

Muscle Spindles in Muscle Control

II. Analysis of Muscle Servo Model

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Abstract

The muscle spindles (MS) have been proposed by Merton (1953), to be the sensors supplying a feedback signal in the muscle length follow-up servo system. This system is analyzed here, based on the two engineering requirements for man made servo systems, namely the system loop gain and the steady state error (Gille, 1959). In the first part the system's linearized transfer function equations are developed. It is shown that the small loop gain found in the reflex studies indicates a small gain under volitional control of movements, i.e. volitional control is being exercised directly by the alpha or gamma system. For the steady state error no definite conclusions can be drawn from the available data (Rosenthal, 1970; Houk, 1963); however, it is shown to be inversely proportional to the steady state loop gain, and the system is thus of type "0" or "1".

1. Introduction

It has been proposed that the "reflex" maintenance of muscle position is achieved by a length follow-up servo mechanism (Merton, 1953). This muscle control model is widely accepted and used extensively to explain the complex animal behavior of posture and locomotion (Roberts, 1967). The present study is an attempt to analyze this muscle control model and see if it can meet the basic engineering requirements for such a system.

The vast literature on servo systems indicates quite clearly that there is no unanimity as to what this "servo" term actually implies. The spectrum of definitions is so wide that it includes practically all closed loop system. In order to avoid confusion and to restrict the analysis to the *muscle* servo system, the term "servo" will not be dealt with any further, but the general characteristics of servo systems, accepted by most writers, will be used.

Servo systems, in the strict sense, have inputs which vary in time, and are designed to make input and output equal. One may add that they are intended to make a low-power input equal to a higher-power output. In purely technological requirements the performance specifications for such a servo system will usually

include the following demands: (a) safety or stability; (b) accuracy, or small steady state errors; (c) high speed of response to varying inputs. These demands will in turn provide the criteria for the effectiveness of the servo system as follows:

(1) *Stability.* This is an obvious requirement, which imposes limitations on the other two requirements [(b) and (c)].

(2) *High Open Loop Gain.* This will be dealt with extensively below. In the meantime, it is sufficient to say that it implies a small steady state error which depends on the type of system. In addition, in the case of the reflexive muscle servo system regulating muscle length, it implies high stiffness or resistance to disturbances.

(3) *Large Bandwidth.* This is a measure of the speed of response of any system; however, it has its limitations on account of noise effects and stability problems.

The muscle control system obviously meets the first requirement for stability under normal conditions. A Nyquist plot of the arm control system shows a considerable margin of stability, as does that of the triceps surae muscle of the cat (Josef, 1972). In the present study the analysis is centered around the loop-gain and the steady state errors as a measure of the system quality in resisting changes in the selected muscle length, and in following input signals.

2. Muscle Control Servo Model

Since only the second requirement of a system to be of a servo type, i.e. accuracy of the output in following a system input, is investigated, we have only to show that the steady state error is acceptably small in order to prove that the system is a "servo" system, and simultaneously demonstrate the type of servo action which the system can provide. A small, or zero, steady state error to a step input function will indicate a "length" servo action, and a zero steady state error

to a ramp input function will indicate a "velocity" servo action. It will be shown later that, if the type of system determines the type of servo, the loop gain determines the value of the steady state error, when it exists. The larger the loop gain, the smaller the steady state error for a system with fixed dynamics, as is the case for standard servo systems. We therefore begin the analysis by examining the system transfer functions and loop gain, in order to point out the effects of a low loop gain on volitional control. Later the influence of low loop gain on the accuracy of system response is analyzed in relation to the steady state errors.

The model is shown in Fig. 1. According to it, the muscle length $L_m(t)$ is maintained regardless of environmental changes by the feedback signal $F_\beta(t)$ transmitted to the spinal cord. This signal, which is proportional to $L_m(t)$, activates the extrafusal fibres so as to oppose any change in $L_m(t)$. The above process can take place in one of the following ways:

(a) In *amphibians*, the control function, $F_\alpha(t)$, arriving from the CNS to the motoneurons, activates simultaneously the muscle and MS motor system, i.e. $F_\gamma(t) = E(t)$. As the muscle contracts, it "unloads" the MS. In view of the above simultaneity, if the muscle and MS contract by the same amount, i.e. $L_\alpha(t) = -L_m(t)$, $F_\beta(t)$ remains unchanged. If, however, because of external loads or internal disturbances, the muscle does not contract by the proper amount, $F_\gamma(t) = E(t)$ activates the MS so as to increase $F_\beta(t)$ (augmented by the MS's own positive feedback) to achieve the desired length. The increase in $E(t)$ is indicated by the plus sign at summing point I for $F_\alpha(t)$ and $F_\beta(t)$, representing the spinal cord. The plus sign at summing point III indicates a positive feedback loop, and the minus at

summing point II – a negative one. It should be noted that the stretch reflex is not pronounced in amphibians.

(b) In *mammals*, the system can be activated volitionally as a servo via the gamma system also, in view of the separate functioning of the alpha and gamma systems. The servo-assisted, or alpha-gamma linkage mode (Eldred, 1953; Granit, 1962) is only operative when both systems are activated simultaneously; otherwise unloading of the MS by the muscle is not compensated by the gamma system [see case (a)]. When the latter is activated alone, $\Delta E(t) = \Delta F_\beta(t)$, and the desired muscle length is achieved when $L_m(t)$ unloads the MS by the necessary amount.

(c) In the reflexive, experimental mode of length servo activation no signals arrive from the CNS, i.e. $F_\alpha(t) = \text{const}$ and for mammals $F_\gamma(t) = \text{const}$. The input is the external load, $T_L(t)$, applied to the muscle via its tendon. If the system is set at $L_m(t_0)$, any increase in $T_L(t)$ increases $L_m(t)$, which in turn stretches the MS, generating $E(t)$ so as to oppose the disturbance and bring $L_m(t)$ back to $L_m(t_0)$. For the mammal, if the MS was slack, say $F_\gamma(t) = 0$, the reflex mode is inoperative, since the MS has a dead zone in its response to change in muscle length. For the amphibian, the MS is more likely to be activated in this mode, as $F_\gamma(t) = E(t)$. [It should be noted that, under certain experimental conditions (Eldred, 1953) the gamma system was activated before the alpha system, in which cases (b) and (c) apply to the mammal.]

The assumptions underlying the model shown in Fig. 1 are as follows:

(1) For simplicity, only the MS loop is considered, as only the MS is presumed to act as the length

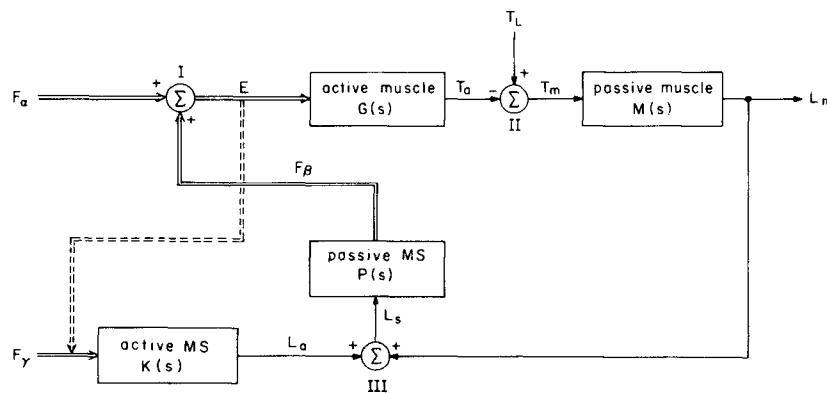


Fig. 1. Block diagram of muscle MS servo control model. (For notation see text.) Dashed line – collaterals of alpha motor axon innervating amphibian MS; Double line – multiple neuronal communication path; Bold line – lumped mechanical variables

feedback sensor in this model. In addition, under reflexive experimental conditions (Granit, 1962) discussed later, the influence of the Golgi tendon organs on the performance of the system is necessarily limited, in view of the smallness of the active muscle forces (Houk, 1967). The main justification, however, for not including the Golgi organs is the demonstration by Rosenthal *et al.* (1970) that they have the same dynamics as the MS and therefore can change only the steady state gain, which will be considered below.

(2) The spinal cord is presumed to act as a simple summing element (number 1), especially for the I_a input, which is known to be excitatory.

(3) The assumed MS input is the change in muscle length, with the length servo as the model for muscle control. When MS length is the assumed input, it is readily related to muscle length, through knowledge of the muscle tension and tendon stiffness.

(4) The transfer functions of the various system components around the $L_m(t_0)(\text{rest})$ point are governed by their anatomical structure. They are non-linear and time-varying and depend on the muscle length, L , and its rate of change (time derivative), \dot{L} , but lend themselves to linear approximation for the purpose of a general analysis of the system. (See also under "Discussion".)

The transfer functions in question are:

(a) $G(s)$ – Characterizing the muscular generation of an active force, $T_a(s)$, in response to an afferent motor activation signal, $E(s)$.¹

(b) $M(s)$ – Characterizing the passive change in length, $L_m(s)$, in response to an applied force, $T_m(s)$, which is made up of an external force, $T_L(s)$, or the active force, $T_a(s)$, or both. In the reflex stretch studies the applied force is $T_L(s)$, but $T_a(s)$ is not zero under these conditions.

(c) $K(s)$ – Characterizing the change in MS length, $L_a(s)$, in response to MS motor activation.

(d) $P(s)$ – Characterizing the MS afferent response, $F_\beta(s)$, to a change in its length, $L_s(s)$, which is a function of both $L_a(s)$ and $L_m(s)$.

The analysis is based on the principle of superposition of inputs, i.e. independent summation of the muscle system responses to various possible inputs. This is done for simplicity, despite the known limitations of this assumption, such as nonlinearity of the MS and spinal-cord responses. Under these circumstances the mammal system can be activated via three different inputs as follows:

1. The main alpha motor input.
2. The gamma servo-assisted MS input.

3. A mechanical disturbance input, T_L , such as an externally applied force or weight.

For the mammal system, the change in muscle length in response to these inputs can be analyzed as follows:

The feedback signal, $F_\beta(s)$ is:

$$\begin{aligned} F_\beta(s) &= P(s) L_s(s) \\ &= P(s) [L_m(s) + F_\gamma(s) K(s)] . \end{aligned} \quad (1)$$

The muscle neuronal activating signal, $E(s)$, is:

$$E(s) = F_\alpha(s) + F_\beta(s) . \quad (2)$$

The change in length in response to this input and an additional disturbance input is:

$$\begin{aligned} L_m(s) &= M(s) T_m(s) \\ &= M(s) [T_L(s) - T_a(s)] . \end{aligned} \quad (3)$$

Substituting $T_a(s) = E(s) G(s)$ and Eq. (1) and (2) into Eq. (3), we have:

$$\begin{aligned} L_m(s) &= M(s) [T_L(s) - G(s) F_\alpha(s) - G(s) P(s) K(s) F_\gamma(s)] \\ &\quad - M(s) G(s) P(s) L_m(s) . \end{aligned} \quad (4)$$

Rearranging Eq. (4), the change in muscle length in response to the three inputs is:

$$\begin{aligned} L_m(s) &= \frac{M(s)}{1 + M(s) P(s) G(s)} \cdot T_L(s) \\ &\quad - \frac{M(s) G(s)}{1 + M(s) G(s) P(s)} \cdot F_\alpha(s) \\ &\quad - \frac{M(s) G(s) P(s) K(s)}{1 + M(s) G(s) P(s)} \cdot F_\gamma(s) . \end{aligned} \quad (5)$$

The first term in Eq. (5) is the muscle response to a mechanical pull and shows an increase in length with increasing T_L . The second and third terms are muscle responses to a neuronal stimulation and show a decrease in length with increasing stimulation.

Using Eq. (5), the servo action can be analyzed in the reflexive mode. In this case $F_\alpha(t) + F_\gamma(t) = \text{const}$ and the only variable input is $T_L(s)$. Evaluating the changes in muscle length about the initial length to this input only:

$$L_m(s) = \frac{M(s)}{1 + M(s) G(s) P(s)} \cdot T_L(s) . \quad (6)$$

The open-loop response for such a disturbance is

$$L_m(s) = M(s) T_L(s) \quad (7)$$

and if the change in muscle length is to be any smaller under closed-loop conditions, then it is necessary that:

$$1 + M(s) G(s) P(s) \gg 1 . \quad (8)$$

¹ The transfer function in the frequency domain, using the Laplace transform variable s , is $G(s) = T_a(s)/E(s)$.

Eq. (8) should apply in the physiologically normal range of operation. It is known, however, from experimental results (Terzuolo) that it does not hold for the spinal cat, nor even for the decerebrate cat, where the loop gain is slightly larger than 5 (Rosenthal, 1970; Houk, 1970). (We shall see later how the stated inequality of Eq. (8) can influence the length steady state error.)

If Eq. (8) were satisfied, the change in muscle length in response to alpha stimulation would be:

$$L_m(s) \cong -\frac{1}{P(s)} \cdot F_\alpha(s) \quad (9)$$

and the muscle response to gamma stimulation would be:

$$L_m(s) \cong -K(s) \cdot F_\gamma(s). \quad (10)$$

Eqs. (9) and (10) show that in these circumstances, i.e. with the servo conditions applying to the reflex case and Eq. (8) satisfied, muscle response to the neuronal input is a function not of the muscle properties, but of the MS characteristics. This is yet to be shown physiologically.

In summation of the mammal case, it can be concluded that a length servo system, if applied to the reflex mode of muscle control, would have explicit implications in volitional control as well. In addition, the requirement of a high loop gain [Eq. (8)] implies the existence of a system which is rigid to external disturbances, which, in reality, is not the case. From the above evidence, we conclude that Eq. (8) is not satisfied, and consequently question the reliability of the length servo system as a functional model for the MS role in muscle control.

In the amphibian system (dashed line in Fig. 1) only two inputs, T_L and F_α , exist, and the MS has its own positive feedback loop. In experiments done on a spinal frog, alternate measurements of the response in this loop to changes in external loading, in both the open and closed loop modes, rendered a ratio of about 1:1.2 respectively in the magnitude of the responses (Inbar, 1972/I). Since an effective servo model necessarily requires the existence of a more significant difference than this, it may be deduced that this configuration also does not apply in the case of amphibians.

3. Steady State Errors

To determine the nature of system stability, the characteristic equation of the system alone is necessary. When evaluating the steady state solution of the system

equation, after transient phenomena have vanished, it is necessary to investigate the steady state error of the system, in relation to the relevant driving function, i.e., a step position function for a position servo, a ramp position function (a step function in velocity) for a velocity servo, etc.

In Fig. 2a block diagram for a unity feedback system is shown. If $H = 1$, and $G(s)$, the forward loop gain, is written in its normal form as:

$$G(s) = K \frac{(1 + \tau_1 s)(1 + \tau_3 s) \dots}{s^n (1 + \tau_2 s)(1 + \tau_4 s) \dots} \quad (11)$$

the transform of the steady state error, which is the difference between the desired output $R(s)$ and the actual output $C(s)$, is:

$$E(s) = R(s) - C(s)$$

$$= \frac{1}{1 + G(s)} \cdot R(s),$$

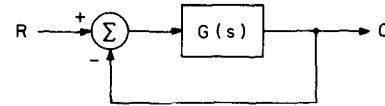
i.e.

$$E(s) [1 + G(s)] = R(s).$$

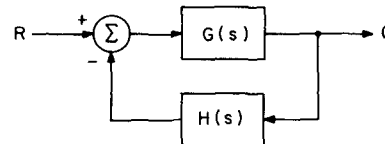
The evaluation of the steady state error, i.e. the evaluation of e when $t \rightarrow \infty$, can be achieved by evaluating $sE(s)$ when $s \rightarrow 0$, as is justified by the final value theorem.

It can be shown that for systems with $H = 1$, the error is a function of n , where n is the power of s in the denominator of Eq. (11). For a system with $n = 0$ the steady state error to a step change in position, namely $R = A/s$ is:

$$\begin{aligned} e_{ss} &= \lim_{t \rightarrow \infty} e(t) = \lim_{s \rightarrow 0} s \frac{A/s}{1 + G(s)} \\ &= \frac{A}{1 + \lim_{s \rightarrow 0} G(s)} = \frac{A}{1 + K}, \end{aligned} \quad (12)$$



a



b

Fig. 2. a: A unity feedback control system; b: A general feedback control system

i.e., the steady state error is a function of the system's DC gain, K . The larger the gain, the smaller the error.

For a system with $n = 1$ the steady state error to a step change in position is zero, and K can be as small as desirable, but finitely small. This is so since $G(s)$ in Eq. (12) will go to infinity when $s \rightarrow 0$ and $e \rightarrow 0$. The same type system, namely type one with $n = 1$, will have a nonzero error for a step change in velocity, i.e., for a ramp position input $r = v \cdot t$. The value of the error will again be a function of the DC gain, smaller for larger K . It should be noted that for a zero type system, i.e. $n = 0$, the steady state error for a ramp input is infinite regardless of K .

For the general case of $H \neq 1$, (Fig. 2b), the actuating signal is $E = R - HC$. For a step input in position, $r = A$,

$$e_{ss} = \lim_{t \rightarrow \infty} e(t) = \lim_{s \rightarrow 0} s \frac{A/s}{1 + GH} = \frac{A}{1 + \lim_{s \rightarrow 0} GH}.$$

It is seen here that, in contrast to the previous case $H = 1$, the error in the usual sense, i.e., the difference between output and input, does not correspond here to the actuating signal. For this kind of system it is simpler, and for the reflex muscle control system more relevant, to evaluate the steady state error with *load disturbances* acting as input and T_m as output. In order to study the steady state error of the muscle servo control loop the block diagram which was used before, Fig. 1, is used again. For the present purpose, however, it is modified to have the disturbance as the input, Fig. 3, and the same procedure is used to evaluate the actuating signal. For a disturbance input a good servo system will have a zero actuating signal for large t , since the output is required to be zero (this will yield also a zero change in muscle length). The analysis to follow is based on a linear model justified by the derivation of the various load small signal transfer functions.

To evaluate the steady state error for load disturbances, the complete transfer function characteristics of the system are needed. Recently Rosenthal *et al.* (1970) published such data on the triceps surae of the cat. These results are taken from an isolated muscle; however, most experiments upon which the servo theory is based (Houk, 1970) were carried out on similar systems.

The steady state error of the modified muscle control system in Fig. 3 is T_m , where T_m represents changes in muscle tension about the mean working tension which the muscle developed in order to main-

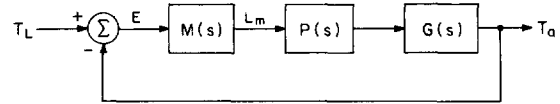


Fig. 3. The modified, and reduced, muscle servo model for reflex studies, with T_L as the disturbance input

tain a certain length, L_0 . If the system is to be of a length servo type, then the variations in L should be zero after some transients caused by the disturbance subside. The test signal is a step change in tension, and when $t \rightarrow \infty$ we require the actuating signal to go to zero.

Analyzing the block diagram as before, we obtain:

$$\frac{T_m(s)}{T_L(s)} = \frac{1}{1 + M(s)P(s)G(s)}.$$

For a step input $T_L = A/s$ we test

$$e_{ss} = \lim_{t \rightarrow \infty} T_m(t) = \lim_{s \rightarrow 0} s T_m(s) = \lim_{s \rightarrow 0} \frac{A}{1 + M(s)P(s)G(s)}. \quad (13)$$

We now substitute M , P and G as given by Rosenthal (1970) and repeated below:

$$G(s) = \frac{K(s + 0.352) \exp(-0.002s)}{(s + 0.157)(s + 6.91)(s + 157)^2}$$

$$M(s) = \frac{(s + 0.28)(s + 2.89)(s + 4.33)}{0.28(s + 0.19)(s + 1.32)(s + 23.2)(s + 345)}$$

$$P(s) = \frac{(s + 0.44)(s + 1.7)(s + 11.3)(s + 200)^2}{(s + 0.82)(s + 2.7)}$$

[In this work Rosenthal *et al.* derived the function

$$\frac{1}{M(s)} = \frac{T_m(s)}{L_m(s)}].$$

Thus we obtain:

$$e_{ss} \cong \frac{A}{1 + K/10^7} \neq 0 \quad (14)$$

Equation (14) indicates a non zero error with a magnitude which depends on the DC gain. It can be seen that if K were of the order of $K/10^7 = 10^2$, the steady state error would be small and the disturbance would be quenched by the servo action. This brings us back to the first part of this paper, where the gain problem was discussed and deduced to be low, from decerebrate cat length-tension measurements, from spinal frog measurements, and from other more

theoretical considerations. The result therefore is that, if it is at all active, the servo action can reduce the step disturbance A to $A/(1 + 5.6)$, as in the case of the decerebrate cat, by a reduction of that amount in muscle tension T_m , but not in muscle length L_m .

However, the results are not that conclusive. In Rosenthal's published results the TF of the passive muscle, $M(s)$, is seen to have a -5 dB/dec slope and -22.5° constant phase behavior. Such a function $M(s)$ can be approximated (Josef, 1972) by the following TF :

$$M(s) = \frac{K'}{s^{1/4}}.$$

If the new TF for $M(s)$ is substituted in equation (13), we get:

$$\lim_{s \rightarrow 0} M(s) P(s) G(s) = \infty$$

and the steady state error to a step change in load is zero. We should remember, however, that if the Nyquist plot at frequencies close to zero falls back to the real axis, then the system is definitely of type 0.

4. Discussion

An important assumption in the foregoing analysis is that the system is linear. Accordingly, conclusions here are confined to the specific case under study.

The change in gain of the measured transfer functions was based on "large-signal" studies of the system. The muscle-tension and MS responses, measured for a total of four or five mm stretches (about 15% of the total muscle length) (Inbar, 1972/I) give no information about the differential gains involved, some of which (such as the MS gain for small perturbations) were found to be high (Matthews, 1969). However, the transfer functions used in the steady state error calculations (Rosenthal, 1970) were derived by small signal analysis.

The follow-up servo system concept has been widely used in the past in studies of the muscular system (Roberts, 1967; Granit, 1962). As such, this model has provided a stimulating background for a large body of research activity. Recently, however, this concept has been challenged by various workers (Matthews, 1966; Houk, 1970) although it still provides the framework for activity in this research area. In the present work we have tried to bring to light the importance of the loop gain to a servo system, and to employ it in the study of the steady state error, particularly to a step position, or step disturbance input.

Though no definite conclusive results could be obtained for the steady state error for a step input, it is interesting to note that the e_{ss} for a ramp input has either a constant value which depends on the loop gain, for a type 1 system, or an infinite value, for a type 0 system.

It is also interesting to note that, for a square (t^2) input, the system must be of a second order for the error to be zero, i.e., for the output to track an acceleration signal, a servo system must be of type 2 ($n=2$). If it is of type 1, the error will be proportional to the loop gain; the higher the gain, the smaller the error.

The present example indicates that at most a type 1 system can simulate the single muscle control system. Furthermore, this is true not only for the single muscle, but also for the human postural control system, as studied by Houk (1963). Using Houk's linear reduced model of the postural control system, the open loop TF is:

$$M(s) \cdot G(s) \cdot P(s) = \frac{T_{iso}}{\frac{jB}{K} s^2 + js + B} \cdot K \frac{\eta T_s + 1}{T_s + 1} \cdot \frac{1}{s} \exp(-st)$$

The pole $1/s$, which comes from Houk's muscle model, is the only pole at the origin thus indicating a first order system. If, however, a different muscle model is used, similar to Houk's simple linear model but with a series and parallel elastic element, then the model will represent a zero order system. However we manipulate the model, it appears that the system is at most of order one. Assuming a constant H , even if not unity, will lead to the conclusion that *volitional* control is not carried out in a servo mode.

Thus our *reflex* system can, at best, be of a length servo type; however, this will only be the case if it can be shown to be a type 1 system. For want of proof to this effect, and due to the obvious fact that volitional control cannot be expected to function under the conditions imposed by a constant steady state error, the original assumption of a fixed-dynamics length control servo system as a model for muscle control is concluded to be rather dubious.

Though the gain was found to be too small for justifying servo action alone, it is, however, large enough to enable the muscular control system to change its own dynamics. That such changes can take place is well known (Houk, 1963; Stark, 1967). A system with such a mechanism clearly belongs to the "adaptive" system category.

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