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A Mechanical Model of the Secondary Endings of Mammalian Muscle Spindles

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Received March 16, 1970

Summary. A mechano-electric model of the secondary endings of the mammalian muscle spindle receptors has been developed. The model involves a mechanical system with second order transfer dynamics connected to a zero order mechano-electric transducer with constant gain.

The mechanical system is supposed to describe the visco-elastic properties of the intrafusal muscle fibres, and this part of the model is identical to that used in connection with an earlier proposed model of the primary endings (Rudjord, 1970).

The general transfer properties of the model are derived, together with a description of the particular response components obtained during a linear extension of the mechanical system.

A simple direct electronic analogue was used for studying the effects of the individual parameters and for a preliminary estimate of an adequate set of parameter values.

With appropriate parameter values, a close correspondence could be obtained between the behaviour of the model and the typical response properties of the secondary endings of the muscle spindles.

The order of magnitude of the best parameter fit also appeared to correspond to the values previously found to yield an adequate description of the transfer properties of the primary endings.

It is further shown that for the best fit of the mechanical parameters, the secondary ending model may be approximated by a simple first order system with lead-lag transfer behaviour.

The transfer properties of this simplified model appear to agree with the reported response properties of typical secondary ending receptors except for extreme rates of stretch or very high vibrational frequencies of stretch during which the simplifying approximation evidently does not apply.

1. Introduction

The mammalian muscle spindles are innervated by afferent fibres both in the group Ia and the group II range of conduction velocities. Branches from a single group Ia fibre innervate the central region of all the intrafusal fibres of a muscle spindle organ. Some of the intrafusal muscle fibres, particularly among the nuclear chain type (see Fig. 1), also receive innervation from group II afferents.

Depending on whether the terminals originate from a group Ia or a group II afferent fibre, the set of sensory terminations that are formed by a single afferent fibre is generally referred to as a *primary ending* or a *secondary ending*, respectively (for review, see Matthews, 1964).

In a previous model study of the primary ending receptors (Rudjord, 1970) a second order mechanical system was proposed as a simplified description of the visco-elastic properties of the system of intrafusal muscle fibres of a spindle organ. Based on this mechanical system, many details of the transfer characteristics of the de-efferented primary endings could be accounted for by the type of deformation occurring in the sensory region of the model, when the system was subjected to imposed length changes. Since the group II afferents are connected to parts of the same mechanical system, some relationship would be expected to exist between the functional properties of the two types of receptor endings. Provided that the mechano-electric transduction taking place in the receptor terminals is basically of the same kind for the group Ia and the group II afferents, the same visco-elastic model of the intrafusal muscle fibre system should also apply for a description of the transfer properties of the secondary endings as well.

In the present study a mechanical deformation of the nuclear chain intrafusal muscle fibres is considered as the direct governor of the response of the secondary ending receptors.

Based on the original mechanical model of the intrafusal muscle fibre system, the present paper investigates to which extent this model also yields an adequate description of the functional properties of the de-efferented secondary endings, that corresponds to the experimental observations on the actual behaviour of the biological prototype.

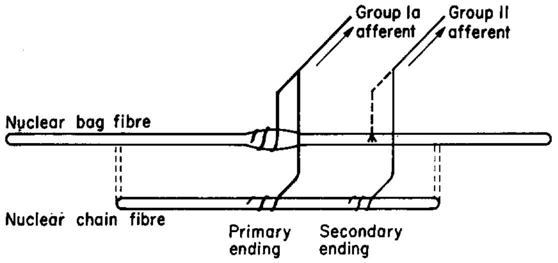


Fig. 1. Schematic representation of an idealized muscle spindle. Only one intrafusal muscle fibre of each kind is shown, together with an indication of the structure and the location of the primary and the secondary ending terminals that are formed by the group Ia and the group II afferent innervation

2. *Histological Structure*

The anatomical structure of the intrafusal muscle fibres as well as the histology of the sensory innervation have been studied by many authors. (For an extensive bibliography, see section B of Eldred *et al.*, 1967.)

The group II afferents appear mainly to innervate the nuclear chain intrafusal fibres (Boyd, 1962). Secondary ending terminations on the chain fibres generally form spiral-like sensory structures covering about 300—500 μm of the nuclear chain fibres. These terminations are always located outside the central region covered by a similar sensory structure originating from branches of the group Ia afferent fibre innervating the muscle spindle. Occasionally, branches from group II afferents innervate the nuclear bag fibres where they terminate in a characteristic type of "flower-spray" endings (Boyd, 1962). This type of secondary ending termination apparently forms a weaker mechanical attachment to the intrafusal fibre than do the spiral-like terminations found on the nuclear chain fibres.

According to Boyd (1962) the main difference between the spiral-like terminations of group Ia and group II afferents is that the coiled structure of the latter consists of fibres that are significantly thinner than the group Ia branches wrapped around the bag region of the nuclear bag fibres. Electron microscope studies show a very firm mechanical attachment of the group Ia coils to the bag structure of the nuclear bag fibres (Landon, 1966). The group Ia fibres innervating the nuclear chain fibres, however, apparently form terminations with a weaker mechanical connection and with a spiral structure that is more similar to that formed by the secondary endings (Boyd, 1962; Landon, 1966). No trough-like structure beneath the windings of these coiled receptor terminations, as that found beneath the coils of the group Ia terminals innervating the bag region (Landon, 1966), is present on the nuclear chain fibres. This applies for both primary and secondary ending terminations on the nuclear chain fibres (Landon, 1966 and personal communication). The histological picture thus indicates that the sensory structures of both primary and secondary endings located on the nuclear chain intrafusal muscle fibres, are fairly equal, and significantly different from the group Ia terminations found on the nuclear bag intrafusal muscle fibres.

3. *Functional Properties*

Within normal physiological ranges of muscle extensions, the firing rate of the secondary endings increases approximately linearly with the passive lengthening of the muscle (Harvey and Matthews, 1961). The slope of the frequency-extension relationship, that may be defined as the static sensitivity of the receptor endings (Whitteridge, 1959) is approximately the same as that found for the primary endings (Jansen and Matthews, 1962; Fehr, 1962; Alnaes *et al.*, 1965). The dynamic sensitivity of the secondary endings seems, on the other hand, to be much lower than that found for the primary endings when the muscle is stretched at a constant velocity to full physiological extension (see Matthews 1964). However, carefully conducted re-investigations using small amplitudes of sinusoidal vibrations applied to the muscle, have shown that except for a very large difference in the absolute firing rate of the two types of endings the transfer characteristics of the primary and the secondary endings are remarkably similar (Matthews and Stein, 1969). The great difference in absolute firing rate, together with some deviations at relatively high frequencies of muscle vibrations, have in an earlier proposed model been ascribed to different transducer properties of the group Ia terminals innervating the nuclear bag and the nuclear chain intrafusal fibres of the muscle spindles (Rudjord, 1970). Alternatively, it might reflect a difference between the deformation properties of the central region and the more polar regions of the intrafusal muscle fibres that is particularly pronounced by very small amplitudes of extension of the system (Brown *et al.*, 1969).

A relationship between the functional characteristics of the primary and the secondary endings involves the following properties:

(1) The position sensitivity of the primary and the secondary endings appears to be approximately equal for stretch amplitudes above ca. 0.5 mm (Harvey and Matthews, 1961).

(2) The response of the secondary endings to linear stretches and to sinusoidal vibrations of the muscle shows an approximately linear transfer behaviour, while the primary endings appear to behave linearly only at very small amplitudes of vibration of the muscle (Matthews and Stein, 1969).

(3) By muscle vibrations at amplitudes within the linear range of the primary endings (<0.2 mm at a vibration frequency of 1 Hz), Bode plots of the frequency response show a remarkably similar dynamic behaviour of the primary and the secondary endings, except for a much higher level of the absolute firing frequency of the former (see Fig. 5 of Matthews and Stein, 1969) corresponding to an overall gain between one and two orders of magnitude greater than that of the secondary endings (see Fig. 4 of Matthews and Stein, 1969).

(4) Bode plots of the phase advance characteristics of the primary endings also demonstrate a linear behaviour of the receptor at small amplitudes of stretch. Within this linear range, the phase advance characteristics of the primary and the secondary endings show a remarkable similarity, particularly for vibration frequencies below about 10 Hz (see Fig. 6 of Matthews and Stein, 1969).

(5) Bode plots of the frequency response of the secondary endings show a marked dependence on the carrier frequency (i.e. the mean discharge frequency of the modulated output signal) that does not appear in the response of the primary endings (Poppele and Bowman, 1969, 1970).

A similar carrier dependent response of crustacean stretch receptors has been found to be due to the encoder (Terzuolo *et al.*, 1968). Poppele and Bowman (1969, 1970) therefore interpret the carrier dependent response of the secondary endings to reflect an encoder system that is quite different from that of the primary endings.

(6) By increasing the vibration amplitude above the linear range of the primary endings, the "amplitude gain" (output/input amplitude ratio) declines rapidly. Fig. 5 of Matthews and Stein demonstrates that at a vibration frequency of 1 Hz the amplitude gain of the primary ending declines rapidly for vibration amplitudes exceeding about 0.2 mm. At a stretch amplitude of about 0.5 mm peak-to-peak value, the amplitude gain has declined to below 1/10 of its level at amplitudes below about 0.2 mm.

At amplitudes of vibration exceeding about 0.5 mm, the output/input ratio of the primary ending appears to remain approximately constant. In this low level region of the amplitude gain, the slope is almost identical to that describing the amplitude gain of a secondary ending subjected to the same input (see Fig. 4 of Matthews and Stein, 1969).

(7) For small amplitude sinusoidal stimuli at frequencies exceeding about 10 Hz, the amplitude gain of the primary endings increases faster with increasing frequency of vibration than does the corresponding output/input amplitude ratio of the secondary endings (see Fig. 5 of Matthews and Stein, 1969).

(8) For small amplitude muscle vibration at frequencies exceeding about 5–10 Hz, the phase advance of the primary endings is greater than the corresponding phase angle obtained for the secondary endings. For vibrational frequencies above 10–20 Hz the response of the primary endings may show a phase advance that exceeds 90°. A phase angle of 90° seems on the other hand to be an upper limit for the secondary endings.

(9) According to Poppele and Bowman (1969, 1970) the frequency response of the primary endings may be accounted for by a transfer function that contains exactly the same terms as the transfer function obtained for the secondary endings, in addition to a particular differentiating term that is characteristic for the primary endings.

(10) At modulation frequencies above ca. 1–2 Hz the amplitude of the frequency modulated response of the primary endings shows a significant temperature dependence, that is not present in the corresponding response pattern of the secondary endings (Poppele and Bowman, 1969, 1970). According to Poppele and Bowman (1969, 1970) the temperature dependency of the primary ending response could always be accounted for by modifying only the differentiating time constant found to characterize the different behaviour of the primary and the secondary endings.

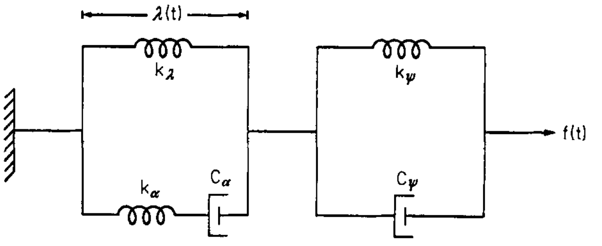


Fig. 2. Mechanical model of the secondary ending receptors. The elastic element k_λ is supposed to describe the mechanical properties of the nuclear chain type of intrafusal muscle fibres on which the secondary ending terminals are supposed to be located. The response of these endings is considered to be proportional to the length $\lambda(t)$ of this element. The other parameters refer to properties of the nuclear bag type of intrafusal muscle fibres. The subscript α indicates parameters of the bag-like sensory region and ψ refers to the lumped parameter representation of the polar region of the nuclear bag fibres

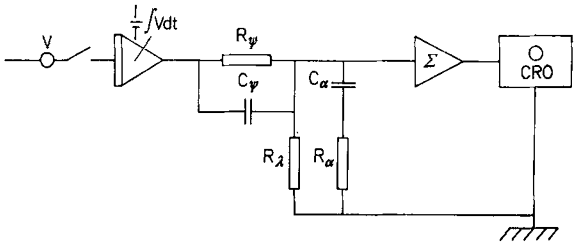


Fig. 3. Direct analogue of the mechanical model used for electronic simulation studies of the system. The resistors correspond to the compliances of the elastic elements appearing in Fig. 2, and the capacitors correspond to the dashpots of the mechanical model. An imposed stretch of the mechanical model is simulated by integrating a constant voltage V, as indicated at left, and applying the output from the integrator to the electronic analogue. In order to avoid loading of the system by the recording device, an operational amplifier Σ is connected to the output of the analogue

Poppele and Bowman (1968, 1969) suggest that the carrier dependent behaviour of the secondary endings reflects an encoder mechanism that is entirely different from that of the primary endings. The hypothesis is based on observations of a similar carrier dependent response of the cructecean stretch receptors (Terzuolo *et al.*, 1968). By intracellular current application, Terzuolo *et al.* could demonstrate a change of the encoder process when the carrier frequency varied.

Such information is not available for muscle spindle receptors and it is thus not possible to decide whether a carrier dependent behaviour reflects properties of the encoder system or properties related to processes that precede the voltage to frequency conversion. The carrier dependency seems to be a resonant phenomenon, and it may merely reflect the very low level of variability present in the discharge pattern. This point of view is supported by the fact that Poppele and Bowman (1970) also found a carrier dependent behaviour in some primary endings with a pronounced regular discharge pattern during steady state conditions.

The observed difference between the variability of the discharge intervals of the two types of receptor endings (Stein and Matthews, 1965) might reflect properties of the encoder system. It seems more likely, however, that it reflects different mechanical or electrical filtering of the preceding governor of the voltage to frequency conversion. Alternatively, different amounts of noise may be introduced by the mechano-electric transduction, or a different spatial integration of the preceding mechanical deformation may yield a different noise pattern in the generator potentials established (Rudjord, 1969a).

4. Model of the Secondary Endings

In the hind leg muscle spindles of the cat the group II flower-spray terminations on the nuclear bag fibres are relatively rare (Boyd, 1962). For the purposes of the present model the contribution from these terminations is therefore disregarded.

Excitation of the receptor endings is supposed to originate from a mechanical extension of the receptor region of the terminals located on the relatively uniform and homogeneous nuclear chain intrafusal muscle fibres.

The coiled secondary ending terminations are supposed to behave as a mechano-electric transducer system in which mechanical deformation is converted into a depolarization of the receptor membrane. The electromotive force which is generated across the membrane, is further supposed to supply current to a common pacemaker of the group II afferent fibre. The resulting train of afferent impulses is modulated according to the time course of the original mechanical deformation of the receptor region of the intrafusal muscle fibre involved. Simple superposition of the generator currents originating from several branches of a group II afferent fibre is proposed and each of these branches is supposed to behave equivalently. The complete system of receptor terminals of an ending may then be approximated by a simple two fibre system as indicated in Fig. 1. Fig. 2 shows a lumped parameter representation of the idealized intrafusal muscle fibre system shown in Fig. 1. This second order visco-elastic system corresponds to that used in connection with an earlier proposed model of the primary endings (Rudjord, 1970). The mechanical properties of the nuclear chain intrafusal muscle fibres are approximated by the purely elastic element k_λ in Fig. 2. Extension of this element is supposed to deform a receptor region to which a linear mechano-electric transducer with zero-order transfer characteristics is connected. The length $\lambda(t)$ is thereby converted into a proportional electrical signal. In the present study this electrical signal is considered as the output of the model.

Any additional transfer dynamics due to the mechano-electric transduction and the impulse generating mechanism is thus disregarded, and the same applies to dynamics of the extrafusal muscle within which the spindle organ is located.

5. Transfer Properties of the Model

The response properties of the proposed model may be described by a general transfer function $H(s)$ that relates an imposed extension $X(s)$ of the mechanical system to the corresponding length change $\lambda(s)$ of the elastic element k_λ:

$$H(s) = \frac{\lambda(s)}{X(s)}\,. \tag{1}$$

The symbol s refers to the complex frequency representation of the time variables, that is obtained through the Laplace transformation

$$F(s) = \int_0^\infty f(t)\, e^{-st}\, dt\,. \tag{2}$$

Experimental studies indicate that the transfer dynamics of the muscle spindle receptors mainly reflect properties of the mechanical system (Edwards, 1955; Lippold *et al.*, 1960). The mechano-electric transduction is therefore supposed to involve a simple constant gain factor μ_λ that relates the deformation of the λ-branch to a proportional electrical quantity that represents the output of the model. The overall transfer function may thus formally be written

$$H_\lambda(s) = \mu_\lambda \frac{\lambda(s)}{X(s)}\,. \tag{3}$$

In terms of the mechanical parameters that according to Fig. 2 define the proposed model, the complete transfer function may be obtained from the set of equations describing the equilibrium state of the system (see Rudjord, 1970):

$$H_\lambda(s) = \frac{\mu_\lambda k_\psi}{k_\psi + k_\lambda} \frac{1 + \left(\frac{C_\psi}{k_\psi} + \frac{C_\alpha}{k_\alpha}\right)s + \frac{C_\psi C_\alpha}{k_\psi k_\alpha}\,s^2}{1 + \left(\frac{C_\alpha}{k_\alpha} + \frac{C_\psi + C_\alpha}{k_\psi + k_\lambda}\right)s + \frac{C_\psi C_\alpha}{k_\alpha (k_\psi + k_\lambda)}\,s^2}\,. \tag{4}$$

6. Response of the Model

Eq. (4) completely defines the response properties of the proposed model. If the Laplace transform $X(s)$ of the input function is known, the corresponding particular response of the model may be computed by inverse transformation of the quantity

$$\mu_\lambda \lambda(s) = H_\lambda(s) \cdot X(s)\,. \tag{5}$$

The available experimental data on the response of the muscle spindle receptors to imposed stretches, have almost exclusively been obtained by stretching the muscle at various rates of constant velocities (see for instance Matthews, 1963). More recently, also sinusoidal vibrations of the muscle has been used (see for instance Matthews and Stein, 1969).

6.1. Ramp Response. The Laplace transform corresponding to an imposed stretch at a constant velocity ϱ given by

$$X(s) = \frac{\varrho}{s^2}\,. \tag{6}$$

According to Eq. (4) and (5), the ramp response of the proposed model then yields

$$H_\lambda^\varrho(s) = \frac{\varrho K_\lambda}{s^2} \frac{1 + a_1 s + a_2 s^2}{(1 + \tau_1 s)(1 + \tau_2 s)} \tag{7}$$

where the parameters are defined according to Eq. (4)

$$K_\lambda = \frac{\mu_\lambda k_\psi}{k_\psi + k_\lambda}\,, \tag{8}$$

$$a_1 = \frac{C_\psi}{k_\psi} + \frac{C_\alpha}{k_\alpha}\,, \tag{9}$$

$$a_2 = \frac{C_\psi C_\alpha}{k_\psi k_\alpha}\,, \tag{10}$$

$$\tau_1 + \tau_2 = \frac{C_\alpha}{k_\alpha} - \frac{C_\psi + C_\alpha}{k_\psi + k_\alpha}\,. \tag{11}$$

The time constants τ_1 and τ_2 represents the inverse roots of the denumerator of Eq. (4).

Inverse transformation of Eq. (7) yields the following time course of the ramp response of the model

$$\begin{aligned} h_\lambda^\varrho(t) &= \varrho K_\lambda(a_1-\tau_1-\tau_2+t) \\ &+ \frac{a_2-a_1\tau_1+\tau_1^2}{\tau_1-\tau_2}\,e^{-t/\tau_1} \\ &- \frac{a_2-a_1\tau_2+\tau_2^2}{\tau_1-\tau_2}\,e^{-t/\tau_2}. \end{aligned} \tag{12}$$

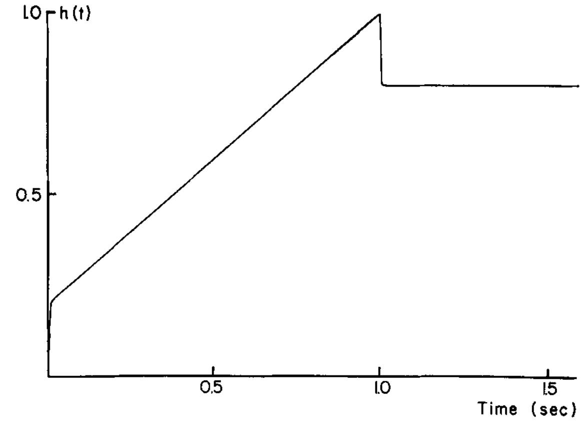


Fig. 4. Computed ramp response of the model with parameters corresponding to the following electrical constants:

$R_\psi = 100\,\mathrm{k\Omega}$, $R_\alpha = 500\,\mathrm{k\Omega}$, $R_\lambda = 1\,\mathrm{k\Omega}$,
$C_\psi = 2.5\,\mu\mathrm{F}$, $C_\alpha = 0.2\,\mu\mathrm{F}$

During conventional experimental conditions, a linear stretch of the muscle may have a duration of the order of one sec by a reasonable rate of stretch to full physiological extension of the muscle. If the receptor endings are not subjected to fusimotor activation the transient phases typically appear to be much shorter (see for instance Matthews, 1963). If thus approximately steady state conditions are obtained (i.e. for $t \gg \tau_1$ and τ_2) the model predicts a constant rate component of the response, given by

$$h_\varrho = \varrho K_\lambda(a_1-\tau_1-\tau_2). \tag{13}$$

This component is superimposed on a pure position response given by

$$h_\chi = \varrho K_\lambda t. \tag{14}$$

The rate response of the system may be defined by Eq. (13) or by the ratio:

$$\eta(t) = \frac{h_\varrho}{h_\chi} = \frac{a_1-\tau_1-\tau_2}{t}. \tag{15}$$

As would be expected, the rate response as given by Eq. (13) is directly proportional to the velocity ϱ of the imposed stretch. It is also proportional to the gain factor K_λ, and it thus contains the same factors as those appearing in the position response h_χ. In order to obtain a quantity that more directly characterizes the rate responsiveness of the system the ratio

$$\eta = \frac{h_\varrho}{h_\chi}\,t \tag{16}$$

appears more adequate. This quantity may easily be determined experimentally, and it will be independent of the time and the velocity of an imposed linear stretch. According to Eq. (16), the rate responsiveness of the present model yields

$$\eta = a_1-\tau_1-\tau_2 = \frac{C_\psi}{k_\psi} - \frac{C_\psi + C_\alpha}{k_\psi + k_\lambda}. \tag{17}$$

If $k_\lambda \gg k_\psi$, this quantity is approximately given by

$$\eta \simeq \frac{C_\psi}{k_\psi}. \tag{18}$$

Fig. 4 shows the unit ramp response of the model computed for a simulated duration of the stretch equal to 1 sec and for parameters as given in the Fig. legend.

A reasonable parameter set was first obtained by real time simulations of the model on the electronic analogue shown in Fig. 3. This analogue also appeared to be convenient for studying the effect of the various parameters on the response properties of the model.

The rate constant of the present model for a particular set of parameters may be calculated directly from Fig. 4, yielding $\eta \simeq 0.23$. As the parameter values corresponding to this ramp response are known, η may also be calculated directly from Eq. (17), or an approximate value may be obtained from the simplified Eq. (18). With the parameter values used in Fig. 4, Eq. (18) yields $\eta = 0.25$. The larger value of η obtained from Eq. (18) reflects the effect of neglecting the last component of Eq. (17).

Experimental estimates of the rate constant of receptor endings may be obtained from adequate frequency displays of the response to constant velocities of stretch. A typical de-efferented secondary ending (Fig. 2 of Matthews, 1963) yields $\eta \simeq 0.35$ for stretch velocities $\varrho > 5$ mm/sec. A slight increase of η appear for $\varrho < 5$ mm/sec.

From frequency displays of the ramp response of typical primary endings (Figs. 5, 7 and 9 of Matthews, 1963), rate constants of about $\eta = 2$ to 2.5 are obtained for stretching rates above ca. 5 mm/sec. For values of ϱ below about 3—5 mm/sec, the rate constant of the primary endings appears to increase significantly. At $\varrho = 5$ mm/sec the rate constant of a particular primary ending (Fig. 7 of Matthews, 1963) yields $\eta \simeq 2$. At $\varrho = 1$ mm/sec (Fig. 9 of Matthews, 1963) the ramp response of the same ending gives $\eta \simeq 3.8$. A stretch velocity of $\varrho = 0.5$ mm/sec further yields $\eta \simeq 5.5$ and for $\varrho = 0.22$ and 0.12 calculations of the rate constants from the frequency display yield $\eta \simeq 6$ and $\eta \simeq 10$, respectively.

The marked increase of the rate constant of the primary endings at very low stretch velocities seems to be a general property of these receptor endings. The effect indicates a nonlinear behaviour of the system. It may reflect the presence of amplitude dependent gain characteristics of these receptors (see Matthews and Stein, 1969) as the behaviour would be a direct consequence of the earlier proposed model interpretation of the nonlinear transfer characteristics of the primary endings (Rudjord, 1969b, 1970).

6.2. Frequency Response. The Laplace operator s may be written as a complex frequency

$$s = \sigma + i\omega.$$

This frequency may be represented by a phasor (or vector) with a magnitude s that rotates at an angular frequency ω in the complex plane.

In the particular case of sinusoidal functions, the real part σ vanishes and the Laplace operator may be replaced by the quantity $i\omega$, where ω represents the angular frequency of the function.

The frequency response of the present model may thus be computed from the general transfer function by replacing S by $i\omega$ in Eq. (4):

$$H_\lambda(i\omega)=K_\lambda\frac{1+a_1 i\omega-a_2\omega^2}{1+b_1 i\omega-b_2\omega^2}\,, \qquad (19)$$

where

$$b_1=\frac{C_\alpha}{k_\alpha}+\frac{C_\psi+C_\alpha}{k_\psi+k_\lambda}\,, \qquad (20)$$

$$b_2=\frac{C_\alpha C_\psi}{k_\alpha(k_\psi+k_\lambda)}\,. \qquad (21)$$

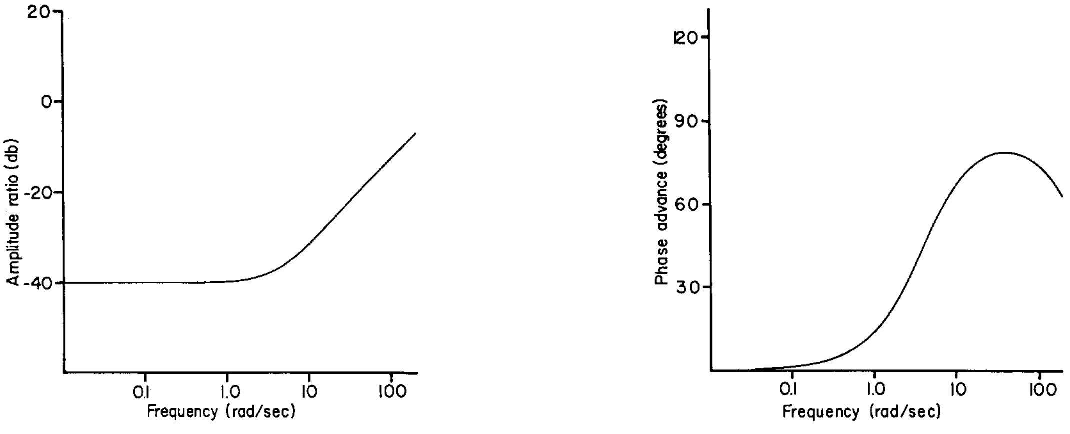
Fig. 5 shows a Bode plot of the frequency response of the model, computed from Eq. (19) for different values of ω, and for the same parameters as used in Fig. 4.

The rate component of the ramp response of this simplified model yields

$$\eta=\frac{C_\psi}{k_\psi}-\frac{C_\psi}{k_\psi+k_\lambda}=\frac{C_\psi}{k_\psi}\cdot\frac{k_\lambda}{k_\psi+k_\lambda} \qquad (24)$$

according to the definition given in Eq. (16).

Eq. (24) thus shows that for a given stiffness ratio $k_\lambda/k_\psi+k_\lambda$ the rate sensitivity increases in direct proportion with the viscous resistance of the lumped polar network of the model. As η is always positive, a true rate sensitivity of the model will be present for all finite values of the parameters involved.



a

b

Fig. 5. Computed frequency response of the model for the same parameters as given in Fig. 4

7. *Lead-Lag Approximation*

In order to obtain a reasonable fast transient response of the present model, the simulation studies suggest that C_α should be small relative to C_ψ. Similarly, a fairly large value of k_α is required. Similar estimations of these parameters appeared to yield the most adequate transfer properties of a corresponding model of the primary endings considered in a previous study (Rudjord, 1970).

If

$$C_\alpha \ll C_\psi \quad \text{and} \quad \frac{C_\alpha}{k_\alpha}\ll\frac{C_\psi}{k_\psi}\,,$$

Eq. (4) may be approximated by the much simpler transfer function

$$\hat{H}_\lambda(s)=\frac{\mu_\lambda k_\psi}{k_\psi+k_\lambda}\;\frac{1+\dfrac{C_\psi}{k_\psi}S}{1+\dfrac{C_\psi}{k_\psi+k_\lambda}S}\,. \qquad (22)$$

Physically, this approximation corresponds to a negligible dynamic load of the α-branch in the proposed mechanical model shown in Fig. 2.

Eq. (22) describes a first order system with simple lead-lag behaviour, corresponding to muscle spindle models that have been proposed earlier by several authors (Vossius, 1960; Stark and Houk, 1962; Houk *et al.*, 1966; Toyama, 1966; Crowe, 1968).

Inverse transformation of Eq. (22) multiplied by ϱ/s^2 yields the following ramp response in the time domain

$$\hat{h}_\lambda^\varrho(t)=\varrho K_\lambda\left(\left(\frac{C_\psi}{k_\psi}-\frac{C_\psi}{k_\psi+k_\lambda}\right)\left(1-e^{-\frac{t(k_\psi+k_\lambda)}{C_\psi}}\right)+t\right). \qquad (23)$$

8. *Conclusions*

(1) An earlier proposed second order model of the system of intrafusal fibres of a muscle spindle used for a description of the behaviour of the primary ending receptors may also be used as a basic element in a model of the secondary endings.

(2) In the proposed model, excitation of the secondary endings is proposed to be proportional to the degree of extension of the nuclear chain intrafusal muscle fibre. The mechanical properties of these fibres are represented by a purely elastic component.

(3) The mechanical parameters used for a model description of the primary ending receptors also fit the model of the secondary endings reasonably well when the simulated transducer gain of the receptor terminals of the secondary endings is chosen identical to that of the group Ia terminals innervating the nuclear chain intrafusal muscle fibres (see Rudjord, 1970).

(4) By adequate parameter selection both the response to linear stretch and to sinusoidal vibrations of the length of the mechanical system yields response characteristics that correspond closely to the general experimental observations on de-efferented muscle spindles.

(5) The proposed model of the secondary endings appears to behave approximately equal to a simple first order lead-lag network, provided that the parameter values of the complete system correspond largely to those used earlier for a best fit of the model to the typical response properties of the primary ending receptors.

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Kongreßmitteilung

Der Erste Europäische Kongreß für Biophysik, organisiert von der Österreichischen biophysikalischen Gesellschaft unter Mitwirkung der Schwestergesellschaften und unter der Patronanz der Internationalen Union für Reine und Angewandte Biophysik (IURAB), findet in Baden bei Wien, 14.—17. September 1971, statt. Anfragen und Anmeldungen an das Sekretariat, Frau E. Weidenhaus, Wiener Medizinische Akademie, Stadiongasse 6—8, A-1010 Wien, Österreich.

Verantwortlich für den Textteil: Prof. Dr. W. Reichardt, 7400 Tübingen, Max-Planck-Institut für biologische Kybernetik, Spemannstr. 38 — Verantwortlich für den Anzeigenteil: Edgar Seidler, 1 Berlin 33, Heidelberger Platz 3. — Springer-Verlag, Berlin · Heidelberg · New York
Druck der Universitätsdruckerei H. Stürtz AG, Würzburg. — Printed in Germany