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Quantitative Studies on the Slowly Adapting Stretch Receptor of the Crayfish

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Summary. In isolated receptors the impulse frequency following "step" stretches had a highly significant correlation with both muscle length and tension; any deviations from linearity were in opposite directions, impulse frequency rising more quickly than linearly with length and more slowly than linearly with tension. The impulse frequency decayed according to a power function of time from application of a step increase in length. A transfer function was derived and used to predict responses to sinusoidal and constant velocity stretches. The experimental data generally agreed with predictions. The deviations that were found could be accounted for by considering quantitatively any non-linearity between frequency and length, the adaptation of the impulse frequency to constant currents, the all-or-none nature of the action potential, and the viscous forces present during dynamic stretch. The approximately linear relationship between impulse frequency and muscle length and muscle tension is discussed. Muscle tension appears to be the more direct causal agent of impulse generation. Possible physical bases for the transfer function are also considered.

Introduction

One step towards a quantitative understanding of the response of a sensory system is the development of a mathematical description for the response of the first order neurone to a variety of stimulus patterns. There have been several notable attempts at such descriptions in recent years (HERMANN and STARK, 1963; CHAPMAN and SMITH, 1963; KIRSCHFELD and REICHARDT, 1964) using the concept of the linear transfer function. The transfer function is closely associated wiht the Laplace transform method for solution of linear differential equations with constant coefficients (CLARK, 1962). A transfer function can be derived in two ways. If complete knowledge of the behaviour of all components of a system is available, and they are linear, the transfer function can be derived directly. The transfer function so derived can be used to correctly predict the response to any input. The alternative method, when complete knowledge of the system is not available, is to measure the response to a simple input pattern, fit the response with an empirical formula and derive a transfer function from this formula. Since this second method relies on an empirical relationship from a limited range of data, it may not correctly predict responses to other types of stimuli. Indeed any deviations noted may be useful in determining other important factors governing the behaviour of the system.

In this paper a transfer function for the slowly adapting stretch receptor of the crayfish is determined from its response to a step change in length of the receptor muscle. This receptor is particularly suited for detailed analysis since with extracellular recording from an isolated preparation stable records can be obtained for many hours and there is exceedingly little variability in its response. The response (frequency of nerve impulses) is also quite linear with muscle length over the physiological range. It is especially important to consider the response to dynamic stimuli such as constant velocity ramp stretches since they have been extremely useful in analysing the function of vertebrate muscle spindles (MATTHEWS, 1964). Therefore, predictions for dynamic stimuli (sinusoidal and constant velocity stretches) are derived and compared with experimental results. Some deviations from the predictions of the transfer function are found though these can be accounted for quantitatively by considering records of muscle tension and any non-linearity present in the relation between impulse frequency and receptor length. The implications of and possible physical basis for the transfer function are discussed. Some of the results have been published previously in abstract form (BROWN, 1965). POPPELE, BORSELLINO and TERZUOLO (1966) have also briefly described the response of the lobster stretch receptor to sinusoidal stretch.

Methods

Preparation. Isolated slowly adapting stretch receptors (R. M. 1; ALEXANDROWICZ, 1951) from the second abdominal segment (occasionally 3rd or 4th segments) of freshwater crayfish (*Astacus sp.*) were used. Dissection was done from the ventral side under saline with incident lighting as described by WIERSMA, FURSHPAN and FLOREY (1953), usually with isolation of the whole length of nerve stretching from receptor to the ventral nerve cord. In some experiments the minimum and maximum length *in situ* of the receptor muscle was measured with a calibrated eyepiece. The increase in length from minimum to maximum was about 35% of the minimum length.

The fast receptor muscle was dissected away and the slow receptor with its natural insertions into pigment tissue at the anterior end of the segment and clear connective tissue at the posterior end, was transferred to the organ bath without crossing any fluid interfaces.

In the organ bath (volume 5 ml) the receptor was attached at one end to the myograph and at the other end to the puller. At both ends this was done by passing the ends of the receptor muscle into a longitudinal slit made in a piece of monofilament nylon (10 lb. breaking strain; SMITH, 1964), and then sliding over this bit of the nylon a small segment of stainless steel tubing, which because of its close fit to the nylon rod pressed the two sides of the slit together. This proved to be a secure form of fixation and, once attached, the receptor did not slip out even under extreme stretches. The nylon rods were stuck with Araldite to the myograph and puller extensions. The extension from the puller passed

through a small hole in the side of the bath which was sealed with vaseline to stop fluid leaks. The extension from the myograph entered the bath from above so that there was no friction to distort the recording of the tension.

Application of Stretch. This was done with an electromagnet (GOODMANS V 47, 3 ohm model) mounted on a horizontal screw thread so that the initial length of the receptor could be adjusted by hand. The initial length was chosen so that the receptor fired at about 1 impulse/sec. This length was generally slightly higher than the minimal length *in situ*. In some cases the receptor fired even when completely slack (cf. EYZAGUIRRE and KUFFLER, 1955). In these cases the muscle was stretched until the background discharge just increased perceptibly. For comparison with the other experiments a frequency 1 impulse/sec less than the background was subtracted from the measured values.

For constant velocity stretches and "step" stretches (ramp rise times of 30—40 msec were used for "steps") ramp voltage wave forms were generated by a transistor circuit (BANNISTER, 1965) and these were amplified to provide a ramp current which was fed to the coil of the electromagnet. Ramp rise times from 10 msec to 8 seconds were available in 30 fixed steps, and the final value of the current at the top of the ramp was varied by 10 fixed resistors in series with the coil, providing 10 different length stretches from 0.1 to 1.0 mm in approximately 0.1 mm steps.

This open loop system was simple and reliable and, because the stiffness of the internal suspension of the moving coil was so much greater than the tensions developed in the receptor, had no zero error. 500 gms displaced the coil by about 1 mm. Maximum recorded tensions from the slow receptor muscle were about 30 mg. wt. However, for long stretches (> 0.7 mm) the velocity of stretch fell off as the movement approached its final length, presumably due to an increase in stiffness of the mounting of the coil at its extremes of movement. The change in slope between the initial part of the stretch and that over the final part was of the order of 15% of the initial slope. As the range of velocities used varied over two orders of magnitude and the minimum difference between the various velocities used was 100%, this seemingly large error for long stretches was ignored.

There was another undesirable feature in the stretching apparatus. Movement did not cease at the end of the ramp, there being a slow onward creep which was over in 2 seconds, and very largely over in 250 msec. This creep was worse for fast rise times when it might amount to 10% of the total length (see Fig. 1 and Fig. 9).

Sinusoidal stretch was applied by driving the electromagnet with a low frequency oscillator (Servo-Mex, TWG 100). The frequency of the stretching was varied from 0.03 c/s to 5 c/s, and its amplitude (peak to peak) was varied from 0.014 to 0.72 mm by means of resistors in series with the current amplifier. x-y plots of applied signal against resultant length showed that the vibrator did not appreciably distort the oscillator waveform. The amplitude was reduced by 8% of its low frequency value at 10 c/s.

Recording of Tension. This was done with an R. C. A. 5734 mechano-electric transducer valve with an extended anode pin of stainless steel tubing having a natural frequency of 130/sec. It was calibrated in the way described by KRNJEVIC and VAN GELDER (1961), and was found to have an output linear with tension. Its compliance was not more than 50 μ/100 mg wt. Drift of the output was greatly reduced by supplying the heaters from a regulated D. C. power supply and mounting the valve in a large brass block.

Recording of Length. The phototransistor circuit of MACHIN (1959) was used, a light metal vane on the extension of the moving coil partly interrupting light from a pea bulb focused on the phototransistor. The output was linear with displacement over the range used (1 mm).

Direct Current Stimulation. Square current pulses were applied to the sensory cell from a battery using a microswitch, the current reaching the nerve via a 20 MΩ resistor and Ag/AgCl electrodes, the cathode in the crayfish saline and the anode on the nerve raised into liquid paraffin. Current was monitored as the voltage drop across a 10 KΩ resistor.

Recording of Action Potentials. This was done conventionally with a pair of silver electrodes on the receptor nerve, which was raised into liquid paraffin. The amplified spikes were used to trigger a circuit which gave a direct display of the instantaneous frequency of discharge (MATTHEWS, 1963a). The frequency of discharge was thus recorded directly, simul-

taneously with the length and tension, by photographing the stationary spots of 2 double-beam oscilloscopes on moving, 70 mm recording paper. Film speeds of 1.22 cm/sec and 1.84 cm/sec were used.

When sinusoidal stretches were being used the recording paper was stationary and the output of the frequency meter was displayed on the y axis of the oscilloscope while the signal from the length transducer was applied to the x axis (see Fig. 7).

Saline. VAN HARREVELD's (1936) solution was used; the pH was about 7.5 at 15° C.

Temperature. In any one experiment the temperature, which was recorded by a thermistor bead in the organ bath, did not vary by more than 3° C; the extreme values were between 13° C and 23° C. All the later experiments were carried out below 18° C by keeping the fluid in the bath 5° C below room temperature with a thermoelectric cooling device.

Length Change of the Sensory Region of the Receptor Muscle. In 3 experiments small glass beads were placed on the receptor muscle on either side of the area innervated by the sensory cell. With powerful lateral illumination these beads acted as small markers, bright enough to produce an image on the film of a Cossor 35 mm oscilloscope camera which was placed with its lens close to the eyepiece of a microscope (magnification × 25). The camera film ran at right angles to the axis of stretching. It was thus possible to record the length changes of the middle region of the receptor muscle during and immediately after an applied stretch of constant velocity.

Analysis and Accuracy of Records. Records of frequency, tension, etc. on the photographic recording paper were measured to the nearest 0.1 mm. The frequency value in mm was converted to readings of impulses/sec by inspection of accurate calibration curves. The voltage output of the instantaneous frequency meter was not exactly linear with frequency over the whole range of frequencies studied. Assumption of linearity would have given an error of ± 2 impulses/sec. By using the calibration curve the accuracy was increased to ± 0.5 impulses/sec.

The movement of the recording paper provided the time base (see above). The film did not run on completely evenly. The variation in speed was 1.5% of the mean value.

Provided the preparation was washed with fresh perfusion fluid between readings, repeated recordings of any one particular stimulus pattern gave reproducible results throughout the course of an experiment though there was a tendency for the responses to decline slowly during a long experiment.

In 4 experiments the discharge of the receptor was recorded on magnetic tape and the intervals were measured and recorded on punched paper tape automatically by a high speed timer and recorder "Histar" (STEIN, 1965). These experiments gave similar results to those recorded more conventionally. Further analysis was done on the English Electric KDF 9 Computer of the Oxford University Computing Laboratory. The statistical analysis was done using a computer program written by Dr. D. F. MAYERS of the Computing Laboratory. In testing for the significance of statistical parameters, it was assumed that they were normally distributed. Values more than three times the standard error in the determination of the parameters were assumed to be statistically significant at the 5% level. These assumptions are not fully justified because of the small sample sizes (GUEST, 1961).

Results

Step Stretches. The time course of the frequency of action potentials generated by the slowly adapting stretch receptor using "step" stretches to various lengths from the same initial length (rise time 40 msec) are shown in Fig. 1. Only four stretches are shown in Fig. 1 for purposes of clarity. At first there is a very rapid decline in the frequency, but the decline becomes increasingly slow with time. The initial length was chosen as described under "Methods" and in this case the stretch receptor fired one nerve impulse/sec at the initial length. As the stretches were increased by steps of about 0.2 mm, the impulse frequency also increased by roughly equal amounts while the tension rose by increasing amounts. This result has been noted by TERZUOLO and WASHIZU (1962). However, KRNJE-

VIC and VAN GELDER (1961) reported a linear relation between frequency and tension and WENDLER and BURKHARDT (1961) described a near-linear relation between frequency and tension. All three groups of workers can not be correct for it is agreed that tension is not linearly related to length (TERZUOLO and WASHIZU, 1962; KRNJEVIC and VAN GELDER, 1961). All previous studies used stretches applied successively one on top of another so that the effects of adaptation accumulated and the muscle was often stretched to lengths greater than the physiological maximum. All stretches used in the present study were kept within the normal physiological range and were applied in random order from the same initial length with a one minute recovery period between stretches. When these precautions were taken, we never encountered the non-linearities due to the phenomenon of "overstretch" first reported by WIERSMA, et al. (1953).

Since a linear relation between input and output is important for the type of analysis to be carried out, and since we could give more carefully controlled stretches to the muscle than had been done previously, we first examined the linearity of the system. The response frequency (for which we shall use the letter y) was measured at two or three different times after the onset of step changes in length of several magnitudes in 13 receptors. The size of the length change will be denoted by x. The best fitting straight line and the best fitting curve (in the sense of least mean square deviations) of the form $y = a_0 + a_1 x + a_2 x^2$ were calculated for 34 cases in all. The linear correlation coefficients and the significance (GUEST, 1961) of the various coefficients were also determined. For comparison, similar calculations were done for the changes in frequency as a function of the change in tension on the same receptors. In all cases response frequency and muscle length were highly correlated (linear correlation coefficients > 0.94) and in over half of the measurements the linear correlation coefficient was greater than 0.98. Even slightly higher values were found for the relation between frequency and muscle tension (linear correlation coefficient always > 0.95 and greater than 0.98 in over 3/4 of the cases examined). The coefficient a_2 for the relation between impulse frequency and muscle length was significantly different from 0 at the 5% level (i.e. there were significant deviations from linearity) in over half the cases that were examined. Significant deviations from linearity in the relationship between impulse frequency and muscle tension were only found under 20% of the time. The directions of the deviations from linearity were also different; in all cases of significant deviation, impulse frequency showed a faster than linear increase with increasing length and a slower than linear increase with increasing tension. If the best values of a_2 are examined for all cases (not only those in which the value was significantly different from zero) much the same result emerges. In over 85% of the cases the best value of the coefficient a_2 relating frequency and length was positive while, just under 60% of the time, the corresponding coefficient relating frequency and tension was negative.

Since the linear correlations between impulse frequency and both muscle length and tension are so high, it is not surprising that both relationships have been reported in the literature by different workers

(TERZUOLO and WASHIZU, 1962; KRNJEVIC and VAN GELDER, 1961). However, the differences in the direction of the deviations from linearity may be important in determining which variable is the more direct causal agent in the generation of nerve impulses. This topic will be discussed later. In most of the results impulse frequency will be considered only as a function
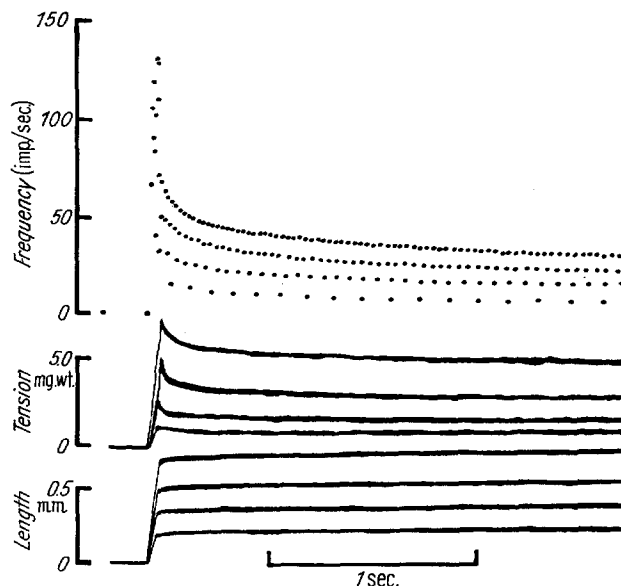

Fig. 1. *Superimposed tracings of the response of a slowly adapting stretch receptor to 4 different length stretches with the same rise time (about 40 msec). The top records show the frequency of discharge. Each action potential is represented by a spot and the vertical displacement is proportional to the reciprocal of the time interval since the previous action potential (i.e. the instantaneous frequency in impulses/sec). The middle records give the tension in the receptor muscle. The bottom records show the changes in length of the muscle measured by the length transducer (Temperature 15° C, Exp. 2)*
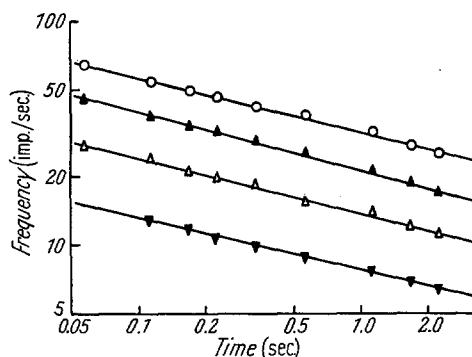

Fig. 2. *The decay of impulse frequency following "step" stretches (40 msec rise time) to different lengths plotted on a log-log scale. Time was measured from the midpoint of the rising phase of the stretch. Data from Fig. 1. The straight lines are calculated best fits; a straight line of negative slope on this plot indicates that the impulse frequency decays as a power function of the time since application of the "step" stretch*

of muscle length and initially a linear relationship between the two will be assumed.

Let us now return to the time course of the change in impulse frequency following a step stretch. In Fig. 2 the response frequencies shown in Fig. 1 have been replotted on a log-log scale. On this scale a power function plots as a straight line, the exponent given by the slope. It will be noted that replotting in this way has linearized the curves of frequency versus time and that the slopes of the decay curve following changes in length of different magnitudes are approxi-

mately equal. The results can thus be summarized by the equation

$$y = a\, x\, t^{-k}.\tag{1}$$

The constant a gives a measure of the sensitivity of the receptor to a unit change of length while k determines the rapidity with which the response decays following the change in length. The best straight line
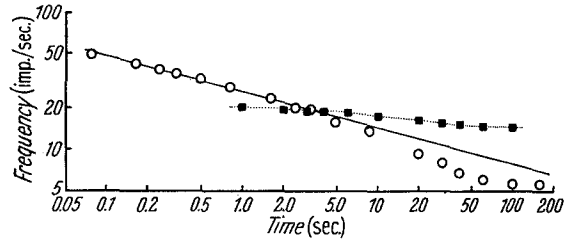

Fig. 3. *Decay of impulse frequency following a "step" change in length of 0.77 mm (circles) compared to that following the sudden application of a constant depolarizing current of 0.37 μA (squares) on a log-log scale.* Same receptor as Fig. 1. See text for explanation of lines drawn through points
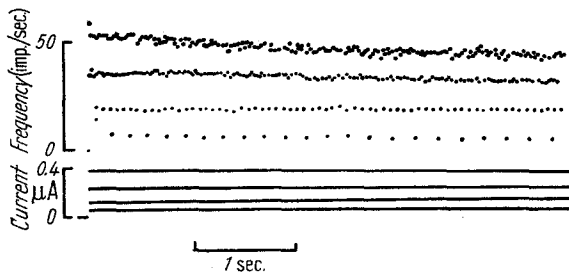

Fig. 4. *Superimposed tracings of the response of a slowly adapting stretch receptor to step depolarizing currents.* Upper records, instantaneous frequency; lower records, applied current. (Temperature 22° C, different receptor from that shown in Fig. 1)
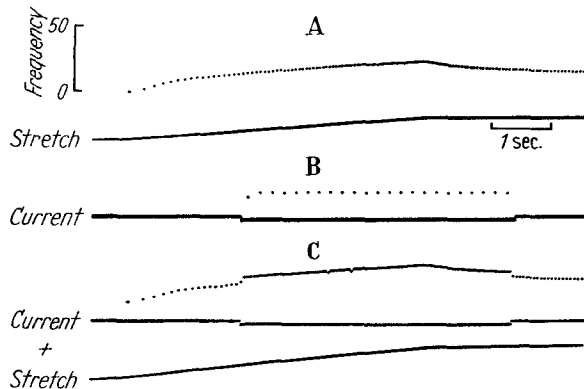

Fig. 5. *Records showing summation of the effects of stretch and depolarizing current. A.* Response to slow constant velocity stretch. *B.* Response to small depolarizing current. *C.* Response to the simultaneous application of stretch and current. Top trace in each record shows instantaneous frequency (scale in *A* applies also to *B* and *C* and represents 50 impulses/sec). Bottom traces signal length and current

on a log-log plot (again in the sense of least mean square deviations) was determined for the first 2.5 seconds of each muscle stretch in 5 receptors listed in the Table. In each of the 31 stretches so analysed the linear correlation coefficient between $\log y$ and $\log t$ was greater than 0.84 and for over 60% of the stretches it was greater than 0.99. The overall mean value for k in these experiments was 0.210 ± 0.015 (mean $\pm$ S.E.). No individual determination varied as much as 0.04 from the mean for that experiment. The largest deviations were in both directions and occurred more frequently for the smaller stretches where measuring errors were greater.

The average value for the constant a varied widely between receptors (from 20.2 to 62.6 impulses mm^{-1} sec^{k-1}) since muscles of different lengths were used. In addition, the value of a tended to increase somewhat as the size of the step stretch was increased because of the non-linearity present in some muscles. The effect of the non-linearities will be analysed more fully later.

In Fig. 3 the response of the same receptor as in Fig. 1 to a step stretch of 0.77 mm lasting 200 seconds is indicated by open circles. The solid line as before is the best fitting power function over the first 2.5 seconds. Two kinds of deviations are noted at long times. Both were characteristic of the results on 7 receptors examined using long stretches although they were often much less marked than in Fig. 3. At about 10 seconds the frequency begins to decay faster than a power function while beyond 100 seconds the decay slows and tends toward a constant value. Hence, with stretches lasting minutes, a small term should be added to the right hand side of Eq. (1) which is independent of time. However, with an isolated preparation, the response tended to decrease somewhat during the course of the experiment and the recovery from such a long stretch was rather slow so that it was difficult to examine the small term with accuracy. Studies using such long-lasting stretches (WENDLER, 1963) indicate that this small term is also fairly linear with extent of stretch. The effect of this correction term on stretches lasting less than 5 seconds is minimal and will not be considered further.

D. C. Current Stimulation. An explanation of the faster than power function decay after ten seconds (or for that matter, the power function decay itself) is not immediately clear. Experiments were therefore carried out in which step currents with a rise time less than 5 msec were applied. The current was also recorded to be certain that it remained constant over the period of stimulation. Currents were applied which gave a similar range of frequencies to those elicited by stretch. Responses to current steps of various sizes are shown in Fig. 4 for comparison with the responses to step stretches. No sharp peak frequency is seen with current stimulation and very little decay in frequency (NAKAJIMA, 1964; WENDLER, 1963) occurs over the first few seconds. The filled squares (■) in Fig. 3 show the response to a long step current. The decline in frequency to constant current is much less marked and of a different character. The responses could always be fitted adequately by a single exponential of the form

$$y = a_e + b_e e^{-t/\tau}.\tag{2}$$

The dotted line in Fig. 3 represents such a curve where

$$a_e = 14.5 \text{ impulses/sec}; \qquad b_e = 5.6 \text{ impulses/sec};$$
$$\tau = 16 \text{ sec}.$$

In contrast, at least three exponentials would be needed to fit the response to stretch adequately.

The time constant and extent of the electrical adaptation seen in Fig. 3 is of about the same size as the deviations from the power function decrease at about 10 seconds following the step stretch. However, it is more reasonable to compare the responses to stretch and current if the applied current was acting

at the site of natural impulse initiation. The evidence shown in Fig. 5 suggests that this is the case. In Fig. 5A the response to a 0.5 mm stretch with a long rise time is shown. Fig. 5B gives the response to a small depolarizing current while Fig. 5C gives the current superimposed on the stretch and it is seen that the response to the two sum. Furthermore, hyperpolarizing currents would slow a discharge due to stretch (not illustrated), and current stimulation was ineffective after crushing the soma of the sensory cell. Although this does not prove unequivocally that the natural and electrical stimuli were acting at the same point these same criteria have been used by LIPPOLD, NICHOLLS and REDFEARN (1960) with the muscle spindles of the cat tenuissimus muscle.

The frequency of discharge at about one second after the onset of stimulation as a function of current strength is shown in Fig. 6. The shape of the curve (linear over the lower portion, but approaching a maximum as the current is increased) is an agreement with previous studies (WENDLER and BURKHARDT, 1961; TERZUOLO and WASHIZU, 1962).

With the external electrodes used, the current was undoubtedly more diffuse than the generator current that normally excited the cell though the above experiment indicates that the mechanically and electrically induced depolarizations sum. The interspike intervals during current stimulation were more irregular than those elicited by stretch. Using intracellular stimulation TERZUOLO and WASHIZU (1962) found a linear region extending to higher frequencies and a higher maximum discharge frequency.

Transfer Functions. If the response to a step stretch is given by Eq. (1), the transfer function, $G(s)$, (CLARK, 1962) can be obtained by dividing the Laplace transform of the response, $Y(s)$, by the Laplace transform of the input, $X(s)$, where the Laplace transform is defined by $F(s) \equiv \int_0^\infty e^{-st} f(t)\, dt$. For Eq. (1) the transfer function is

$$G(s) = \frac{Y(s)}{X(s)} = \frac{\int_0^\infty e^{-st} a\, x t^{-k} dt}{\int_0^\infty e^{-st} x\, dt} = a\, \Gamma(1-k)\, s^k \qquad (3)$$

where $\Gamma(1-k)$ is the gamma function which is tabulated in the *C. R. C. Standard Mathematical Tables* (HODGMAN, ed., 1957).

From the transfer function the response to an arbitrary input can be predicted. In particular, the prediction for sinusoidal stretches is given by (CHAPMAN and SMITH, 1963)

$$y = a\, x\, \Gamma(1-k)\, (2\pi f)^k \sin(2\pi f t + k\pi/2) \qquad (4)$$

where f is the frequency of sinusoidal stretching in cycles/second. Eq. (4) predicts that the amplitude of the response will increase as the k-th power of the stimulus frequency and that there will be a constant phase lead of $k\pi/2$ radians or $90k$ degrees.

Similarly the transfer function can be used to predict the response to a ramp stretch. Consider a ramp of length x lasting t_1 seconds with a constant velocity $v = x/t_1$ over this time. If it is further assumed that the muscle remains stretched the amount x for times $t \geq t_1$, then the Laplace transform of the input waveform is

$$X(s) = (v/s^2)(1 - e^{-st_1}). \qquad (5)$$

Multiplying Eq. (5) by the transfer function of Eq. (3) and taking the inverse transform yields the predicted response frequency as a function of time.

$$y = \frac{a v t^{1-k}}{1-k} \qquad t \leq t_1,$$
$$= \frac{a v (t^{1-k} - (t - t_1)^{1-k})}{1-k} \quad t > t_1. \qquad (6)$$

Hence, on the linearly rising phase of the ramp, the response frequency should increase according to the $(1-k)$-th power of time and, when the stretch reaches the final length, it should begin to decline as the difference of two power functions. In the "Appendix" it is shown that:
1. for $t/t_1 \gg 1$, this difference reduces to Eq. (1);
2. the fastest convergence to Eq. (1) results when time is measured from the midpoint of the ramp ($t_1/2$) and
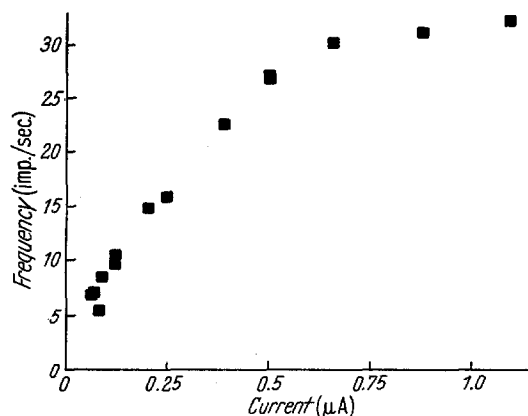

Fig. 6. *Frequency of discharge as a function of the strength of applied depolarizing current.* Frequencies measured one second after application of current and plotted on linear coordinates. Same receptor as Fig. 1

3. for times shortly after the end of the ramp, the frequency predicted by Eq. (6) will be higher than that given by Eq. (1) if time is measured from the midpoint of the ramp. However, the error is only 0.5% at t_1 seconds after the end of the ramp.

These last results extend the intuitive idea that the time taken to attain the final length will not seriously affect the instantaneous frequency measured at times long compared to the time taken to reach the final length.

If the velocity of the ramp, v, and the time t_1, are varied so that the same final length is reached at different rates, the peak frequency should increase as the k-th power of the velocity as can be seen by substitution in Eq. (6). The maximum frequency, y_m, will occur at $t = t_1$, as discussed above, so

$$y_m = \frac{a v t_1^{1-k}}{1-k} = \frac{a x^{1-k} v^k}{1-k}. \qquad (7)$$

Thus, there are in theory at least five simple ways of determining the constant k:
1. the exponent of the power function decay in response frequency with time after step stretches,
2. the exponent of the power function increase in amplitude of the response as a function of frequency of sinusoidal input,
3. the phase lead to sinusoidal stretches ($90k$ degrees),
4. the exponent of the increase in peak frequency with velocity using ramp stretches,

5. the exponent $(1 - k)$ of the increase in response frequency with time on the linearly rising phase of ramp stretches.

These determinations of k could be used to give four separate determinations of the constant a. In practice as will be indicated, the first determination is the most accurate and in the next sections we will compare the results for sinusoidal and ramp stretches with the average values determined from several step stretches of different length.

Sinusoidal Stretches. The inverse of each interresponse interval was directly displayed on the y-axis of the oscilloscope at the end of the interval. The term "instantaneous frequency" has been used to distinguish this sort of measurement from an average
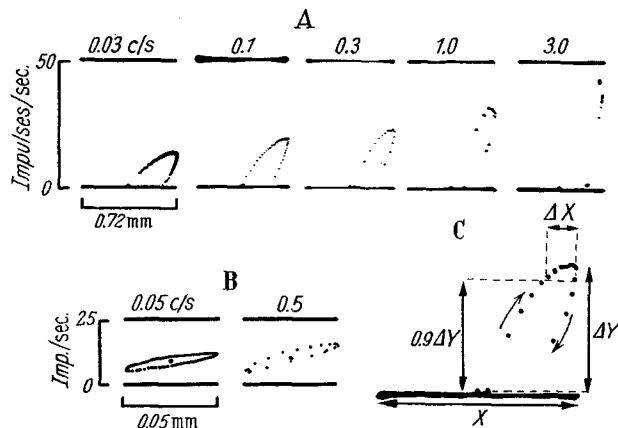

Fig. 7. *The response of the slowly adapting stretch receptor to sinusoidal stretches at various cyclic frequencies.* Each record is the photograph of an x-y plot displayed directly on an oscilloscope (see "Methods"). The y-coordinate gives the instantaneous frequency while the x-coordinate is the measured length. A. Responses to sinusoidal stretches of 0.72 mm peak to peak at frequencies from 0.03 to 3 c/s. At the resting length (midpoint of the sine wave) the receptor was firing just less than 1 impulse/sec. Same receptor as Fig. 1 (Exp. 2). B. Response of a different receptor to 0.05 mm peak to peak stretches after being stretched to give a background discharge of about 10 impulse/sec. (Tracings of actual records.) C. Enlargement of 0.3 c/s record of A to show method of analysis of records (explanation in text)

frequency measured over a number of intervals. However, uncertainty still remains since it is not clear to what part of the interval the instantaneous frequency refers, and this uncertainty limits the time resolution of the analysis to half an interspike interval.

If the response frequency measured the average generator current over a single interval, it would be more appropriate to display the frequency in the middle of the interval. In fact, the average is weighted in favour of currents occurring towards the end of the interval since a) the nerve is refractory immediately following a nerve impulse and b) the depolarization produced by current will decay from the time of its occurrence so that a current toward the end of the interval will contribute more to the threshold depolarization than one early in the interval. Hence, the "instantaneous frequency" can be thought of as referring to some point in time in the latter half of the interspike interval. PARTRIDGE (1965) has recently considered this problem in more detail.

For sinusoidal analysis there will be a limit of accuracy for phase information of $180 f/y$ degrees where f is the cyclic frequency of stretching and y the "instantaneous" response frequency. A similar uncertainty is involved in measuring the maximum frequency change (the response amplitude to sinusoidal stretching). At high stimulus frequencies the peaks will be rounded off by the averaging and the measured amplitude will be artificially low. A further difficulty

arises from the fact that the responses tend to occur locked in phase with the stimulus so that only a few isolated points are obtained from many cycles instead of a complete curve. Finally, with a small resting discharge, the receptor will go silent for half a cycle. In practice, this means that sinusoidal frequencies above 5/sec could not be analysed accurately.

Records of the responses to different frequencies of sinusoidal stretching are shown in Fig. 7 A using an x-y plot as described in "Methods". Fig. 7 C illustrates the method of analysis of these records. The measurement of peak frequency minus resting discharge (Δy) gives the amplitude of the response to sinusoidal input. This amplitude is plotted as a function of input frequency in Fig. 8 A on a log-log scale, and the solid line represents the best fitting straight line on this plot. The correlation coefficient of such a plot was always greater than 0.96. No corrections for the effects discussed above of high sinusoidal frequencies have been made. The constant k determined in this way was 0.278 compared to the average value of 0.244 determined from 5 step stretches in the same experiment. The results of the 5 experiments in which sinusoidal stretches were applied from the same muscle length

Table 1
Determinations of Decay Constant k

Exp.	Steps mean k	Sines (amplitude) Deviation	Ramps (peak) Deviation	Ramps (rising phase) Deviation
1	0.224	− 0.005	+ 0.134	− 0.115
2	0.244	+ 0.034	+ 0.149	− 0.040
3	0.204	+ 0.039	+ 0.111	− 0.206
4	0.223	− 0.043	+ 0.158	− 0.020
5	0.157	+ 0.058	+ 0.126	+ 0.038
Mean ± S.E.	0.210 ± 0.015	+ 0.017 ± 0.018	+ 0.136 ± 0.008*	− 0.069 ± 0.042

Determinations of Sensitivity Constant a

	mean a	% Deviation	% Deviation	% Deviation
1	37.4	+ 2.1	+ 18.2	+ 26.5
2	36.1	− 1.4	− 10.5	− 4.2
3	62.6	− 15.5	+ 21.1	+ 48.6
4	20.2	+ 6.9	+ 11.9	+ 22.8
5	53.0	− 10.9	− 15.1	− 11.7
Mean ± S.E.	41.9 ± 7.3	− 3.8 ± 4.1	+ 5.1 ± 7.5	+ 16.4 ± 10.9

Comparison of constants in transfer function determined from application of various types of stretch in the 5 receptors on which all measurements were made using stretches from the same resting length. All values were determined from best fitting straight lines on log-log plots. The slope on each plot gave a value for k [steps, Eq. (1); sines (amplitude), Eq. (4); ramps (peak), Eq. (7)] or $1 - k$ [ramps (rising phase), Eq. (6)]. The intercept on the log-log plot, together with the value of k determined from the slope was then used to determine a. The mean value of k determined from between 5 and 7 "step" stretches in each receptor provided the most accurate values of k and a. The values determined from other inputs are listed as deviation or % deviations from the mean values using the "step" stretches. A significant deviation (indicated by an asterisk) was found for one mean value and large, but non-significant deviations in two others. The reasons for these deviations are discussed in the text. Measurements of the phase lead of the response to a sinusoidal input gave a fifth method for determining k [Eq. (4)]. These values agreed with those determined from "step" stretches (Fig. 8 B) but are not listed in the Table because of the difficulties in obtaining a "best" value. The receptor in Exp. 4 had a higher resting discharge (2.9 impulses/sec) than the others and this was corrected for as explained under "Methods" before analysing the responses to step or ramp stretches.

as the "step" stretches are summarized in the Table. The deviations were both positive and negative and were not significant. The value of the constant a so determined (Exp. 2) was 35.6 compared to an average value of 36.1 determined from the "step" stretches. Again positive and negative deviations are seen in the Table and they were not significant.

The amount of phase lead in Fig. 7A is indicated qualitatively by the openness of the curves or by the shift of the x-coordinate of the peak frequency away from the peak length. Zero phase difference between input and output would plot as a straight line. Phase lags were never seen over this frequency range.

For small phase leads such as those found here, it is very difficult to measure the shift of the peak frequency away from the peak length accurately, since the position varies as the cosine of the phase angle. Instead, we have measured the difference between the position on the rising and falling phase of the stretch (Δx in Fig. 7C) that gave the same response frequency. This difference was then divided by the peak to peak extent of the stretch (x). Since the uncertainties in time discussed above are inversely proportional to the frequency, we have chosen as high a response frequency (0.9 Δy) as was consistent with accurate measurement of Δx. For a linear system, the phase lead will then be equal to $\sin^{-1}(2.294 \, \Delta x/x)$. Measurement errors produced differences in phase lead of $\pm 1°$. Similar but less reliable results were obtained when the phase lead was calculated from the change in position at half the peak frequency or as the x-coordinate of the peak, though the phase lead tended to be somewhat greater, when measured at lower impulse frequencies. The curved arrows of Fig. 7C show the direction of movement during the stretching. Placing the points at the end of the interval reduces the openness of the curve on both sides of the loop and hence the error limits for the estimated phase lead will be asymmetrical.

Fig. 8B shows the measured values of phase lead (horizontal lines) together with estimated error limits (vertical lines) from measurement errors and time uncertainties. The effects of neuronal variability, or time for conduction of the action potential along the nerve (only about 1 msec) were not taken into account. The dashed line is the value predicted from the transfer function using the average value of k determined for the same receptor from 5 step stretches to different lengths. Because of the rapidly increasing error bounds as the stimulus frequency is increased, it is difficult to calculate a best value for k from the phase data, but it is clearly in agreement with the result predicted by the transfer function. This was true of all experiments that were analysed fully.

Implicit in these calculations is the idea that one can fill in the silent half cycle with fictitious negative frequencies. If a small sinusoidal stretch is applied to a receptor that has been stretched so that it exhibits a large background discharge, this assumption is not needed; the frequency always remains positive. Results obtained in this way are shown in Fig. 7B. The behaviour is qualitatively similar, increasing sensitivity with increasing input frequency and roughly constant phase lead (openness of loop). However, the sensitivity was found to be greater than predicted from the transfer function. This is due to the non-linearity of the system when stretched to this degree.

Ramp Stretches. In Fig. 9 the responses to ramp stretches of varying velocity to the same final length are shown for the receptor of Experiment 2. The transfer function predicts that the peak frequency should increase as the k-th power of the velocity; it also predicts that the response frequency should increase

as the $1 - k$-th power during the rising phase of the ramp. In Fig. 10A and 10B the results are plotted on a log-log scale and the solid lines represent best fitting straight lines on this plot. The linear correlation coefficient on this sort of plot was always greater than 0.96. The value for k determined from the peak response frequency using different velocities was 0.393 while that from the rising phase was 0.204. The average
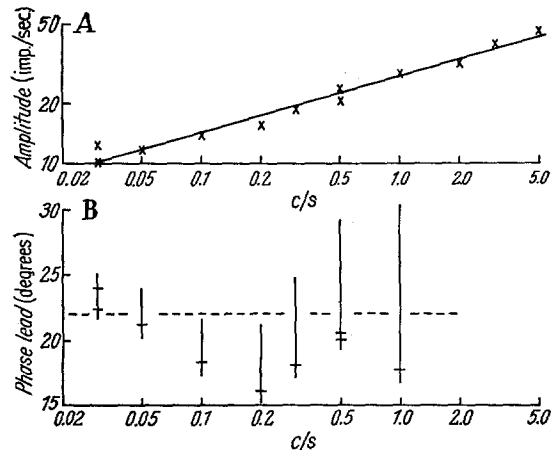

Fig. 8. *Response to sinusoidal stretches. A.* Peak impulse frequency minus resting discharge (amplitude) plotted as a function of the rate of sinusoidal stretching on a log-log scale. Straight line gives calculated best fit. *B.* Phase lead (linear scale) plotted as a function of the rate of sinusoidal stretching (logarithmic scale). Vertical lines represent uncertainty in estimation of phase angle; the horizontal lines intersect them at the measured experimental values. The dashed line is the predicted value of phase lead using the transfer function derived from response to "step" stretches. Same receptor as in Fig. 7A and Fig. 1
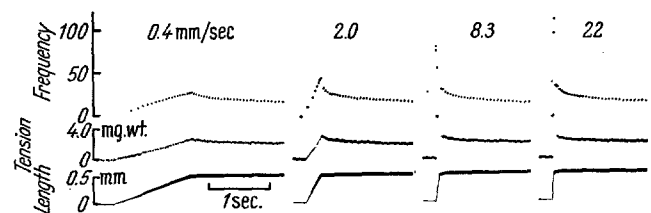

Fig. 9. *Responses of a slowly adapting receptor to stretches of 4 different velocities (values given above the records) to the same final length (0.5 mm).* The top records show instantaneous impulse frequency. The middle records give the tension in the receptor muscle. The bottom records show the changes in length of the muscle measured by the length transducer. Same receptor as Fig. 1 (Exp. 2). Rising phase of tension records in the two fastest stretches was too faint to reproduce
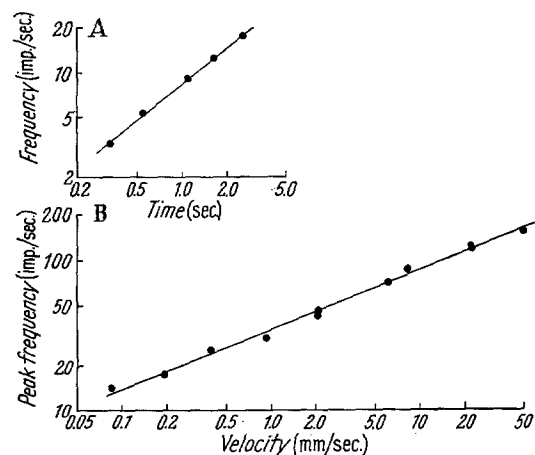

Fig. 10. *Responses to ramp stretches.* Same receptor as Fig. 1. Straight lines are calculated best fits. *A.* Impulse frequency during a constant velocity (0.19 mm/sec) ramp stretch plotted as a function of time on a log-log scale. *B.* The peak impulse frequency as a function of the velocity of stretching (mm/sec) to the same final length (0.5 mm) plotted on a log-log scale

value determined from five step stretches was 0.244. The Table gives the results from this and other experiments and it is seen that the average value of k determined from the peak response frequency is higher than predicted and that from the rising phase of the long ramps lower. (Only for the longest, slowest ramps could enough points be measured to determine the constants.)

A possible source of deviations is the significant non-linearities between impulse frequency and muscle length found in some receptors. The effect of non-linearities would be most marked on the rising phase of a ramp stretch since other measurements (e.g. decay following steps, sinusoidal amplitudes and phase leads, peak frequency) are taken at a roughly constant position and are relatively insensitive to the non-linearities present. In the following section the effect of non-linearities is considered in detail and later the reasons for the deviations in peak response as a function of velocity are analysed.

Non-Linearities. Eq. (1) assumes that the output frequency is directly proportional to the input length at all times. The initial length was chosen so that the zero order term (the constant value at $x=0$) was small, but it was shown earlier that second order terms (terms in x^2) were sometimes significant. If we include this second order term, Eq. (1) for the response to a step stretch would become

$$y = (a_1 x + a_2 x^2) t^{-k}. \tag{8}$$

The response can be considered to result from two processes, one which converts x to $a_1 x + a_2 x^2$, and a decay process with transfer function $\Gamma(1-k) s^k$ (corresponding to the time decay t^{-k}).

Hence, if the input were a ramp, $x = v\,t$, the first process would convert the ramp to $a_1 v\,t + a_2 v^2 t^2$, which would then be the input to the decay process. By multiplying the Laplace transform of this last expression by the transfer function of the decay process and taking the inverse transform, a new prediction for the response to a ramp input can be made. This prediction taking into account the second order term is given by Eq. (9).

$$y = \frac{a_1 v\,t^{1-k}}{1-k} + \frac{2a_2 v^2 t^{2-k}}{(2-k)(1-k)}. \tag{9}$$

The first term of Eq. (9) corresponds to the prediction of Eq. (6) and the second term represents an additional term. It is clear that on a log-log plot of frequency against time the best fitting slope will be higher than predicted by Eq. (6). If the slope is assumed to be $1-k$, (from consideration of only the first term) the prediction of the value of k will be low as actually found. The prediction of Eq. (9) for impulse frequency as a function of time was calculated using values of a_1, a_2 and k determined from the step stretches. The calculated line fell virtually on the best fitting line of Fig. 10A; any residual deviations were within measurement error. This result applied as well to the experiments in which the maximum deviations in k were found. The insensitivity to non-linearities of the value of k determined from the peak frequency can be easily demonstrated. If the length of stretch x is kept constant while the velocity v and the time t_1

for the stretch are varied, we have from Eq. (9) for the peak frequency, y_m,

$$y_m = \left(\frac{a_1 x^{1-k}}{1-k} + \frac{2a_2 x^{2-k}}{(2-k)(1-k)} \right) v^k. \tag{10}$$

The slope, k, on a log-log plot of y_m against v will remain unchanged although the straight line on this plot will in general be shifted up or down the y-axis.

Similar calculations could be made for sinusoidal stimulation and the effect of the second term would be to introduce a second harmonic. Third or higher order terms could be introduced, if present, in an analogous way.

Another source of non-linearity arises if the muscle does not move smoothly and uniformly to its new length. With a quick ramp stretch large acceleration forces are present and initially a wave will spread down the muscle and the receptor may undergo an extra stretch and release. This is evident as small oscillations in some of the tension records (not those illustrated) and as a single or double high frequency impulse followed by one or two low frequency impulses. Oscillations have also been seen in vertebrate muscle subjected to similar ramp stretches (Matthews, 1963b). This effect might be advanced as the cause of the high value of k which results from measuring the peak frequency as a function of the velocity at which the muscle is stretched to the final length. This is unlikely for three reasons:

(1) Neglecting velocities above 10 mm/sec (the highest velocity attained in sinusoidal stimulation) has very little effect on the value of k.

(2) Averaging over the top two or three impulses does not sufficiently reduce k although oscillations in frequency lasting more than one or two impulses were never seen.

(3) Direct, continuous photomicroscopy of glass beads placed on the part of the muscle innervated by the sensory cell failed to show oscillations during ramp stretches, although the light was not sufficiently intense to record the fastest stretches.

Viscous Tension. A more likely possibility is that muscle tension is the causal agent generating the nerve impulses. If this were the case the viscosity of the muscle would add considerably to the muscle tension during high velocity stretches and one would thus expect a higher impulse frequency. From Fig. 1 and Fig. 9, it can be seen that the muscle tension approaches a steady value quite quickly after the end of a stretch. As a measure of viscous tension we subtracted the tension 1 second after the end of the stretch from the peak tension. This measure is *not* a linear function of velocity, increasing more slowly than the velocity as velocity is increased. It does, however, increase more quickly than the k-th power (k, as determined from the "step" stretches, varied between 0.15 and 0.25) and was of the right order of magnitude to account for the deviations found in the value of k determined from the curves of peak frequency vs velocity (Table). A more exact comparison must await better methods for measuring the very small tensions in the muscle fibre.

Consideration of the response to sinusoidal stretching adds further support to this hypothesis. The amplitude of the sine response was measured near the peak length where the velocity was very small and

linear function of velocity. In addition, the predictions of this model are not linear with length. Increasing the length x does not increase x_1 directly, but only indirectly through a decrease in t_0. Thus, rather than being proportional to length, the curve would be shifted along the time axis in disagreement with the records of Fig. 1. An analogous kinetic model in which inactivation of a depolarizing chemical is proportional to the n-th power of its concentration can also be developed, but with some of the same difficulties.

A more likely hypothesis is that the power function is a convenient representation although one without a simple physical basis. A power function could be approximated over a certain range of times by a series of exponential decay processes with different time constants. At least three decay processes are involved, the decay of tension at a constant overall length, the decay of generator current at a constant tension (see Wendler, 1963) and the decay of impulse frequency to a constant current. Only the last of these seems to be a simple exponential process. Wendler and Burkhardt (1961) have used the analogy of a chain of effects between stimulation and excitation (Wirkungskette zwischen Reiz und Erregung). Imposing a variety of inputs on the first link of the chain has already indicated several complications not included in the simple structure of Eq. (1) and further studies are needed to elucidate the nature and extent of the decay processes. However, for many purposes, the power function and its corresponding transfer function should be a useful tool for analysis of the more complex systems of which the stretch receptor is only one part.

The power function also seems a useful way to encode information. It can be thought of as a fractional differentiation of the input signal (Chapman and Smith, 1963). Information is thus available about muscle position and velocity. The two are also separable in time since velocity will be signalled by a high frequency burst which we have shown dies away quickly after the end of a dynamic stretch leaving a well-maintained discharge which depends on the final length of the muscle.

Appendix

Eq. (6), the predicted response to a ramp input, can be expanded in powers of (t_1/t) for times greater than t_1. The result is

$$y = a\,x\,t^{-k}\left[1 + \left(\frac{k}{2}\right)(t_1/t) + \frac{k(k+1)}{6}(t_1/t)^2 + \cdots\right]. \quad (A.1)$$

For $t \gg t_1$, all terms except the zero order term can be neglected and Eq. (A.1) reduces to Eq. (1), the response to a step input. A better fit to the results at times when the first order term [the term in (t_1/t)] can not be neglected results from measuring times from the midpoint of the ramp. This approximation can also be expanded in powers of (t_1/t) to give

$$y = a\,x\,(t - t_1/2)^{-k} = a\,x\,t^{-k} \times$$
$$\times \left[1 + \left(\frac{k}{2}\right)(t_1/t) + \frac{k(k+1)}{8}(t_1/t)^2 + \ldots\right]. \quad (A.2)$$

Comparing Eq. (A.2) to the exact expansion given by Eq. (A.1), it can be seen that, if times are measured from the midpoint of the ramp, the first order term will be right and the error in the second order term is only $\frac{1}{4}$ as great as if times were measured from the

start of the ramp. The fact that the first order term is exact (and will only be exact if time is measured from the midpoint of the ramp) ensures that the convergence to Eq. (1) will be fastest when time is measured from the midpoint of the ramp. It is a result of the quantity $t_1/2$ in the approximation of Eq. (A.2) that second (and higher) order terms are smaller than those of Eq. (A.1). Since all the terms of Eq. (A.1) are positive, this approximation will underestimate the prediction of Eq. (6) for times shortly after the end of the ramp. If we assume $t = 2t_1$, (the frequency is measured t_1 seconds after the end of the ramp) and assume a value of 0.2 for k, the first order term of Eq. (A.1) is 0.05 and the second order term is 0.01. The error is only $\frac{1}{4}$ of this last figure and, because of the rapid convergence of the series, the total error in the approximation of Eq. (A.2) is unlikely to appreciably exceed 0.5%.

Note added in Proof. A paper by Borsellino, Poppele and Terzuolo in the Symposia on Quantitative Biology Vol. 30, pp. 581—586 (1965) has recently become available. In this paper a transfer function for the lobster stretch receptor was derived. Differences between their results and ours presumably arise from differences in their experimental animal, size of stretch (microns as compared to tenths of a millimetre), type of stretch (only sinusoidal inputs over a rather different frequency range were used), and analysis procedures. With the smaller, higher frequency stretches used, their results were dominated by the discrete, all-or-none nature of the action potential output and the transfer function for the specific transducer properties of the receptor organ itself was only obtainable by a subtraction procedure. This procedure was not needed in the present work over the range of amplitude and frequency of stretches used. Finally, their analysis was based on the averaged output of a track-and-hold device which introduced substantial delays. The frequency averaged during an interval was the inverse of the *preceding* interspike interval.

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Eine Theorie über das Spektrum von Selbstlauten

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Zusammenfassung. Zweck des vorliegenden Aufsatzes ist es, die Form des Spektrums von Sprechsignalen, wie z. B. von Selbstlauten, zu erklären.

Summary. The aim of this paper is to explain — from the mathematical point of view — the vowels spectrum.

Wie bekannt ist, werden in der modernen experimentellen Phonetik weitgehend Geräte verwendet, die automatisch das Spektrum von Sprechsignalen anzeigen können. In Abb. 1 ist das Spektrum des Selbstlautes *a* aus der rumänischen Sprache wiedergegeben, so wie man es mit dem Apparat „Sonograph" erhält. Dieses Spektrum weist die allgemeinen Merkmale jedes Selbstlautspektrums auf.

Das Spektrum der Selbstlaute ist im allgemeinen dadurch gekennzeichnet, daß die Komponenten eine in gewissen Bereichen stetig veränderliche Frequenz aufweisen, während die Maxima sich ungefähr in der Mitte der Bereiche befinden und diese Mittenfrequenzen alle ganze Vielfache einer Grundfrequenz sind.

Im folgenden werden die allgemeinen Merkmale dieser Spektren ausgehend von den physiologischen und physikalischen Grundlagen der betreffenden Vorgänge erklärt.

Wie bekannt ist [1], ändert sich der Luftdruck als Funktion der Zeit — im Falle eines reinen Selbstlautsignals, d. h. entsprechend eines einzigen gesprochenen Selbstlautes — wie in Abb. 2 angegeben, das vom Schirm eines Zweistrahloszillographen erhalten wurde. An einen Eingang wurde das Signal angelegt, das von einem Mikrophon erzeugt wird, in welches der betreffende Selbstlaut gesprochen wird. An dem anderen Eingang wurde ein Markierungssignal bekannter Frequenz angelegt. Die waagerechte Geschwindigkeit des Elektronenstrahls ist in diesem Bild verhältnismäßig klein (geringe Frequenz der Zeitbasis). Für eine große Geschwindigkeit (höhere Frequenz der Zeitbasis) erhält man Abb. 3. Ein ähnliches Bild erhält man auch,

wenn man die zeitliche Luftdruckveränderung mit Hilfe eines Kymographen untersucht.

In einem früheren Aufsatz [2] wurde versucht, das Spektrum der Selbstlaute auf Grund der zeitlichen Luftveränderung zu erklären.
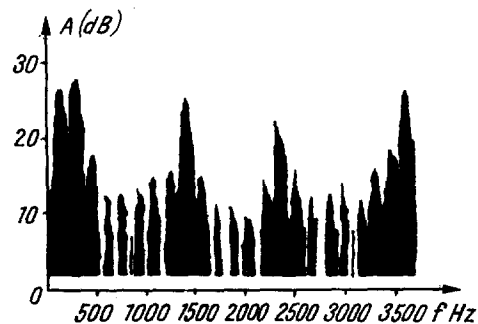

Abb. 1. Spektrum des *a*-Selbstlautes

Bezeichnet man mit $p(t)$ den Luftdruck als Funktion der Zeit, so kann man unter Berücksichtigung der Formen in Abb. 2 und 3 den Luftdruck als

$$p(t) = a(t)\, v(t) \tag{1}$$

angeben, wo $v(t)$ das periodische Signal und $a(t)$ dessen Amplitude bedeutet.

Wie aus Abb. 2 ersichtlich, kann man annehmen, daß $a(t)$ eine ungefähr trapezförmige Änderung aufweist, die in Abb. 4 angegeben und durch folgende Beziehungen gekennzeichnet ist:

$$a(t) = \begin{cases} k_1 t & 0 \leqq t \leqq t_1 \\ k_0 & t_1 \leqq t \leqq t_2 \\ k_2 - k_3 t & t_2 \leqq t \leqq t_3. \end{cases} \tag{2}$$

Berücksichtigt man (1) und die Tatsache, daß $v(t)$ eine periodische Funktion ist,

$$v(t + T) = v(t),$$