AN ANALYSIS OF IMPULSE DISCHARGES
FROM THE SPINDLE RECEPTOR

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The response of spindle receptors to muscle stretch, as represented by either the amplitude of the receptor potential or the frequency of impulse discharges, is composed of two components; dynamic and static ones (KATZ, 1950). The dynamic response occurs in the phase of muscle extension, and depends upon the velocity of muscle lengthening, while the static component is maintained during sustained extension, relating to the muscle length (KATZ, 1950). The former represents the process of the 'differentiation' involved in the transducer action of the spindle receptors. It can not be explained in terms of the electrical properties of the nerve membrane at the sensory terminals (KATZ, 1950). Instead there have been suggestions that it may occur due to visco-elastic properties of the spindle receptors (B. H. C. MATTHEWS, 1931; KATZ, 1961; R. ITO and F. ITO, 1963; P. B. C. MATTHEWS, 1964).

The aim of the present work is to examine the validity of the hypothesis of the mechanical 'differentiation' just mentioned. When a muscle is pulled, changes in the spindle receptor will occur in the following sequence; (i) an increase of muscle length raises the tension along the sensory portion of the intrafusal muscle fibres, (ii) the tension increase over the sensory portion of the intrafusal muscle fibres develops a receptor potential across the nerve membrane, (iii) the receptor potential leads to impulse discharge through the sensory nerve fibres. The energy is transformed in turn relating to the following quantities; the muscle length \( l \), tension in the sensory portion \( p \), receptor potential and impulse frequency \( f \).

In frog toe muscle KATZ (1950) found an approximately linear relation between the amplitude of the receptor potential and the frequency of the impulse discharges. A similar observation was made on stretch receptor cells of the crayfish (TERZUOLO and WASHIZU, 1962). Experiments on crayfish stretch receptor cells further revealed that impulse frequency is proportional to the tension recorded along the receptor muscle (KRNIJEVIC and GELDER, 1961). Therefore, as the basis of the present work, a simple relation will be
assumed between \( f \) and \( p \);

\[ f = k(p - P') \quad (1) \]

where \( k \) is a constant and \( P' \) threshold tension for initiating impulses. If this were so, the impulse frequency during alteration of the muscle length \( (l) \) would be determined by the relation of \( l \) versus \( p \). The functional form of the latter would be given if the mechanical properties of the spindle receptor were known. A simple visco-elastic model will thus be described below.

In Results the frequency of impulse discharges is measured in frog sartorius muscle during muscle stretch at constant velocities as well as under sustained extension at various lengths. It will be shown that the impulse frequency follows the theoretical prediction to the extent that the model can be regarded as representing the transducer action of the spindle receptor, at least the main part of it. The parameters of the model will be derived from the characteristics of the spindle discharge patterns.

MODEL

The visco-elastic property of muscle fibres has been represented by a model comprising a spring and a dash-pot in parallel (Hill, 1922; Gasser and Hill, 1924; Levin and Wyman, 1927). This model may be applied not only to the extrafusal muscle fibres, but also to the intrafusal muscle fibres which belong to the spindle receptor. Within the muscle spindle, as diagrammatically shown in Fig. 1A, an afferent fibre (\( N \)) branches over several intrafusal muscle fibres and terminates in their sensory portions (\( S \)) (Gray, 1957; Katz, 1961). Since striations are absent or attenuated in the sensory portion (Robertson, 1956; Gray, 1957; Katz, 1961; F. Ito, Toyama and R. Ito, 1964), the viscosity may be assumed to be considerably smaller than that of the muscular portion (\( M \)) (B. H. C. Matthews, 1931; Katz, 1961; R. Ito and F. Ito, 1963; P. B. C. Matthews, 1964). Furthermore, frog muscle spindle con-

**Fig. 1.** A, schematic drawing of a spindle receptor. \( N \); sensory nerve fiber. \( M \); muscular portion with striation. \( S \); sensory portion. B, visco-elastic model of the spindle receptor. \( G_1 \); spring representing the elasticity of the sensory portion. \( G_2 \); that for muscular portion. \( \eta \); dash-pot denoting the viscosity of the muscular portion. \( l \); length of the model. \( p \); tension along \( G_1 \).
tains only one type of intrafusal muscle fibres (BARKER and COPE, 1962), and in
this respect it is simpler than its mammalian counterpart which involves two
types of intrafusal muscle fibres; the nuclear bag and nuclear chain fibres.

The simplest visco-elastic model of the spindle receptor is thus given in
FIG. 1B, in which the elasticities of the sensory and muscular portions of the
intrafusal muscle fibres are represented by springs $G_1$ and $G_2$ respectively,
and the viscosity of the muscular portion by a dash-pot $\gamma$. The viscosity of
the sensory portion is neglected for the reason mentioned above. In this
model of the spindle receptor, the tension along the sensory portion of the
intrafusal muscle fibres ($p$) is given by that of the spring $G_1$. When the
model is expanded from the initial length ($L_i$) to the final length ($L_s$) at a
constant velocity (FIG. 2A), $p$ will change in the manner illustrated in FIG. 2B:
It consists of two terms, $p_1$ and $p_2$, as separately shown in FIG. 2C and D
(see Appendix). While the model is being stretched, $p_1$ rises exponentially,
and reaches $P_d$ at the time $T_s$ when the stretch has ceased. After $T_s$, it
decreases exponentially, while the model is kept at the expanded length. On
the other hand, $p_2$ increases from $P_i$ to $P_b$ in parallel with the length increase
from $L_i$ to $L_s$.

As the model of the whole spindle receptor system, it will further be
assumed that impulses are generated at a frequency ($f$) which is related to
$p$ in the equation (1). Thus, like $p$, $f$ would be separated into two fractions,
$f_1$ and $f_2$, in the following way,

\[
\begin{align*}
  f_1 &= kp_1, \\
  f_2 &= k(p_b - P').
\end{align*}
\]

Like $p_1$, $f_1$ would be raised only transiently during, and shortly after the
period of stretch. Therefore, as shown in FIG. 2D, the impulse frequency at
the steady state before or long after single stretches, $F_i$ or $F_b$, would represent
$f_2$ alone at these moments. On the other hand, the frequency $F_s$ at the
cessation of stretch would be a sum of $f_1$ and $f_2$ at this time. Thus $(F_s - F_b)$
will give $F_d$ that is the $f_1$ component at that moment. As will be described
in Appendix, $F_a$ is given as function of the stretch velocity by

\[
F_a = kAv(1 - \exp(-\Delta L/vB)),
\]

while $F_i$ and $F_b$ are related to the muscle length by

\[
\begin{align*}
  F_i &= kC(L_i - L_0) + k(P_b - P'), \\
  F_b &= kC(L_s - L_0) + k(P_b - P'),
\end{align*}
\]

respectively. Here $v$ is the stretch velocity, $\Delta L$ net length increase produced
by stretch, i.e. $(L_s - L_i)$, $L_0$ the standard length of the model, $P_0$ tension in
$G_1$ at $l = L_0$, and $A, B, C$ are constants relating to $G_1, G_2, \gamma$ (see the equations
(10), (11), (12) in Appendix). These equations provide the basis for the ex-
perimental test of the actual spindle discharge in Results.
FIG. 2. An illustration of the behaviour of the visco-elastic model of FIG. 1B. A, time course of the length increase at constant velocity stretches. $l$; length of the model. $L_0$; standard length. $L_i$; initial length. $L_s$; final length. $\Delta L$; net length increase produced by stretch. B, time course of the change in tension $p$ or impulse frequency $f$. $P_0$, tension at $l=L_0$; $P_i$, initial tension before stretch; $P_s$, that at the end of stretch; $P_b$, that long after the end of stretch; $P_d=P_s-P_b$. C, the dynamic component of $p_1$ or $f_1$ of $p$ or $f$. D, the static component $p_2$ or $f_2$ of $p$ or $f$.

METHODS

The experiments were carried out on sartorius muscles (20–30 mm in length) of Rana nigromaculata at room temperatures of 18–21°C. They were excised with the muscle nerve attached. On the muscle surface a spindle receptor was identified microscopically (cf. F. Ito, Toyama and R. Ito, 1964) and its innervation was isolated by cutting all other nerve fibres in their intramuscular course. The muscle with a functionally isolated receptor was laid in a Ringer bath made of perspex plates. The Ringer solution had the following ionic composition: Na 112.8, K 2.7, Ca 3.6, Cl 117.3, HCO$_3$ 1.8 m-equiv./1. The pelvic end of the muscle was fixed on a glass hook which was attached to a micrometer (MM of FIG. 3). The position of the glass hook was read on the micrometer, the error being within 0.1 mm. The other end of the muscle was fixed on a stretcher which was a lever (L) of a pen-motor (PM). The stretcher was driven by a current generator to produce a linear increase of muscle length. The free end of the stretcher moved over a slit, and its position was signalled by measuring with a photocell the amount of light passing through the slit. The extent of stretch was controlled with a stopper (ST) that limited the movement of the stretcher.

Muscle length was displayed on one beam of a dual beam cathode ray oscilloscope (FIG. 4). Platinum-platinum black electrodes were used for recording impulses from the nerve trunk which was lifted just above the Ringer solution. Nerve impulses were amplified with an A.C. amplifier and displayed on another beam of the oscilloscope. Impulse discharges were recorded continuously during and after muscle stretch, together with muscle length, on moving film.
FIG. 3. An illustration of the Ringer bath with the device for stretching the muscle. The upper and lower diagrams show the top and side views, respectively. M; sartorius muscle. RE; recording electrode. PM; pen-motor used as a stretcher. L; lever of the pen-motor. ST; stopper. MM; micrometer. PC; photocell. MS; microscope. Lp₁ and Lp₂; lamps for illuminating the muscle and the photocell, respectively.

RESULTS

1. General observations. The muscle was initially extended to the resting length in situ, which was arbitrary taken as the standard muscle length $L_0$. From the $L_0$-length the muscle was subjected to a series of stretches at eight different velocities. Similar tests were repeated with the initial muscle length increased by 2 mm, and then further by another 2 mm. In each single stretch the muscle was maintained for 3 sec at the final length attained, as shown in the lower traces of Fig. 4, and kept relaxed for at least 15 sec before the next trial. Fig. 4 illustrates the impulse discharges from a spindle receptor during such trials from the length of $L_0 + 2$ mm. The discharge frequency was measured at the moment of initiation of each impulse as the mean of the reciprocals of the preceding and succeeding two intervals of discharges, and was plotted in Fig. 5 for stretches at four different velocities. As shown in
FIG. 4. The response of a spindle receptor to muscle stretch at four different velocities (A, 2.0 mm/sec; B, 6.0 mm/sec; C, 12 mm/sec; D, 35 mm/sec). In each record the stretch started at the moment indicated by an arrow, from the initial muscle length of $L_0 + 2$ mm. The continuous traces registered the impulses discharged from a spindle receptor and those with blanking at 100 c/sec indicated the muscle length. Note that the initial and later halves of the slowest stretch are indicated in the upper and lower records of A, respectively.

the inset diagram of Fig. 5, the impulse frequency changed in the three successive phases; (i) a transient rise immediately following the onset of stretch, which decayed rapidly; (ii) a progressive increase during the period when the muscle was being stretched; (iii) a gradual decline to a certain low value within one or two seconds after the muscle attained the final length.

Comparison between the curve in Fig. 2B for the tension rise in the spindle model and that in Fig. 5 for the discharge frequencies from the actual muscle spindle reveals a close similarity of their time courses except for the initial transient rise in the latter defined above as the phase (i). This initial frequency rise, however, varied greatly in its degree from case to case, and was even absent in some preparations. This contrasts to the constant appearance of the later phases of frequency rise. The possible cause for the phase (i) will be discussed later.

2. Testing the equations (5) and (6). After the muscle reached the final length of stretch, as shown in Fig. 5, the frequency fell to the same steady
FIG. 5. The impulse frequency plotted against time. The moment of the onset of stretch was taken as zero time. Four sets of plotting points (○, △, ●, ▲) are for A, B, C, D of FIG. 4, respectively. The time course of increase of the muscle length for each trial of stretch is indicated at the bottom. The inset diagram indicates the three phases (i), (ii), (iii) of increase in the impulse discharge.

value in spite of the different velocities of extension. This is to be expected for the frequency $F_{ib}$, which according to the equation (6) would be related merely to $L_s$, but not to the stretch velocity. In the case of FIG. 6 $F_i$ and $F_b$ were measured during trials of stretch from three different initial muscle lengths and are plotted as function of the muscle length at the time of measuring them. The plotting points fall on a straight line which is drawn by the equations (5) and (6) with $kC = 25$ impulses/sec/mm, and $k(P_0 - P') = -35$ impulses/sec.

FIG. 6. $F_i$ (○) and $F_b$ (●) plotted against the amount of muscle extension. Explanation is in the text.
In nine out of fifteen spindle receptors examined in the present experiment, $F_i$ and $F_b$ were related linearly to the muscle length over a range of the latter from 1 to $1.35 \times L_o$. The values of $kC$ and $k(P_0-P')$ calculated for these receptors are listed in Table 1. In the remaining six, however, the linear relation was restricted within a relatively small range of length increase (less than $0.25 \times L_o$), over which there was a saturation phenomenon in the impulse frequency.

3. Testing the equation (4). $F_d$ was measured in the way shown in Model as $(F_i-F_b)$ and was plotted in Fig. 7 against the stretch velocities. Three sets of the plotted points were obtained in three trials of stretch from different initial muscle lengths, and they lie along the same curve. Hence $F_d$ is independent of the initial muscle length, but it is related to the stretch velocity, just as expected from the equation (4). The curve in Fig. 7 is drawn by the equation (4) with $kA=12$ impulses/mm, $B=0.15$ sec.

![Fig. 7. $F_d$ plotted against the stretch velocity. The initial muscle length, $L_o$ (△), $L_o+2$ mm (○), $L_o+4$ mm (●).](image)

In all cases examined, $F_d$ was found to be independent of the initial muscle length as far as $F_i$ and $F_b$ are linear functions of the muscle length. Values of $kA$ and $B$ were shown for the nine receptors in Table 1 in comparison with $kC$ and $k(P_0-P')$.

4. Reconstruction of the whole time course of spindle discharge. From the values of $kA$, $B$, $kC$ and $k(P_0-P')$ calculated above, the whole time course of the spindle discharge can be reconstructed for the model of Fig. 1B under the same conditions of stretch as in Figs. 4 and 5. In Fig. 8A–D, the response predicted for the model is indicated by solid lines at four different stretch velocities, while the actual frequency change in Fig. 5 is shown by interrupted lines. These ideal and actual curves may be said to agree with each other reasonably well except for the following two points; (i) the model response lacked the initial transient phase of the frequency rise, as already mentioned...
above, and (ii) after the muscle was extended at a relatively fast velocity, the actual impulse frequency fell considerably faster than in the ideal curves (Fig. 8C and D).

**DISCUSSION**

The three characteristic frequencies of the spindle discharge \(F_d, F_i, F_b\) produced by muscle extension altered in a fashion that is described for the simple model of the spindle receptor (Figs. 6 and 7). The whole time course of the spindle discharge conformed to that expected for the model (Fig. 8).

As listed in Table 1, the coefficients \(kA, B, kC\) of the equations (4), (5), (6) were calculated in nine preparations from the curves relating \(F_i\) and \(F_b\) to \((L_1-L_0)\) and \((L_2-L_0)\), or \(F_d\) to \(v\), respectively (Figs. 6 and 7). The obtained values had only small variations, so that they may be taken as reflecting the fundamental properties of spindle receptors. From the coefficients \(kA, B, kC\) as shown in Appendix, the parameters of the model can be given in the form of \(G_1/G_2, \eta/G_2\) and \(kG_1\). \(\eta/G_2\) would represent the time constant of length change in the striated portion of the intrafusal muscle fibres in the case where they are kept isotonic. About 600 msec obtained here is in approximate agreement with 200-300 msec, which has so far been given for the isotonic shortening of the whole sartorius muscle (RITCHIE and WILKIE, 1958). To this extent, the visco-elastic parameters in the striated portion of the intrafusal muscle fibres appear to be of the same order as those of the extrafusal muscle fibres. \(G_1/G_2\) of about 3, on the other hand, would indicate the
difference of the elastic properties between the striated and non-striated portions of the intrafusal muscle fibres. On the other hand, there was a wide variation in $k(P_0 - P')$ of Table 1. Since $kA$, $kC$, and $kG_1$ in Table 1 had a relatively small variation, $k$ itself would not fluctuate greatly. But rather it may be that in the present experiments the standard length $L_0$ could not be determined accurately, so that the value $P_0$ may have varied greatly from case to case.

Thus it may be said that the model in Fig. 1B represents the major portion of the behaviour of the real muscle spindle. The dynamic and static responses of the muscle spindle can now be discriminated on the basis of this model: As shown in the equation (4), the relation of the dynamic response to the stretch velocity depends upon the coefficient $A$, which includes the viscosity of the striated portion of the intrafusal muscle fibres (see the equation (10) in Appendix). On the other hand, in the equations (5) and (6), the static response is merely determined by the muscle length, the proportion constant $C$ comprising the elasticities of both striated and non-striated portions of the intrafusal muscle fibres (see the equation (12)). The large viscosity of the striated portion thus is essential for effecting the ‘differentiation’ in the spindle response.

Two discrepancies have been pointed out between the responses of the model and of the real spindle. Firstly, the initial transient rise of the impulse frequency (phase (i) specified in Results) should arise from a factor or factors due to the difference in elastic properties between the striated and non-striated portions of the intrafusal muscle fibres. On the other hand, there was a wide variation in $k(P_0 - P')$ of Table 1. Since $kA$, $kC$, and $kG_1$ in Table 1 had a relatively small variation, $k$ itself would not fluctuate greatly. But rather it may be that in the present experiments the standard length $L_0$ could not be determined accurately, so that the value $P_0$ may have varied greatly from case to case.

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Two discrepancies have been pointed out between the responses of the model and of the real spindle. Firstly, the initial transient rise of the impulse frequency (phase (i) specified in Results) should arise from a factor or factors
which are not involved in the model in Fig. 1B. Though a systematic investigation was not made, it was a general impression that this transient frequency rise was prominent when the muscle was pulled from a relatively relaxed state. A possibility may be pointed out that the muscle was transiently pressed by the neighbouring extrafusal muscle fibres which would have transverse shift particularly when pulled from a relaxed state. Secondly, after the stretch ceased, the fall of the impulse discharge was rapider than that expected from the model. A relevant observation, however, has been made upon the tensile behaviour of the glycerinated muscle fibres (Ohnishi 1962). When a glycerinated muscle was pulled in the same manner as was adopted for living muscle in the present experiment, the tension rose and fell along curves closely resembling those in Figs. 5 and 8. The fall of the tension was indeed faster than was expected for a model with constant visco-elastic parameters, because the viscosity of the glycerinated muscle decreased as it was extended. This thixotropic change of the viscosity became more prominent when the stretch was done at higher velocities. Consequently, it is possible in the present cases that the viscosity of the intrafusal muscle fibres decreased by its thixotropic nature at relatively high stretch velocities, though the fastest stretch adopted was no greater than the maximum velocity of the physiological contraction of the sartorius muscles (Ritchie and Wilkie, 1958; Jewell and Wilkie, 1958).

APPENDIX

When the spindle model shown in Fig. 1B is extended from the standard length $L_0$, its mechanical behaviour concerning the length ($l$), tension rise ($p$) and time ($t$) is generally given by the following equations,

$$x = l - L_0 = x_1 + x_2$$
$$y = p - P_0 = G_1 x_1 = G_2 x_2 + \eta \frac{dx_2}{dt}.$$  

(7)

Here $x$ and $y$ are increases of the length and tension from their respective standard values $L_0$ and $P_0$, $x_1$ and $x_2$ are the length increases for $G_1$ and $G_2$ from their standard lengths, respectively. When the stretch is of a constant velocity as shown in Fig. 2A ($l = L_0 + vt$ at $0 \leq t \leq T_s$, $l = L_s$ at $t \geq T_s$), the equation (7) can be solved to yield,

$$p = p_1 + p_2$$
$$p_1 = A v [1 - \exp (-t/B)] \quad \text{for} \quad 0 \leq t \leq T_s$$
$$= A v [1 - \exp (-T_s/B)] \exp \left[1 - (t - T_s)\right] \quad \text{for} \quad t \geq T_s$$
$$p_2 = C (l - L_0) + P_0,$$

(8)

where $T_s$, $A$, $B$, $C$ are given by the following equations
Pd, Pi, Pb (see Fig. 2) are thus given as

\[ T_v = \Delta L/v, \]  
\[ A = \gamma G_1 / (G_1 + G_2)^2, \]  
\[ B = \gamma / (G_1 + G_2), \]  
\[ C = G_1 G_2 / (G_1 + G_2). \]  

By the equations (2) and (3), these values Pd, Pi, Pb are converted to the spike frequency Fd, Fi, Fb as described in the equations (4), (5), (6). The three quantities G1/G2, n/G2, kG1 relating to the parameters of the model, were derived from the equations (10)-(12) in the following way.

\[
\frac{G_1}{G_2} = \frac{A}{BC}, \\
\frac{\eta}{G_2} = B(1 + A/BC), \\
kG_1 = kC(1 + A/BC).
\]

Table 1 lists their values calculated from kA, B, kC for each preparations.

**SUMMARY**

1. Impulses discharged from single spindle receptors of frog's sartorius muscle were recorded during stretch at various velocities and their patterns were analysed on the basis of a visco-elastic model of the muscle spindle.
2. The model comprises a spring (G2) and a dash-pot (77) in parallel, and a spring (G1) in series with them; G1 represents the elasticity of the sensory portion of the intrafusal muscle fibres, and G2 and 77 the elasticity and viscosity of the muscular portion, respectively. It is further assumed that the impulse frequency is related linearly to the tension along G1.
3. The spike frequency was measured as Fi before stretch, as F3 at the time when the muscle attained the final length and as Fb long thereafter. In good agreement with the prediction from the model, both Fi and Fb were linearly related to the muscle length at the time of measuring them, while Fd measured as (Fs-Fb) was merely determined by the stretch velocity. The whole time course of the actual spindle response also conformed to that of the ideal response of the spindle model.
4. The parameters of the model were determined by the relations of Fi or Fb versus muscle length and of Fd versus stretch velocity.
5. The actual spindle response differed from the behaviour of the model in two points: Firstly, the former showed an initial transient rise of the
frequency which might be caused by pressure exerted upon the spindle by the neighbouring extrafusal muscle fibres. Secondly, the decay of the spindle discharge at the cessation of stretch was accelerated with an increase of the stretch velocity, which might be due to thixotropic property of the intrafusal muscle fibres.

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