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THE EFFECTS OF TEMPERATURE ON THE DYNAMIC AND STATIC SENSITIVITIES OF THE FROG MUSCLE SPINDLE

(THE RELATION BETWEEN DYNAMIC TENSION AND DYNAMIC BY STATIC INDEX RATIO)

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ABSTRACT

This work was performed to know the function of the muscle spindle as the transducer under various temperatures. In this field not so many have been reported except for studies made by Matthews and by Ottoson. In this report the effect of various temperatures on the so-called dynamic and static indices by Matthews *et al.* and on the generator potential was studied in the muscle spindle of frog sartorius muscle. The results are summarized as follows; the generator potential remained almost unchanged in the broad range of temperature and the dynamic tension was found to have the tight relation with dynamic/static index ratio.

INTRODUCTION

Ottoson (1965)[1] has found that the receptor potential of an isolated frog muscle spindle remained almost unchanged in amplitude in the range of 3 to about 25°C but decreased above 25°C. He has presumed that those changes by temperature change may depend on a number of factors, such as the visco-elastic property of the intrafusal fibers and their attachment to the sensory endings and the tendons, and also on the electrical property of the sensory membrane. From his results that the decay time of the static phase of the receptor potential is related almost linearly to temperature whereas the curve for the dynamic fall has an exponential course, he considered that changes in the visco-elastic property of the structures forming the spindle might affect only the time course of the different parameters of the receptor. The relationship between the muscle spindle response and the visco-elastic properties of the muscle fibers has been noted by Matthews (1964)[2] and by Toyama (1966)[3]. Recently Nakajima and Onodera (1969)[4] pointed out that the difference

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between the slowly and rapidly adapting stretch receptors of crayfish was not due to difference in the generator adaptation between the two receptor types but depended on the difference of the simple visco-elastic property of the receptor muscle. The present study was intended to determine the role of excitability of the axon membrane and visco-elastic property of the muscle fibers which were affecting to the response of the frog muscle spindle to stretch at various temperatures.

METHODS

The experiments were performed on specimens of *Rana nigromaculata* weighing about 40 g. Thirty seven sartorius muscles were dissected out with its nerve and the 9th dorsal spinal root. The isolated root-nerve-muscle preparation was set in Ringer's solution in a Perspex box. The bottom of the box was formed with an insulated active surface of a thermoelectric unit, by which the temperature of the Ringer's solution was controlled between 5 and 30°C.

Stretching. Both ends of the muscle studied terminate in tendons. The tendon at one end was fixed on a glass hook attached to the movable anode of a mechanoelectric transducer (RCA 5734). The position of the glass hook was read by a micrometer with an accuracy of 0.1 mm. The tendon at the other end was attached with a thread to an electromagnetic stretcher, which consisted of a pen-motor and a lever as has been described by Toyama (1966)[2] and Ito (1968 a)[5]. The threads were kept as short as possible to keep the stretching condition correct. The stretcher was driven by a current generator to produce a linear increase of muscle extension. The current generator was controlled to act for 4 seconds by an electric timer. The extent of stretch was adjusted with a stopper which limited the movement of the lever. After the amount of stretch reached 2 mm, the muscle was left at this state. The muscle was kept relaxed for 15 sec before the next trial of stretching. The free end of the lever moved in front of slit, and muscle length was measured with a phototube by the amount of light passing through the slit. Tension and displacement of the muscle were simultaneously displayed on different traces which were made by means of a chopper operation at 25 Kc/sec from one beam of a dual beam oscilloscope.

Recording. The discharge of single afferent fiber from a muscle spindle was recorded from a subdivided dorsal root filament. The filament was hung with a pair of platinum electrodes in liquid paraffin. The ending studied was identified as muscle spindle ending by its behaviour during isometric as well as isotonic contraction elicited by stimulating the 9th ventral root with single and tetanic shocks (Matthews, 1931[6]; Ito, 1968 b[7]). The conduction velocities of the afferent impulses along the isolated filament were also available for identifying, and this value ranged from 25 to 30 m/sec (Ito, Toyama and Ito, 1964[8]; Matthews and Westbury, 1965[9]). The discharges recorded were displayed on the other beam of the oscilloscope through a differential C-R coupling amplifier. During and after muscle stretch, the discharges, the tension and displacement of the muscle were simultaneously photographed on film. The frequency of the discharges was represented manually by the reciprocal of the mean value of the successive two intervals of spike initiations and was plotted at the time of the middle spike. In nine experiments for recording generator potentials at different temperatures, the single afferent axon of a spindle receptor was isolated in its intramuscular course until the capsule of the spindle receptor was beheld clearly. The preparation was placed in a Ringer's pool in a perspex box, and the nerve was passed into another Ringer's pool through a liquid paraffin pool (1 mm width) situated in a 1 mm wide slit at the center of a partition between the two Ringer's pools. The potential difference led with a pair of calomel electrodes were displayed on one beam of a dual beam oscilloscope through a high input impedance D-C amplifier. Negativity at the sensory ending displayed as the upward deflection. The paraffin gap method has been described in detail by Ito (1968c[10]; 1969[11]).

RESULTS

Spontaneous discharge at various temperatures

All the muscle spindles tested discharged spontaneously at 15 to 21 impulses/sec at 20°C in the muscle length *in situ* (l_0). Fig. 1 shows representative records and the frequency of the spontaneous discharge from an isolated spindle

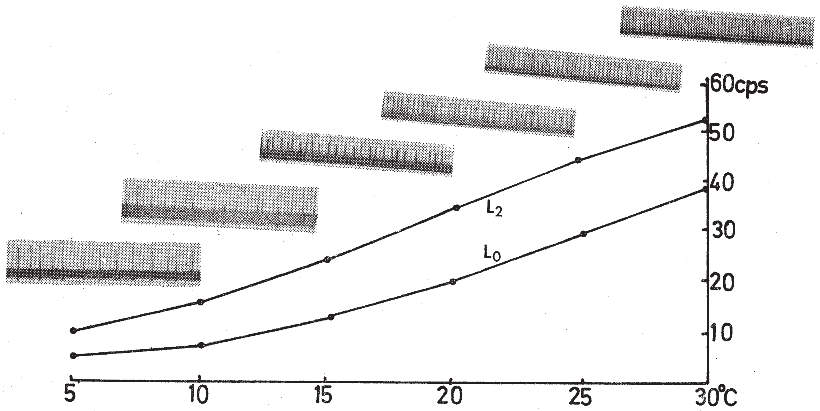

FIG. 1. Effects of temperature on the spontaneous discharge of a spindle receptor. Each record was obtained for 1 sec at temperature of 6 steps from 5 to 30°C at the muscle length of l_{0+2} mm. Graphical illustration of discharge frequency (ordinate) at the muscle length of l_{0+2} and l_0 with temperature (abscissa).

receptor at different temperatures. The receptor discharged at 20.5 impulses/sec at 20°C. When the temperature was raised to 25 and to 30°C, the discharge frequency increased 29.2 and 38.6 impulses/sec respectively. By lowering the temperature to 15, 10 and 5°C, the frequency decreased to 12.4, 7.7, and 5.1 impulses/sec. The relationship curve of the spontaneous discharge to the temperature appeared to be approximately linear in the range between 15 and 30°C. The temperature coefficient (Q_{10}) was calculated to be from 2.4 to 1.4. When the muscle was fixed at the initial length of l_{0+2} extended by 2 mm from the *in situ* length (l_0), the frequency of the spontaneous discharge was 34.1 impulses/sec at 20°C. The frequency depended linearly upon the temperature in the range from 5 to 25°C, the mean slope was 16.8 spikes/10°C in this case. There is no appreciable difference between two Q_{10} values at the l_0 muscle length and at l_{0+2}. From the above result, it is assumed that the dependence of the discharge frequency upon the temperature may be due to a change in the excitability of the sensory nerve ending rather than a change in the tension in the sensory region of the intrafusal muscle fibers.

Static and dynamic sensitivities at various temperatures

Fig. 2 shows a typical example of the response of a muscle spindle during stretch at four different velocities from l_0 length. In each record, the afferent discharge, tension development, and length of the muscle were simultaneously recorded on the upper, middle, and lower traces, respectively. A transient rise of tension development appeared following the onset of the stretch, but no initial acceleration of afferent discharges was observed. The discharge frequency increased during the dynamic phase of the stretch, and then fell rapidly after the completion of the stretch. A constant frequency higher than the resting frequency was attained 0.5 sec after the completion of stretch. According to Jansen and Matthews (1962) [12] and Crowe and Matthews (1964) [13] the frequency of the discharge, measured 0.5 sec after the completion of stretch, was called the "static index" of the sensory ending. They called the difference in frequency between the last point obtained during the dynamic phase of stretching and this static index, the "dynamic index" of the sensory ending to the stretch. In Fig. 3 the dynamic and static indices of the discharge frequency were plotted correspondingly above each spike in the record of a muscle spindle receptor, where the muscle was stretched by 2 mm from l_{0+2} mm initial length at 10 mm/sec velocity at 25°C Ringer's solution. The tension measured at 0.5 sec after stretching completion was called the "static tension" of the muscle, and the difference in tension between the peak tension at the completion of the stretch and this static tension was termed the dynamic tension "ΔT", as shown in the tension record in Fig. 3.

When the muscle was stretched at a constant velocity by 2 mm from the different initial muscle length of l_0 or l_{0+2} mm, the static tension increased in

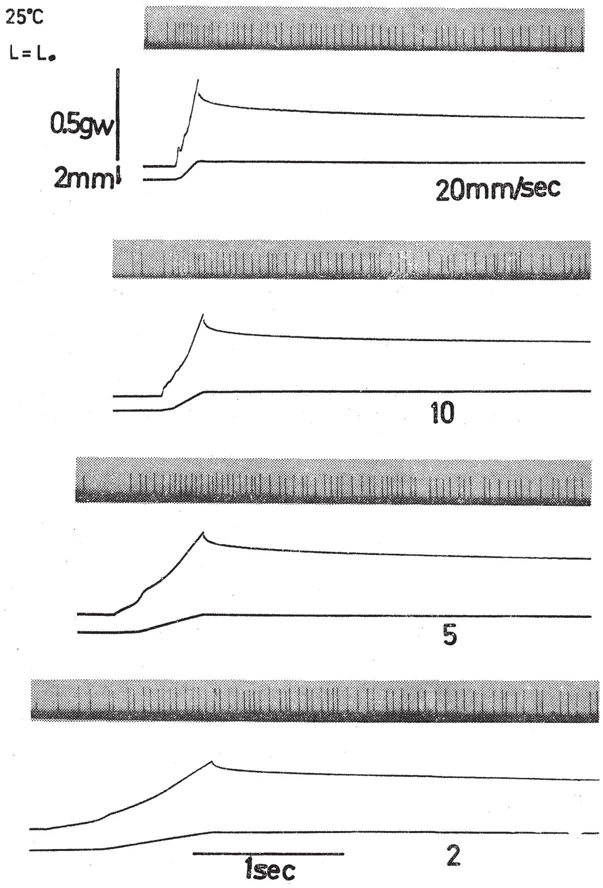

FIG. 2. Responses of a spindle receptor to extensions by 2 mm from l_0 initial length at stretch velocities of 2, 5, 10 and 20 mm/sec, recorded simultaneously with the displacement of the muscle (lower lines) and with the tension of the muscle (middle lines).

the latter. Fig. 4 shows a simultaneous record of the discharge of a spindle receptor (upper traces), the tension (middle traces), and the displacement (lower traces) of the muscle, during further stretch by 2 mm from l_{0+2} mm initial length at different temperatures. The static indices of the discharge frequency increased linearly with a slope of 16.1 spikes/10°C, as similar as the frequency of spontaneous discharges as mentioned in the preceding chapter. With raising surrounding temperature, the ΔT appeared to decrease, while the dynamic index of the discharge frequency increased. Fig. 5 shows the dependence of the dynamic indices of a spindle receptor upon the temperature at different velocities of muscle stretching. The increase of the dynamic index

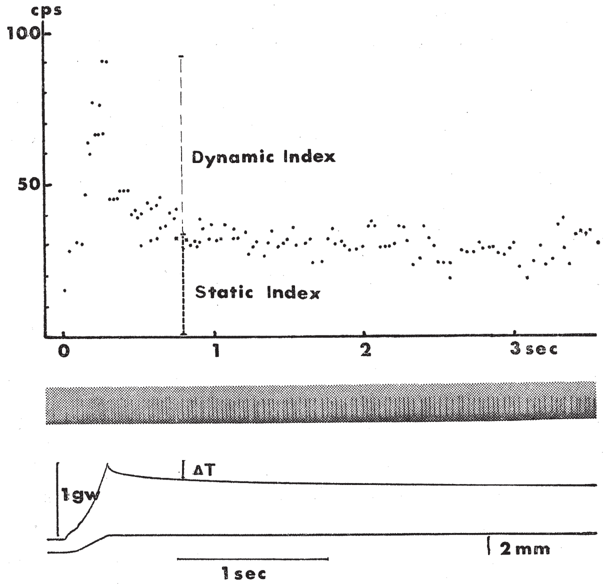

FIG. 3. A representative illustration of dynamic and static indices plotted correspondingly above each spindle receptor spike discharge (upper line of the record) during the muscle stretch by 2 mm from l_{0+2} mm initial length at velocity of 10 mm/sec, and simultaneous record of the displacement (lower line) and the tension of the muscle (middle line) in which ΔT was shown.

by raising temperature appeared to occur more steeply, if the muscle stretch was done at higher velocities or in longer initial muscle length. Toyama (1966)[3] has supposed that the dynamic index may depend largely upon the low elastic properties of the sensory region against the contractile region of the muscle. In other words it is considered that the dependence of the dynamic index upon temperature may be partly due to the dependence of the visco-elastic properties of muscle fibers upon temperature and also the dependence of sensitivities in sensory nerve endings upon temperature. The ratio of the dynamic index to the static index obtained from many records was calculated in order to clarify the temperature effects on the visco-elastic properties by removing those on the nerve ending sensitivities. In the case shown in Fig. 6, the ratio shows 200% when the muscle was stretched at 20 mm/sec by 2 mm from the initial length of l_0 at 5°C. The ratio decreased almost linearly by raising temperature, reaching 109% at 30°C. The slope of the ratio to the temperature was calculated as −36%/10°C at l_0 initial length. When the muscle was stretched at 10, 5 and 2 mm/sec by 2 mm from l_0, the ratios decreased linearly with the mean slope of −32.0, −15.2, and −15.0%/10°C

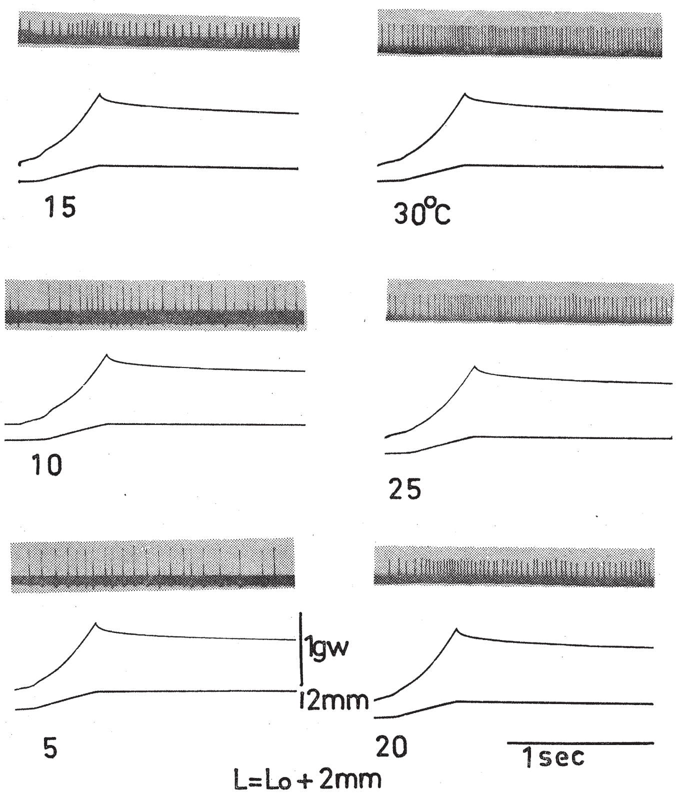

FIG. 4. Responses of a spindle receptor at different temperatures of 6 steps from 5 to 30°C during muscle stretch by 2 mm from l_{0+2} mm initial length at velocity of 5 mm/sec, recorded simultaneously with the displacement (lower line) and with the tension of the muscle (middle line).

respectively. Almost the similar values were obtained in muscle stretched at different velocities by 2 mm from l_{0+2} mm. At 20 mm/sec stretch velocity, the ratio was 200% at 5°C and decreased linearly with the slope of −36.8%/10°C by raising temperature. The value of the slope decayed with the decrease of stretch velocity, as following −30.8, −14.9, and −13.6%/10°C at 10, 5, and 2 mm/sec respectively. In twenty eight preparations tested, values of the ratio and of the slope were observed within the range shown in Fig. 6. It is noticeable that there is no appreciable difference between the values of the ratio at l_0 and l_{0+2} mm initial length. This implies that the increase of the initial muscle length effects the similar influence on both the static and the dynamic sensitivity of the spindle receptor.

Fig. 7 shows ΔT denpending on temperature and also on stretch velocity in comparison with the ratio of dynamic index/static index, the latter also

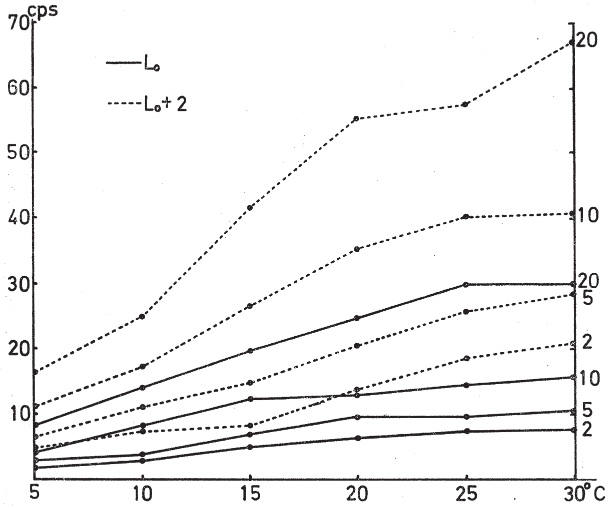

FIG. 5. Relation between temperature and dynamic indices of a spindle receptor during muscle stretch at different velocities from 2 to 20 mm/sec (showing on the right side vertical scale) by 2 mm from l_0 (solid line) and from l_{0+2} mm initial muscle length (dotted line).

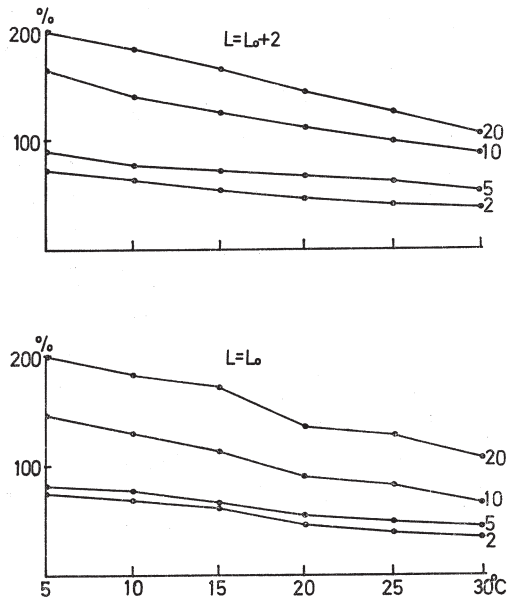

FIG. 6. Change in ratio of dynamic and static indices with temperature. A spindle receptor was stretched by 2 mm from l_{0+2} (upper graph) and from l_0 mm initial length (lower graph) at velocities of 2, 5, 10, and 20 mm/sec (showing on the right end of each line).

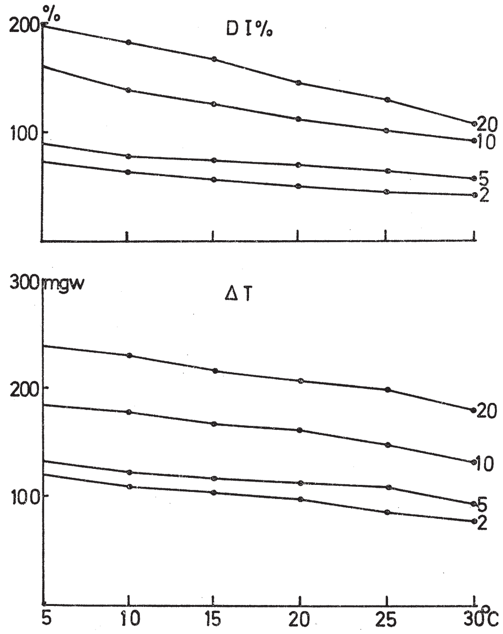

FIG. 7. Comparison between ΔT (lower graph) and ratio of dynamic and static indices (upper graph) depending upon temperature. A spindle receptor was stretched by 2 mm from l_{0+2} at velocities of 2, 5, 10, and 20 mm/sec (showing on the right end of each line).

depends upon temperature as well as upon stretch velocity. When the muscle was stretched at 20 mm/sec by 2 mm from l_0, the amount of the ΔT decreased almost linearly from 240 mg at 5°C to 182 mg at 30°C. Consequently the slope of tension to temperature was calculated to be −23.2 mg/10°C. Decreases in the stretch velocity to the values of 10, 5, and 2 mm/sec resulted in decays in the ΔT getting to 184, 133, and 120 mg respectively at 5°C, and also in decays in the slope of tension to temperature to −20.0, −15.2, and −15.0 mg/10°C respectively. Almost the similar negatively sloped ΔT like the impulse rate were also observed at different velocities. It is concluded that the ratio of dynamic/static indices depends upon the ΔT.

Generator potential at different temperatures

Fig. 8 shows responses of an isolated spindle receptor recorded by means of a paraffin gap method at different temperatures of Ringer's solution. At 19°C (room temperature), a spike discharge occurred at the summit of the dynamic component in the generator potential, and was succeeded by static one, which was not visible in most cases due to being cancelled by the after-hyperpolarization lasting for about 50 msec after the spike, as illustrated in

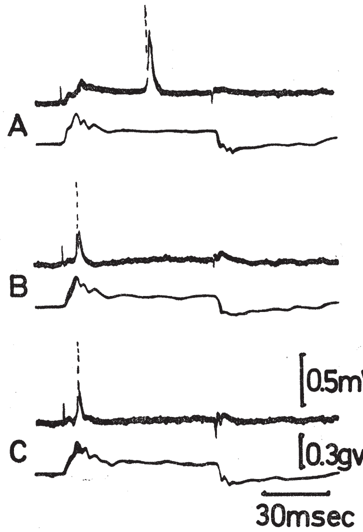

FIG. 8. Response of an isolated spindle receptor to brief stretch at different temperatures (A–14°C, B–19°C, C–24°C). Tension indicated on lower trace. Calibration; 1 sec, 1 mV and 0.3 g.

Fig. 8 B. With rise in temperature to 24°C, the amplitude of the generator potential slightly decreased, and the spike seemed to occur after shorter latency (Fig. 8 C). At the temperature below 15°C, a prominent generator potential often occurred without spike discharge, or sometimes a spike appeared with a considerable latency after the dynamic component of the generator potential as if spontaneous discharge. In this case, the spike did not appear to be triggered by the generator potential.

DISCUSSION

Matthews (1931)[6] demonstrated that the initial frequency of discharge of a muscle spindle in response to stretch increased with rise in temperature but that the adaptation of the frequency was accelerated so that the response gradually became briefer at higher temperatures. This finding has been confirmed by Ottoson's study (1965)[1] on isolated spindles of the frog's toe muscle. He showed that the amplitude of the receptor potential remained almost unchanged from 3 to about 25°C and decreased with higher temperatures while the time course of the rise and the fall of the potential changed with temperature within the range from 2 to 35°C. The receptor potential of the isolated Pacinian corpuscle undergoes similar changes by cooling (Ishiko and Loewenstein, 1960[14]; Inman and Peruzzi, 1960)[15]. Observation by Burkhardt (1956)[16] on the temperature effects on the stretch receptor of the crayfish shows that the receptor potential increases in amplitude with decreasing temperature.

The observations in the present study on the isolated spindle have confirmed the findings mentioned above and also provided an information about the temperature effect on the differentiation between mechanisms of initiation of spike and of generator potential. Namely, the static sensitivity decays although the amplitude of the generator potential remains almost unchanged with decrease in temperature from 25°C to 15°C. This has been also supported by the facts that with decrease in temperature the frequency of spontaneous discharge and the static index decreases with Q_{10} of 1.4–2.4 in the mean while the amplitude of the generator potential remained unchanged or slightly increased. However, it is generally accepted that the static sensitivity depends upon the amplitude of the static component in the generator potential.

As shown in Fig. 7, rise in temperature resulted in a linear decay of the dynamic sensitivities in which the static components had been removed and the dynamic/static index ratios were calculated, the decreases of ΔT were almost in parallel with them. This result agrees with the hypothesis by Lippold *et al.* (1960)[17] that the dynamic fall of the discharge frequency is mainly dependent on mechanical factors. Matthews (1964)[2] and Toyama (1966)[3] have assumed the viscosity and elasticity in the mechanical factor and presented a model consisted of a dash-pot and of a spring respectively. From the present results, the decrease in ΔT in the muscle tension by raising temperature may be considered due to a relative increase in the elasticity or to a relative decrease in the viscosity of the muscle. Similarly, the decrease in the dynamic sensitivity with rise in temperature may be due to a relative increase in the elasticity or to a relative decrease in the viscosity of the polar region along the intrafusal muscle fibers belonging to the receptor. The present study could not determine whether the raising of temperature provides a decrease of the viscosity or an increase of the elasticity.

SUMMARY

1) The responses of isolated spindle receptors of the frog's sartorius muscle were recorded at different temperatures.

2) The frequency of spontaneous discharges at different initial lengths of the muscle increased almost linearly by raising temperature with temperature coefficient (Q_{10}) of the value from 2.4 to 1.4 in the mean.

3) Static and dynamic indices of the discharge frequency, and static tension and dynamic tension (ΔT) of the muscle were obtained during muscle stretch by 2 mm from different initial lengths at different stretch velocities. The static index increased nearly with same temperature coefficient as that for spontaneous discharge, while the dynamic by static index ratio and the dynamic tension (ΔT) decreased almost linearly by raising temperature. The ratio/temperature slope depended on the stretch velocity from -36.8 to $-15.0\%/10°C$ respectively.

4) By means of a paraffin gap method, it was verified that the amplitude of generator potential remained almost unchanged in the temperature range from 5 to 30°C. Below 15°C nerve spikes appeared with a considerable and unstable delay after the dynamic phase of the generator potential, so that the spikes could not be clearly attributed to the generator potential.

5) Effects of temperature on the excitability for initiation of spikes and the visco-elastic properties of muscle fibers were discussed.

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