}_j \\ &\quad + C R_j F, \\ V_{11} &= C + \{ (s + \delta_1) [s + \delta_2 + \theta_3 + \theta_6(1 - \theta_2 \theta_4) H_2 Z_2] \tilde{P}_1 \\ &\quad - \theta_4 (s + \delta_2) (s + \delta_1 + \theta_1) \tilde{Q}_1 \} H_1 \\ V_{12} &= \{ \theta_2 (s + \delta_1) (s + \delta_2 + \theta_3) \tilde{P}_1 \\ &\quad - (s + \delta_2) [s + \delta_1 + \theta_1 + \theta_5(1 - \theta_2 \theta_4) H_1 Z_1] \tilde{Q}_1 \} H_2 \\ V_{21} &= \{ (s + \delta_1) [s + \delta_2 + \theta_3 + \theta_6(1 - \theta_2 \theta_4) H_2 Z_2] \tilde{P}_2 \\ &\quad - \theta_4 (s + \delta_2) (s + \delta_1 + \theta_1) \tilde{Q}_2 \} H_1 \\ V_{22} &= C + \{ \theta_2 (s + \delta_1) (s + \delta_2 + \theta_3) \tilde{P}_2 \\ &\quad - (s + \delta_2) [s + \delta_1 + \theta_1 + \theta_5(1 - \theta_2 \theta_4) H_1 Z_1] \tilde{Q}_2 \} H_2 \\ X_1 &= V_{10} V_{22} - V_{20} V_{12} \\ X_2 &= V_{20} V_{11} - V_{10} V_{21} \\ X &= V_{11} V_{22} - V_{12} V_{21} \end{aligned}$$

We now combine Eqs. (2.15), (2.16), and the second formula in (2.10) with $j=1$ and $j=2$. We then find

$$(2.17) \quad \begin{aligned} V_{11} U_1 + V_{12} U_2 &= V_{10} \\ V_{21} U_1 + V_{22} U_2 &= V_{20} \end{aligned}$$

whose solution is of the form

$$(2.18) \quad U_j(s) = X_j(s)/X(s) \quad (j=1,2)$$

Further, by combining Eqs. (2.15), (2.18), and the first formula in (2.10), we find

$$(2.19) \quad U(x) = \frac{Y(s)}{X(s)} + Y_0(s),$$

where $Y_0 = Y_0(s)$ and $Y = Y(s)$ are defined by the following equations:

$$(2.20) \quad \begin{aligned} Y_0 &= \frac{s + \delta_1}{C} \{ (s + \delta_2 + \theta_3 + \theta_6 H_1 Z_1) C_1 + \theta_2 \theta_6 H_2 Z_2 C_2 \} \tilde{P} \\ &\quad + \frac{s + \delta_2}{C} \{ \theta_4 \theta_5 H_1 Z_1 C_1 + (s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1) C_2 \} \tilde{Q}, \\ Y &= \frac{s + \delta_2}{C} \{ \theta_4 (s + \delta_1 + \theta_1) H_1 X_1 + (s + \delta_1 + \theta_1 + \theta_5) (1 - \theta_2 \theta_4) H_1 Z_1 H_2 X_2 \} \tilde{Q} \\ &\quad - \frac{s + \delta_1}{C} \{ \theta_4 (s + \delta_2 + \theta_3) H_2 X_2 + (s + \delta_2 + \theta_3 + \theta_6(1 - \theta_2 \theta_4) H_2 Z_2) H_1 X_1 \} \tilde{P} \end{aligned}$$

The movement of the antagonistic neuromuscular system described in Fig. 2 is completely determined by Eqs. (2.18) and (2.19).

Before closing this section, we note that the functions

- (i) \tilde{P} , \tilde{Q} , R , \tilde{P}_j , \tilde{Q}_j , and R_j are determined by muscle properties;
- (ii) H_j , Z_j , and C are determined by the gains in the sensory pathways and/or in the γ -motoneuron pathways;
- (iii) C_1 and C_2 are determined by the neural inputs on α - and γ -motoneurons, by the (inhibitory) activities from Renshaw cells and IA interneurons, and by gains in the sensory feedback and γ -motoneuron pathways;
- (iv) V_{j1} , V_{j2} , X and Y are determined by the muscle properties, and by the gains in the sensory feedback and γ -motoneuron pathways;
- (v) V_{j0} , X_j , and Y_0 are determined by the properties of the muscles, by the external load, by the neural inputs on α - and γ -motoneurons, by the neural activities of Renshaw and IA interneurons, and by the gains in the sensory feedback and γ -motoneuron pathways.

The general system equations in the time domain can be established by invoking the inverse Laplace transforms of Eqs. (2.18) and (2.19). This process involves lengthy calculations and yield rather complicated functional differential equations. However, computer simulations can be implemented by using Eqs. (2.18) and (2.19) only.

Before considering the behavior of the general case, we shall briefly discuss some physiologically significant special cases. These discussions will give some insight on the complicated functioning of the antagonistic neuromuscular system.

3. Systems governed by α -motoneurons

When an antagonistic neuromuscular system is governed by α -motoneurons only, and if there is not any external load, then we have

$$(3.1) \quad \begin{aligned} F &= I_{\gamma_1} = I_{\gamma_2} = I_{A_1} = I_{A_2} = \mathbf{R}_1 = \mathbf{R}_2 = Z_1 = Z_2 = 0 \\ \theta_1 &= \theta_2 = \theta_3 = \theta_4 = \theta_5 = \theta_6 = 0. \end{aligned}$$

In this case Eqs. (2.13), (2.14) and (2.16) reduce to

$$(3.2) \quad \begin{aligned} C_j &= I_{\alpha_j} \\ C &= (s + \delta_1)(s + \delta_2) \\ V_{j0} &= (s + \delta_1)(s + \delta_2)(I_{\alpha_1}\tilde{P}_j + I_{\alpha_2}\tilde{Q}_j) \\ V_{11} &= (s + \delta_1)(s + \delta_2)(1 + H_1\tilde{P}_1) \\ V_{12} &= -(s + \delta_1)(s + \delta_2)H_2\tilde{Q}_1 \\ V_{21} &= (s + \delta_1)(s + \delta_2)H_1\tilde{P}_2 \\ V_{22} &= (s + \delta_1)(s + \delta_2)(1 - H_2\tilde{Q}_2) \end{aligned}$$

and

$$(3.3) \quad \begin{aligned} X &= (s + \delta_1)^2(s + \delta_2)^2(1 - \tilde{X}) \\ X_1 &= (s + \delta_1)^2(s + \delta_2)^2\tilde{X}_{1\alpha} \\ X_2 &= (s + \delta_1)^2(s + \delta_2)^2X_{2\alpha} \\ Y &= (s + \delta_1)^2(s + \delta_2)^2\tilde{Y}_\alpha \\ Y_{0\alpha} &= I_{\alpha_1}\tilde{P} + I_{\alpha_2}\tilde{Q} \end{aligned}$$

where

$$(3.4) \quad \begin{aligned} \tilde{X} &= H_1\tilde{P}_1 + H_2\tilde{Q}_2 + H_1H_2(\tilde{P}_1\tilde{Q}_2 - \tilde{Q}_1\tilde{P}_2) \\ \tilde{X}_{1\alpha} &= (I_{\alpha_1}\tilde{P}_1 + I_{\alpha_2}\tilde{Q}_1)(1 - H_2\tilde{Q}_2) + (I_{\alpha_1}\tilde{P}_2 + I_{\alpha_2}\tilde{Q}_2)H_2\tilde{Q}_1 \\ \tilde{X}_{2\alpha} &= (I_{\alpha_1}\tilde{P}_2 + I_{\alpha_2}\tilde{Q}_2)(1 + H_2\tilde{Q}_2) - (I_{\alpha_1}\tilde{P}_1 + I_{\alpha_2}\tilde{Q}_1)H_1\tilde{P}_2 \\ \tilde{Y}_\alpha &= [(I_{\alpha_1}\tilde{P}_2 + I_{\alpha_2}\tilde{Q}_2)(1 + H_2\tilde{Q}_2) - (I_{\alpha_1}\tilde{P}_1 + I_{\alpha_2}\tilde{Q}_1)H_1\tilde{P}_2]H_2\tilde{Q} \\ &\quad - [(I_{\alpha_1}\tilde{P}_1 + I_{\alpha_2}\tilde{Q}_1)(1 - H_2\tilde{Q}_2) + (I_{\alpha_1}\tilde{P}_2 + I_{\alpha_2}\tilde{Q}_2)H_2\tilde{Q}_2]H_1\tilde{P}. \end{aligned}$$

Hence,

$$(3.5) \quad U_j = \tilde{X}_{j\alpha}/(1 - \tilde{X}), \quad U = Y_{0\alpha} + \tilde{Y}_\alpha/(1 - \tilde{X}).$$

Thus, we have

$$(3.6) \quad U_j = \tilde{X}_{j\alpha} + \tilde{X}U_j$$

and

$$(3.7) \quad U = (\tilde{Y}_\alpha + Y_{0\alpha} - Y_{0\alpha}\tilde{X}) + \tilde{X}U.$$

Eqs. (3.6) and (3.7) differ only on their forcing terms.

We now put

$$(3.8) \quad \tilde{\Gamma} = \tilde{P}_1\tilde{Q}_2 - \tilde{Q}_1\tilde{P}_2 \quad (\tilde{\Gamma}(s) \Leftrightarrow \tilde{\gamma}(t)).$$

It can easily be verified that

$$(3.9) \quad H_1H_2 = F_{01}F_{02} \sum_{i=1}^3 \sum_{j=1}^3 H_{i1}H_{j2}(1 + \lambda_{1ij}s + \lambda_{2ij}s^2 + \lambda_{3ij}s^3 + \lambda_{4ij}s^4)e^{-s(t_{i1} + t_{j2})}$$

where

$$(3.10) \quad \begin{aligned} \lambda_{1ij} &= \tau_{1i1} + \tau_{2i1} + \tau_{1j2} + \tau_{2j2} \\ \lambda_{2ij} &= \tau_{1i1}\tau_{2i1} + \tau_{1j2}\tau_{2j2} + (\tau_{1i1} + \tau_{2i1})(\tau_{1j2} + \tau_{2j2}) \\ \lambda_{3ij} &= \tau_{1i1}\tau_{2i1}(\tau_{1j2} + \tau_{2j2}) + \tau_{1j2}\tau_{2j2}(\tau_{1i1} + \tau_{2i1}) \\ \lambda_{4ij} &= \tau_{1i1}\tau_{2i1}\tau_{1j2}\tau_{2j2} \end{aligned}$$

Then, the inverse Laplace transforms of Eqs. (3.6) and (3.7) yield the functional differential equations

$$(3.11) \quad u_j(t) = \tilde{x}_{j\alpha}(t) + L(u_j)(t)$$

and

$$(3.12) \quad u(t) = [\tilde{y}_\alpha(t) + y_{0\alpha}(t) - \int_0^t y_{0\alpha}(\sigma)x(t - \sigma)d\sigma] + L(u)(t)$$

where the integro-differential operator L is defined by the equation

$$(3.13) \quad \begin{aligned} L(v)(t) &= F_{01} \sum_{i=1}^3 \left\{ H_{i1} \int_0^t [v(\sigma - t_{i1}) + (\tau_{1i1} + \tau_{2i1})\dot{v}(\sigma - t_{i1}) \right. \\ &\quad \left. + \tau_{1i1}\tau_{2i1}\ddot{v}(\sigma - t_{i1})]\tilde{P}_1(t - \sigma)d\sigma \right\} \\ &+ F_{02} \sum_{i=1}^3 \left\{ H_{i2} \int_0^t [v(\sigma - t_{i2}) + (\tau_{1i2} + \tau_{2i2})\dot{v}(\sigma - t_{i2}) \right. \\ &\quad \left. + \tau_{1i2}\tau_{2i2}\ddot{v}(\sigma - t_{i2})]\tilde{Q}_2(t - \sigma)d\sigma \right\} \\ &+ F_{01}F_{02} \sum_{i=1}^3 \sum_{j=1}^3 \left\{ H_{i1}H_{j2} \int_0^t [v(\sigma - t_{i1} - t_{j2}) + \lambda_{1ij}\dot{v}(\sigma - t_{i1} - t_{j2}) \right. \\ &\quad \left. + \lambda_{2ij}\ddot{v}(\sigma - t_{i1} - t_{j2}) + \lambda_{3ij}\ddot{v}(\sigma - t_{i1} - t_{j2}) \right. \\ &\quad \left. + \lambda_{4ij}v^{(4)}(\sigma - t_{i1} - t_{j2})\tilde{\gamma}(t - \sigma)d\sigma \right\}. \end{aligned}$$

Let us note that the operator L simplifies considerably when the system is not acceleration sensitive, i.e. $\tau_{2ij}=0$, $i=1,2,3$, $j=1,2$, and, the forcing terms in Eqs. (3.11) and (3.12) are simpler when

$$(3.14) \quad i_{\alpha_j}(t) = \delta(t) \Leftrightarrow I_{\alpha_j}(s) = 1,$$

i.e. the neuromuscular system is activated by a single initiation shock. Another relatively simple case is

$$(3.15) \quad i_{\alpha_j}(t) = \delta(t) + \mu \sin(\Omega t + \phi) \Leftrightarrow I_{\alpha_j}(s) = 1 + \frac{s \sin \phi + \Omega \cos \phi}{s^2 + \Omega^2},$$

i.e. an initiation shock followed by a persistent harmonic oscillation, where μ , Ω , and ϕ are constants, $\mu \geq 0$, $\Omega > 0$.

Now let $\phi = \phi(t)$ be a given sufficiently smooth function for $t \geq 0$ such that $\phi(t) = 0$ for $t < 0$. Consider the functional differential equation

$$(3.16) \quad v(t) = \phi(t) + L(v)(t) \quad (t \geq 0).$$

Put

$$(3.17) \quad t_0 = \max_{i,j} (t_{i1} + t_{j2}).$$

Let $\phi_\kappa = \phi_\kappa(t)$ ($\kappa=0,1,2,3,4$) be certain given sufficiently smooth functions on the interval $-t_0 \leq t \leq 0$. Then the functional differential equation (3.16) subjected to the initial conditions

$$(3.18) \quad v^{(\kappa)}(t) = \phi_\kappa(t) \quad (-t_0 \leq t \leq 0; \kappa=0,1,2,3,4)$$

admits a unique continuous solution for $t \geq 0$ and this solution can be constructed by continuous continuation into the future (cf. Oğuztörel, 1966).

The essential properties of the solutions of the functional differential equation organically depend on the form of the natural modes of the system. These modes correspond to the roots of the transcendental equation $1 - \tilde{X} = 0$, i.e.

$$(3.19) \quad H_1 \tilde{P}_1 + H_2 \tilde{Q}_2 + H_1 H_2 \Gamma - 1 = 0.$$

Eq. (3.19) has infinitely many roots in the complex s -plane and all these roots accumulate only at infinity. Further, the conjugate complex of a (characteristic) root is also a root since all the constants involved in Eq. (3.19) are real. Let $s = \rho \pm i\Omega$ be a pair of characteristic roots with multiplicity μ , where ρ and Ω are real and $i = \sqrt{-1}$, $\Omega > 0$. Then the corresponding natural mode is of the form

$$(3.20) \quad e^{\rho t} [A_\mu(t) \cos \Omega t + B_\mu(t) \sin \Omega t],$$

where $A_\mu(t)$ and $B_\mu(t)$ are polynomials of degree $\mu - 1$ with arbitrary coefficients.

It can be easily verified that Eq. (3.19) has a principal part in the sense of Pontryagin (cf. Pontryagin, 1942), and by a theorem of Pontryagin, all the characteristic roots, except finitely many, have negative real parts.

4. Systems governed by γ -motoneurons

When an antagonistic neuromuscular system is governed by γ -motoneurons only, and if there is not any external load exerting on the system, then

$$(4.1) \quad \begin{aligned} F &= I_{\alpha_1} = I_{\alpha_2} = I_{1A_1} = I_{1A_2} = R_1 = R_2 = 0, \\ \theta_1 &= \theta_2 = \theta_3 = \theta_4 = \theta_5 = \theta_6 = 0. \end{aligned}$$

In this case we have

$$(4.2) \quad \begin{aligned} C_j &= I_{\gamma_j} H_j Z_j \\ C &= (s + \delta_1)(s + \delta_2) \\ V_{j0} &= (s + \delta_1)(s + \delta_2)(I_{\gamma_1} H_1 Z_1 \tilde{P}_j + I_{\gamma_2} H_2 Z_2 \tilde{Q}_j) \\ V_{11} &= (s + \delta_1)(s + \delta_2)(1 + H_1 \tilde{P}_1) \\ V_{12} &= -(s + \delta_1)(s + \delta_2) H_2 \tilde{Q}_1 \\ V_{21} &= (s + \delta_1)(s + \delta_2) H_1 \tilde{Q}_2 \\ V_{22} &= (s + \delta_1)(s + \delta_2)(1 - H_2 \tilde{Q}_2) \\ X &= (s + \delta_1)^2 (s + \delta_2)^2 (1 - \tilde{X}_\gamma) \\ X_1 &= (s + \delta_1)^2 (s + \delta_2)^2 \tilde{X}_{1\gamma} \\ X_2 &= (s + \delta_1)^2 (s + \delta_2)^2 \tilde{X}_{2\gamma} \\ Y &= (s + \delta_1)^2 (s + \delta_2)^2 \tilde{Y}_\gamma \\ Y_0 &= (s + \delta_1)^2 (s + \delta_2)^2 \tilde{Y}_{0\gamma} \end{aligned}$$

where

$$(4.3) \quad \begin{aligned} \tilde{X}_\gamma &= \tilde{X} = H_1 \tilde{P}_1 + H_2 \tilde{P}_2 + H_1 H_2 \Gamma \\ \tilde{X}_{1\gamma} &= (I_{\gamma_1} H_1 Z_1 \tilde{P}_1 + I_{\gamma_2} H_2 Z_2 \tilde{Q}_1)(1 - H_2 \tilde{Q}_2) + (I_{\gamma_1} H_1 Z_1 \tilde{P}_2 + I_{\gamma_2} H_2 Z_2 \tilde{Q}_2) H_2 \tilde{Q}_1 \\ \tilde{X}_2 &= (I_{\gamma_1} H_1 Z_1 \tilde{P}_2 + I_{\gamma_2} H_2 Z_2 \tilde{Q}_2)(1 + H_2 \tilde{Q}_2) - (I_{\gamma_1} H_1 Z_1 \tilde{P}_1 + I_{\gamma_2} H_2 Z_2 \tilde{Q}_1) H_1 \tilde{P}_2 \\ \tilde{Y} &= H_2 \tilde{X}_2 \tilde{Q} - H_1 \tilde{X}_{1\gamma} \tilde{P} \\ \tilde{Y}_{0\gamma} &= I_{\gamma_1} H_1 Z_1 \tilde{P} + I_{\gamma_2} H_2 Z_2 \tilde{Q} \end{aligned}$$

Thus,

$$(4.4) \quad \begin{aligned} U_j &= \tilde{X}_{j\gamma} + \tilde{X} U_j \\ U &= (\tilde{Y}_\gamma + \tilde{Y}_{0\gamma} - \tilde{Y}_{0\gamma} \tilde{X}) + \tilde{X} U \end{aligned}$$

or, equivalently,

$$(4.5) \quad \begin{aligned} u_j(t) &= \tilde{x}_{j\gamma}(t) + L(u_j)(t), \\ u(t) &= [\tilde{y}_\gamma(t) + \tilde{y}_{0\gamma}(t) - \int_0^t \tilde{y}_{0\gamma}(\sigma) x(t - \sigma) d\sigma] + L(u)(t), \end{aligned}$$

where L is the functional differential operator defined by Eq. (3.13). Hence, $u(t)$ and $u_j(t)$ satisfy the same functional differential equation, Eq. (3.16), with different forcing

terms. It is interesting to note that the natural modes in the present case are the same as in the previous case. This represents an extension of a result previously obtained for a single muscle with γ -inputs (Oğuztöreli and Stein, 1981).

5. Systems governed by IA_j interneurons

In this section we consider antagonistic neuromuscular systems governed by IA_j interneurons only. We assume here also that $F=0$, i.e. there is not any external force acting on the system. In this case we have

$$(5.1) \quad \begin{aligned} F=I_{\alpha_1}=I_{\alpha_2}=I_{\gamma_1}=I_{\gamma_2}=\mathbf{R}_1=\mathbf{R}_2=0, \\ \theta_1=\theta_3=\theta_5=\theta_6=0, \end{aligned}$$

and

$$(5.2) \quad \begin{aligned} C_1 &= -\theta_2 I_{IA_2}, \quad C_2 = -\theta_4 I_{IA_1} \\ C &= (s + \delta_1)(s + \delta_2) \\ V_{j0} &= -(s + \delta_1)(s + \delta_2)(\theta_2 I_{IA_2} \tilde{P}_j + \theta_4 I_{IA_1} \tilde{Q}_j) \\ V_{11} &= (s + \delta_1)(s + \delta_2)(1 + \tilde{P}_1 - \theta_4 \tilde{Q}_1) H_1 \\ V_{12} &= (s + \delta_1)(s + \delta_2)(\theta_2 \tilde{P}_1 - \tilde{Q}_1) H_2 \\ V_{21} &= (s + \delta_1)(s + \delta_2)(\tilde{P}_2 - \theta_4 \tilde{Q}_2) H_1 \\ V_{22} &= (s + \delta_1)(s + \delta_2)(1 + \theta_2 \tilde{P}_2 - \tilde{Q}_2) H_2, \end{aligned}$$

and

$$(5.3) \quad \begin{aligned} X &= (s + \delta_1)^2 (s + \delta_2)^2 (1 - X^*) \\ X_1 &= (s + \delta_1)^2 (s + \delta_2)^2 X_1^* \\ X_2 &= (s + \delta_1)^2 (s + \delta_2)^2 X_2^* \\ Y &= (s + \delta_1)^2 (s + \delta_2)^2 Y^* \\ Y_0^* &= -(I_{IA_2} \tilde{P} + I_{IA_1} \tilde{Q}), \end{aligned}$$

where

$$(5.4) \quad \begin{aligned} X^* &= \{\theta_4 \tilde{Q}_1 + \tilde{Q}_2 - \tilde{P}_1 - \theta_2 \tilde{P}_2 + (\tilde{P}_1 - \theta_4 \tilde{Q}_1)(\tilde{Q}_2 - \theta_2 \tilde{P}_2) \\ &\quad + (\theta_2 \tilde{P}_1 - \tilde{Q}_1)(\tilde{P}_2 - \theta_4 \tilde{Q}_2)\} H_1 H_2 = \Gamma^* H_1 H_2 \\ X_1^* &= \{(1 + \theta_2 \tilde{P}_2 - \tilde{Q}_2)(\theta_2 I_{IA_2} \tilde{P}_1 + \theta_4 I_{IA_1} \tilde{Q}_1) \\ &\quad + (\theta_2 \tilde{P}_1 - \tilde{Q}_1)(\theta_2 I_{IA_2} \tilde{P}_2 + \theta_4 I_{IA_1} \tilde{Q}_2)\} H_2 \\ X_2^* &= \{(1 + \tilde{P}_1 - \theta_4 \tilde{Q}_1)(\theta_2 I_{IA_2} \tilde{P}_2 + \theta_4 I_{IA_1} \tilde{Q}_2) \\ &\quad + (\theta_4 \tilde{Q}_2 - \tilde{P}_2)(\theta_2 I_{IA_2} \tilde{P}_1 + \theta_4 I_{IA_1} \tilde{Q}_1)\} H_1 \\ Y^* &= (\theta_4 H_1 X_1^* + H_2 X_2^*) \tilde{Q} - (\theta_4 H_2 X_2^* + H_1 X_1^*) \tilde{P}. \end{aligned}$$

Then we have

$$(5.5) \quad \begin{aligned} U_j &= X_j^* + X^* U_j, \\ U &= (Y^* + Y_0^* - X^* Y_0^*) + X^* U \end{aligned}$$

which yield the following functional differential equations:

$$(5.6) \quad \begin{aligned} u_j(t) &= x_j^*(t) + L^*(u_j)(t), \\ u(t) &= [y^*(t) + y_0^*(t) - \int_0^t y_0(\sigma) x^*(t - \sigma) d\sigma] + L^*(u)(t), \end{aligned}$$

where

$$(5.7) \quad \begin{aligned} L^*(v)(t) &= F_{01} F_{02} \sum_{i=1}^3 \sum_{j=1}^3 H_{i1} H_{j2} \int_0^t \{v(\sigma - t_{i1} - t_{j2}) + \lambda_{1ij} \dot{v}(\sigma - t_{i1} - t_{j2}) \\ &\quad + \lambda_{2ij} \ddot{v}(\sigma - t_{i1} - t_{j2}) + \lambda_{3ij} \ddot{v}(\sigma - t_{i1} - t_{j2}) \\ &\quad + \lambda_{4ij} v^{(4)}(\sigma - t_{i1} - t_{j2})\} \gamma^*(t - \sigma) d\sigma \end{aligned}$$

where λ 's are given by Eqs. (3.10).

Let us note that the natural modes of the present system is determined by the roots of the transcendental equation

$$(5.8) \quad \begin{aligned} \{\theta_4 Q_1 + Q_2 - P_1 - \theta_2 P_2 + (P_1 - \theta_4 Q_1)(Q_2 - \theta_2 P_2) \\ + (\theta_2 P_1 - Q_1)(P_2 - \theta_4 Q_2)\} H_1 H_2 - 1 = 0. \end{aligned}$$

Eq. (5.8) has also a principal part in the sense of Pontryagin. Further, the functional differential equation

$$(5.9) \quad v(t) = \phi(t) + L^*(v)(t)$$

subjected to the initial conditions (3.18) admits a unique continuous solution for $t \geq 0$.

6. Systems governed by Renshaw Cells

In this section we briefly discuss the movement of an antagonistic neuromuscular system which is governed by Renshaw cells only. As before, we assume that there is not any external load acting on the system. In this case we have

$$(6.1) \quad \begin{aligned} F=I_{\alpha_1}=I_{\alpha_2}=I_{\gamma_1}=I_{\gamma_2}=I_{IA_1}=I_{IA_2}=0 \\ \theta_2=\theta_4=0, \end{aligned}$$

and

$$(6.2) \quad \begin{aligned} C_1 = C_2 = V_{10} = V_{20} = X_1 = X_2 = Y_0 = 0, \\ C = (s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1)(s + \delta_2 + \theta_3 + \theta_6 H_2 Z_2) \\ V_{11} = (s + \delta_2 + \theta_3 + \theta_6 H_2 Z_2)[(s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1) + (s + \delta_1)H_1 \tilde{P}_1] \\ V_{12} = -(s + \delta_2)(s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1)H_2 \tilde{Q}_1 \\ V_{21} = (s + \delta_1)(s + \delta_2 + \theta_3 + \theta_6 H_2 Z_2)H_1 \tilde{P}_2 \\ V_{22} = (s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1)[(s + \delta_2 + \theta_3 + \theta_6 H_2 Z_2) - (s + \delta_2)H_2 \tilde{Q}_2] \\ X = (s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1)(s + \delta_2 + \theta_3 + \theta_6 H_2 Z_2) \tilde{X}^* \\ CY = (s + \delta_2)(s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1)H_2 Z_2 \tilde{Q} - (s + \delta_1)(s + \delta_2 + \theta_3 + \theta_6 H_2 Z_2)H_1 Z_1 \tilde{P} \end{aligned}$$

where

$$(6.3) \quad \tilde{X}^* = [(s + \delta_1 + \theta_1 + \theta_5 H_1 Z_1) + (s + \delta_1)H_1 \tilde{P}_1] [(s + \delta_2 + \theta_3 + \theta_6 H_2 Z_2) - (s + \delta_2)H_2 \tilde{Q}_2] + (s + \delta_1)(s + \delta_2)H_1 H_2 \tilde{Q}_1 \tilde{P}_2.$$

We now write the X^* in the following form

$$(6.4) \quad \tilde{X}^* = (\delta_1 + \theta_1)(\delta_2 + \theta_3) + (\delta_1 + \delta_2 + 2\theta_3)s + s^2 + \Gamma_1 H_1 + \Gamma_2 H_2 + \Gamma_{12} H_1 H_2,$$

where

$$(6.5) \quad \begin{aligned} \Gamma_1 = s^2 \tilde{P}_1 + \theta_5(1 + \delta_2 + \theta_3)Z_1 + \delta_1(\delta_2 + \theta_3)\tilde{P}_1 \\ \Gamma_2 = -s^2 \tilde{Q}_2 + \theta_6(1 + \delta_1 + \theta_1)Z_2 - \delta_2(\delta_1 + \theta_1)\tilde{Q}_2 \\ \Gamma_{12} = \theta_6(s + \delta_1)Z_2 \tilde{P}_1 - \theta_5(s + \delta_2)Z_1 \tilde{Q}_2 + \theta_5 \theta_6 Z_1 Z_2 - (s + \delta_1)(s + \delta_2)\Gamma, \end{aligned}$$

where Γ is defined by Eq. (3.8).

According to Eqs. (2.18), (2.19), and (6.2)–(6.5), we have

$$(6.6) \quad \begin{aligned} U_1 = U_2 = 0, \\ U = \tilde{Y}^* + \tilde{X}^* U, \end{aligned}$$

where

$$(6.7) \quad \tilde{Y}^* = C^{-1}Y.$$

Thus, we have the relationships

$$(6.8) \quad \begin{aligned} u_1(t) = u_2(t) = 0 \\ u(t) = \tilde{y}^*(t) + \tilde{L}^*(u)(t), \end{aligned}$$

where $\tilde{L}^*(u)(t)$ is defined by the following equation:

$$(6.9) \quad \begin{aligned} \tilde{L}^*(u)(t) = (\delta_1 + \theta_1)(\delta_2 + \theta_3)u(t) + (\delta_1 + \delta_2 + \theta_3)\dot{u}(t) + \ddot{u}(t) \\ + F_{01} \sum_{i=1}^3 H_{i1} \int_0^t [u(\sigma - t_{i1}) + (\tau_{1i1} + \tau_{2i1})\dot{u}(\sigma - t_{i1}) \\ + \tau_{1i1}\tau_{2i1}\ddot{u}(\sigma - t_{i1})]\gamma_1(t - \sigma)d\sigma + \\ + F_{02} \sum_{i=1}^3 H_{i2} \int_0^t [u(\sigma - t_{i2}) + (\tau_{1i2} + \tau_{2i2})\dot{u}(\sigma - t_{i2}) \end{aligned}$$

$$\begin{aligned} + \tau_{1i2}\tau_{2i2}\ddot{u}(\sigma - t_{i2})]\gamma_2(t - \sigma)d\sigma \\ + F_{01}F_{02} \sum_{i=1}^3 \sum_{j=1}^3 H_{i1}H_{j2} \int_0^t [u(\sigma - t_{i1} - t_{j2}) + \lambda_{1ij}\dot{u}(\sigma - t_{i1} - t_{j2}) \\ + \lambda_{2ij}\ddot{u}(\sigma - t_{i1} - t_{j2}) + \lambda_{3ij}\ddot{u}(\sigma - t_{i1} - t_{j2}) \\ + \lambda_{4ij}u^{(4)}(\sigma - t_{i1} - t_{j2})]\gamma_{12}(t - \sigma)d\sigma, \end{aligned}$$

where λ 's are defined by Eqs. (3.10). Let us note that the natural modes of the system under consideration are determined by the roots of the transcendental equation $\tilde{X}^* = 0$, i.e.

$$(6.10) \quad (\delta_1 + \theta_1)(\delta_2 + \theta_3) + (\delta_1 + \delta_2 + 2\theta_3)s + s^2 + \Gamma_1 H_1 + \Gamma_2 H_2 + \Gamma_{12} H_1 H_2 = 0.$$

Eq. (6.10) has also a principal part in the sense of Pontryagin. Further, Eq. (6.9) subjected to the initial conditions (3.8) admits a unique continuous solution for $t \geq 0$.

7. Systems with no feedback

The absence of feedback is of particular importance in the study of neuromuscular systems. In this case,

$$(7.1) \quad H_1 = H_2 = G_1 = G_2 = 0.$$

Further, by virtue of Eqs. (2.13), (2.14), (2.16), (2.8), and (7.1), we have

$$(7.2) \quad \begin{aligned} C_1 = I_{\alpha_1} - \theta_2 I_{1A_2} \\ C_2 = I_{\alpha_2} - \theta_4 I_{1A_1} \\ C = V_{11} = V_{22} = (s + \delta_1 + \theta_1)(s + \delta_2 + \theta_3) \\ V_{12} = V_{21} = Y = 0 \\ V_{j0} = (s + \delta_1)(s + \delta_2 + \theta_3)[I_{\alpha_1} - \theta_2 I_{1A_2}]\tilde{P}_j + (s + \delta_2)(s + \delta_1 + \theta_1)[I_{\alpha_2} - \theta_4 I_{1A_1}]\tilde{Q}_j \\ + CR_j F \\ X_j = (s + \delta_1 + \theta_1)(s + \delta_2 + \theta_3)V_{j0} \\ X = (s + \delta_1 + \theta_1)^2(s + \delta_2 + \theta_3)^2 \end{aligned}$$

$$Y_0 = \frac{s + \delta_1}{s + \delta_1 + \theta_1} \tilde{P}[I_{\alpha_1} - \theta_2 I_{1A_2}] + \frac{s + \delta_2}{s + \delta_2 + \theta_3} \tilde{Q}[I_{\alpha_1} - \theta_4 I_{1A_1}]$$

and

$$(7.3) \quad \begin{aligned} U_j = \frac{s + \delta_1}{s + \delta_1 + \theta_1} \tilde{P}_j [I_{\alpha_1} - \theta_2 I_{1A_2}] + \frac{s + \delta_2}{s + \delta_2 + \theta_3} [I_{\alpha_2} - \theta_4 I_{1A_1}] \\ + \frac{R_j}{(s + \delta_1 + \theta_1)(s + \delta_2 + \theta_3)} F \end{aligned}$$

and

$$(7.4) \quad U = Y_0.$$

Thus, putting

$$(7.5) \quad \begin{aligned} \tilde{P} &= \frac{s + \delta_1}{s + \delta_1 + \theta_1} \tilde{P}, & \tilde{Q} &= \frac{s + \delta_2}{s + \delta_2 + \theta_3} \tilde{Q}, \\ \tilde{P}_j &= \frac{s + \delta_1}{s + \delta_1 + \theta_1} \tilde{P}_j, & \tilde{Q}_j &= \frac{s + \delta_2}{s + \delta_2 + \theta_3} \tilde{Q}_j, \\ \tilde{R}_j &= \frac{1}{(s + \delta_1 + \theta_1)(s + \delta_2 + \theta_3)} R_j, \end{aligned}$$

with $\tilde{P}(s) \Leftrightarrow \tilde{p}(t)$, $\tilde{P}_j(s) \Leftrightarrow \tilde{p}_j(t)$, $\tilde{Q}(s) \Leftrightarrow \tilde{q}(t)$, $\tilde{Q}_j(s) \Leftrightarrow \tilde{q}_j(t)$, and $\tilde{R}_j(s) \Leftrightarrow \tilde{r}_j(t)$, and passing to the inverse Laplace transforms, we find

$$(7.6) \quad \begin{aligned} u_j(t) &= \int_0^t \{ [i_{a_1}(\tau) - \theta_{2i_{IA_2}}(\tau)] \tilde{p}_j(t - \tau) + [i_{a_2}(\tau) - \theta_{4i_{IA_2}}(\tau)] \tilde{q}_j(t - \tau) \\ &\quad + f(\tau) \tilde{r}_j(t - \tau) \} d\tau, \\ u(t) &= \int_0^t \{ [i_{a_1}(\tau) - \theta_{2i_{IA_2}}(\tau)] \tilde{p}(t - \tau) + [i_{a_2}(\tau) - \theta_{4i_{IA_1}}(\tau)] \tilde{q}(t - \tau) \} d\tau \end{aligned}$$

Eqs. (7.6) completely determine the movement of the antagonistic neuromuscular system in the absence of feedback.

8. Discussion

Production of a movement $u(t)$ is defined by Eq. (2.5) which is a convolution integral containing terms depending on the two neural inputs n_1 and n_2 and external forces f . These inputs are convolved with functions p , q and r , which in the Laplace domain share a common denominator $W(s)$. $W(s)$ is a fourth-order polynomial in s (Eq. 2.8) the coefficients of which are all non-negative (Eq. 2.9). Thus, there can be no complex conjugate roots in the Laplace domain with zero or positive real parts and hence no maintained or growing oscillatory solutions in the time domain (Pontryagin, 1942) resulting from the properties of the muscle and the load. This result is a generalization of a result for a single muscle (Stein and Oğuztörel, 1976). Although there are some specialized muscles in insects capable of generating oscillations (Pringle, 1967), for example to produce the patterns in flying (myogenic flight), other insects generate oscillatory patterns of neural activity for this purpose (neurogenic flight). In vertebrate muscles only small, maintained oscillations have been observed under special conditions in the absence of oscillatory neural inputs (Huxley, 1974).

Thus, these analytic results support the concept that maintained oscillations of a limb do not arise solely from interactions of muscles with each other or with a mass-spring load.

Oscillatory movements can arise either from (1) oscillations arising in feedback pathways, (2) in spinal circuitry such as shown in Fig. 2 or oscillatory inputs from the brain or, for example, a spinal locomotion generator distinct from the connections shown in Fig. 2 (reviewed in Grillner, 1981; Stein and Lee, 1981). Oscillatory solutions in the absence of oscillatory inputs are associated with complex conjugate roots of a transcendental equation such as (3.19). Even with the simplification of Section 3 (i.e., the system is governed by inputs to α -motoneurons only), there can be many, but only finitely many, maintained or growing oscillations. Interestingly, the same transcendental equation arises when the system is governed by inputs to γ -motoneurons or coactivation of combinations of α - and γ -motoneurons (Section 4). This again is an extension of a result obtained for a single muscle (Stein and Oğuztörel, 1981).

The presence of the inhibitory connections from IA interneurons (Section 4) or Renshaw Cells (Section 5) will modify the natural modes. The reason for this result is that the IA interneurons link the antagonistic α -motoneurons and hence introduce an additional feedback route. Similarly, the Renshaw Cells introduce a central feedback pathway onto α -motoneurons but not γ -motoneurons. Thus, as described by Miller and Scott (1977), these connections can introduce oscillations which are not present if only connections from the motoneurons to muscles and feedback from the muscles back to motoneurons are considered. The nature of these oscillations can be studied by solving the transcendental equations given in each section, even in the absence of numerical solutions for the full time-course of the response to any pattern of inputs.

One final point of interest is that the effect of the inhibitory interneurons is to modify oscillations involving the feedback pathways from muscle. With the connections shown in Fig. 2 in the absence of feedback (Section 6), the solutions again have the form of convolution integrals (Eq. 7.6). As indicated by the symbol (\approx), the functions p , q and r are modified, but only by products involving simple lag terms in the denominator (no complex terms). Similarly, the input depends on algebraic sums of the descending inputs to α -motoneurons and IA interneurons, which can not introduce new oscillations. This result would not apply if a more complex model including the adaptation of α -motoneurons was used (Stein *et al.*, 1974a,b; Oğuztörel, 1979). However, these theoretical results are in agreement with the experimental findings of Jordan *et al.* (1979) that a locomotion generator distinct from the spinal connections shown in Fig. 2 is required to account for locomotion observed in the absence of feedback.

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