

A NON-LINEAR MECHANICAL MODEL OF A NON-SPIKING MUSCLE RECEPTOR

BY C. S. BERGER AND B. M. H. BUSH

*Department of Electrical Engineering, Monash University,
Clayton, Victoria, Australia 3168, and Department of Physiology,
University of Bristol, Bristol, England*

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The sensory response of a mechanoreceptor is generally assumed to be a compound function of its mechanical and electrochemical properties. In a muscle receptor such as the mammalian muscle spindle or crayfish stretch receptor, the former depend upon the visco-elastic elements of the receptor muscle and its linkages with the sensory endings, while the latter properties reside within the sensory neurone itself. Analysis of these systems is complicated, however, by the difficulty in defining the precise stimulus obtaining at the site of transduction, and by the possible modifying influence of the impulse encoding process.

One approach to the problem of evaluating the contribution of mechanical factors to the sensory response is to compare the experimentally recorded response with that of an appropriate model derived from the known structure. The well-defined morphology of the crab coxal muscle receptor (Alexandrowicz & Whitear, 1957; Whitear, 1965), together with the absence of regenerative impulses in its afferent nerve fibres (Bush, 1976), makes this an attractive preparation for such an approach. In this paper we show that a non-linear mechanical model, obtained by identifying parts of the receptor muscle system with simple mechanical elements, can reproduce the principal features of the intracellularly recorded afferent responses to constant velocity stretches.

The salient structural components of the crab receptor are illustrated schematically in Fig. 1A. The two main sensory afferents (S and T fibres) produce characteristically distinct, graded receptor potentials in response to ramp function (constant velocity) stretch, as represented by the continuous curves in Fig. 2. The S signal comprises a position plus velocity component, while the T signal has an initial sharp rise (depolarization) followed by a progressive decay during the velocity step (ramp). However, whereas the shape of the S response remains qualitatively the same for different velocities, the decay of the T signal during the ramp decreases relatively with velocity, and may even become negative (i.e. the depolarization now *increases* throughout the ramp) when the velocity is sufficiently small (see figs. 4C and 5A in Bush & Roberts, 1971). The T response is thus markedly non-linear. Furthermore, reciprocal variations in amplitude were sometimes seen in the S and T responses – i.e. when subjected to repetitive pulls over a long period, the S response suddenly increased while the T response simultaneously decreased (see fig. 11, *loc. cit.*).

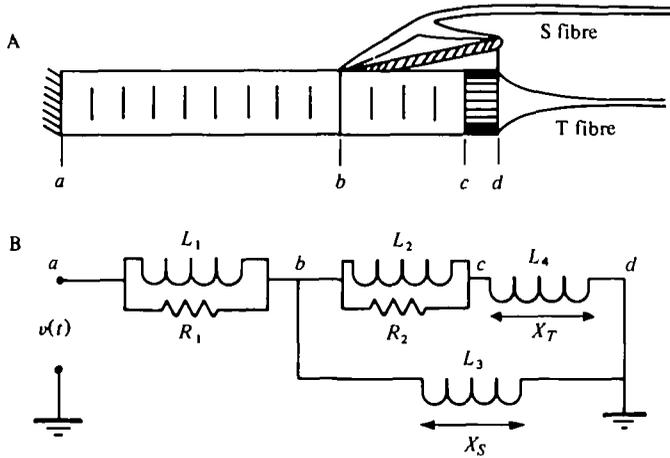


Fig. 1. (A) Schematic diagram of the crab muscle receptor organ, illustrating the essential features of the connections between the S and T fibres and the receptor muscle (*a-d*, greatly truncated). The S fibre bifurcates peripherally to attach to two flanking strands of connective tissue (only one shown), which lie in parallel with about a third of the muscle (*b-d*). The T fibre ends in a short proximal tendon which lies in series with the receptor muscle (*c-d*). (B) Mechanical analogy of the receptor system (see text).

The present study assumes that for positive velocity stretches, the S and T responses are proportional to the length of the connective tissue components in which each sensory fibre inserts. The receptor muscle is modelled by two lumped parameter sections corresponding to the muscle segments *a-b* and *b-c* represented in Fig. 1A. Each muscle segment is modelled by a spring (elastic force L_1 , L_2) in parallel with a damper (viscous force R_1 , R_2). The parallel connective tissue and the series tendon are assumed to have negligible viscous damping and are thus modelled by springs only (L_3 , L_4). The mechanical analogy of the complete receptor system is therefore as shown in Fig. 1B. The velocity/force relationships for the spring and damper are respectively $v = L(di/dt)$ and $v = iR$, where v is velocity, i is force, $1/L$ is stiffness of the spring, and $1/R$ is the viscous friction of the damper. The variables X_S and X_T denote the extensions which cause the electrical signals in the S and T fibres, respectively.

An attempt was made to simulate the experimental results shown in Fig. 2 with linear elements. The transfer functions relating the extensions of the tissue corresponding to the T and S responses, X_T and X_S respectively, to velocity stretches (v) are:

$$\frac{X_T(s)}{V(s)} = \frac{(s + \omega_1)(s + \omega_2)}{s^2 + s\alpha_1 + \alpha_2} \quad \text{and} \quad \frac{X_S(s)}{V(s)} = \frac{(s + \omega_1)(s + \omega_3)}{s^2 + s\alpha_1 + \alpha_2},$$

where s is the Laplace variable and $\omega_1 = R_1/L_1$, $\omega_2 = R_2/L_2$, $\omega_3 = \omega_2 + R_2/L_4$,

$$\alpha_1 = R_1 \left(\frac{1}{L_1} + \frac{1}{L_3} \right) + \frac{R_2}{L_2}, \quad \alpha_2 = \frac{R_1 R_2}{L_2 L_4} \left(\frac{L_2 + L_4}{L_1} + \frac{L_3 + L_4 + L_2}{L_3} \right); \quad L_5 = \frac{L_3 L_4}{L_3 + L_4}.$$

Note that only the two zeros, ω_2 and ω_3 , differ in the two transfer functions. Nevertheless this difference was sufficient to qualitatively model the different responses of the

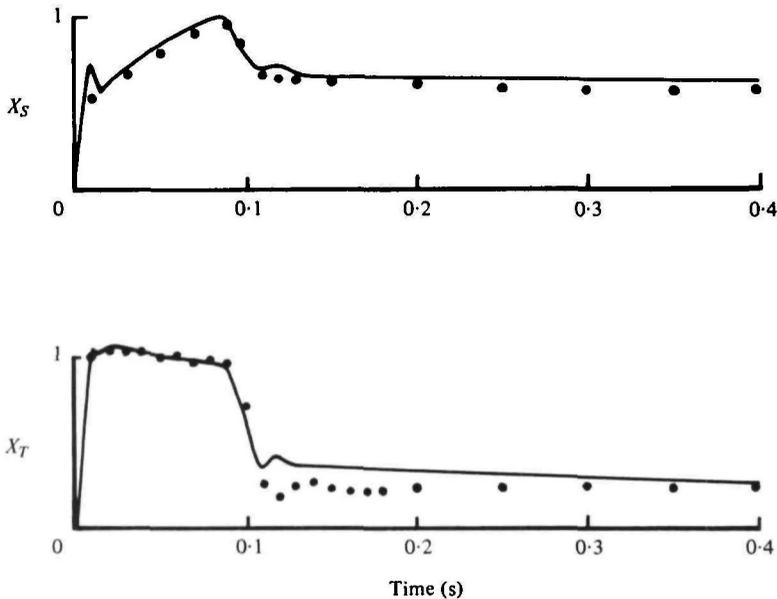


Fig. 2. Comparison of typical experimental recordings (solid curves, drawn from fig. 4E of Bush & Roberts, 1971) with the computer simulation results (dotted points). X_S , S fibre response; X_T , T fibre response. Parameter values for these responses were: velocity of stretch = 5 mm/s, duration of stretch = 0.09 s. $R_1 = 63$, $R_2 = 3.16$; $L_1 = 17 + 61.2v_1$, $L_2 = 0.927 + 9.99v_2$; $L_3 = 1.37$, $L_4 = 0.246$.

S and T fibres during the application of the velocity step. Simple but tedious calculations show, however, that the values of ω_1 and ω_2 required to produce the decay in the T signal during the velocity step were too small to match the response remaining after the step. It was thus necessary to introduce non-linear elements into the model and make the ω 's decreasing functions of velocity. The above equations show that this could be done by making either the muscle compliances L_1 and L_2 , or the viscous frictions $1/R_1$ and $1/R_2$, increasing functions of velocity. Although it may seem less physiologically plausible the former device was chosen, as it simplified the calculations of the initial conditions for the subsequent optimisation of parameters. Accordingly the compliances were made to vary with velocity thus:

$$L_1 = C_1 + C_2 \cdot v_1 \quad \text{and} \quad L_2 = C_3 + C_4 \cdot v_2,$$

where the C 's are constants and v_1 and v_2 are the velocities of stretch of the corresponding muscle segments. The model was simulated on a digital computer.

The parameters were optimized by using a Simplex subroutine to minimise the cost function,

$$\bar{y} = \int_0^{0.45} (y_S - K_S x_S)^2 + (y_T - K_T x_T)^2 dt,$$

where y denotes the experimental result, x the model extension, and K the transfer constant relating extension to electrical signal. The cost function was found to have many local minima; a suitable set of results was only obtained after the linear model

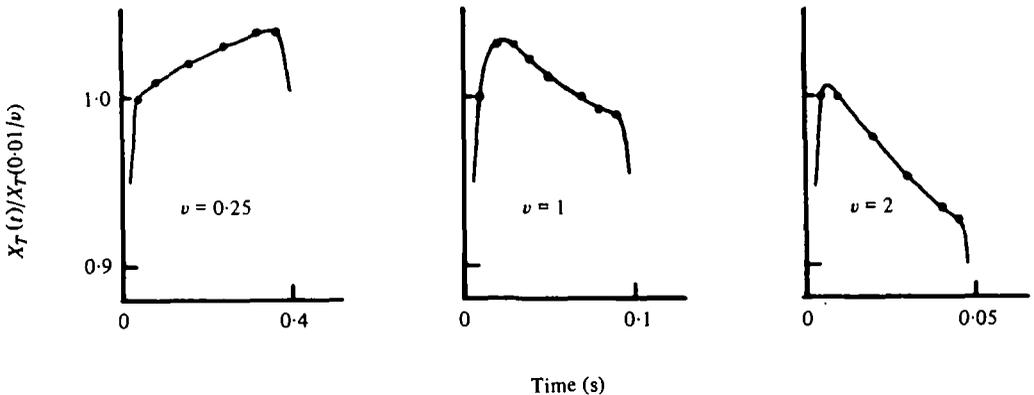


Fig. 3. Computer simulation of relative decays in the T fibre response to stretches of different velocities ($= v \times 5$ mm/s). Results are normalised to the first predicted point, at $t = 0.01/v$ s.

was used to obtain a reasonable initial condition. The final result is shown in Fig. 2. These responses may not represent the globally optimum model parameter, but were nevertheless considered close enough to justify the model.

The model was also subjected to velocity steps of twice and one quarter the original value. The S fibre response remained qualitatively the same, whereas the decay in the T fibre response decreased with velocity as in the experimental results (Fig. 3). This provides additional support for the non-linearity introduced above. The reciprocal variations in the T and S responses, referred to above, can be explained by considering a sudden decrease in stiffness of the spring denoted L_2 . If the total muscle extension were maintained constant, then the second muscle segment would expand allowing the series tendon to shorten, while the parallel connective tissue would extend as the total stiffness of the second half of the muscle system ($b-d$) would have decreased.

Tension monitored in the receptor muscle complex during and following constant velocity stretch resembles the mean (or sum) of the concomitant S and T receptor potentials (Bush & Godden, 1974; Bush, 1976). This too is consistent with the analysis presented here, since the lengths of the two connective tissue components containing the S and T endings are proportional to their respective tensions, and the overall tension equals the sum of these two tensions. The length change accompanying a controlled ramp function input (Bush, 1976) should also follow from the model. Experiments involving dissection of the receptor complex into separate parts, though technically difficult, may eventually permit a more direct test of the model.

In addition to the foregoing response features, the model can simulate the symmetrical negative velocity response of the S fibre during receptor shortening, and also that of the T fibre when the muscle is simultaneously tetanised (see Bush & Godden, 1974). The very different release response of the T fibre in the passive receptor probably reflects ionic events in the sensory dendrites (cf. Mirolli, 1979), as do the small potential oscillations sometimes seen after stretching. A corollary of the good fit to the experimental data of an anatomically realistic mechanical model such as the present one, is that the 'adaptation' displayed in the S and T responses can be largely explained in terms of the mechanical properties of the sense organ. A similar interpretation might be suggested for the frog and mammalian muscle spindles (see, for

example, Hunt & Ottoson, 1975) and the crayfish slowly adapting abdominal stretch receptor. In the 'fast' crayfish receptor, however, accommodation of the spike generator evidently contributes significantly to the overt impulse adaptation (Nakajima & Onodera, 1969).

It may be concluded that the characteristic velocity responses of the crab's coxal muscle receptor can be generated by an appropriate combination of simple mechanical elements. The present model is not unique, as an infinite number of combinations of different L and R values will produce the same result. Different forms of non-linear equations for L_1 and L_2 could probably have been used or, alternatively, non-linear R_1 and R_2 could also have given the desired non-linear effect (but with more computational complexity). A unique model, with global optimum, can only be obtained by using a more testing input signal such as a pseudo random input (or 'white noise'), as applied recently to insect tactile hairs (French & Wong, 1977) and in progress on the crab coxal receptor (Bush, DiCaprio & French, 1978).

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