ANALYSIS OF NERVE-MUSCLE JUNCTIONAL POTENTIALS

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There are three kinds of muscle fibres in function such as twitch fibre, slow fibre and intrafusal fibre, in the frog's skeletal muscle. The electric characteristics of twitch fibre were detailed by Fatt and Katz (1), and the junctional potential and the innervation in slow fibre were investigated by Kuffler and Vaughan (2, 3), moreover the characteristics and the innervation of intrafusal fibre being clarified by Koketsu and Nishi (4, 5). These three fibres different in their appearance may be due to difference of membrane resistance, fibre radius, length constant, membrane time constant, or effective resistance. When the focal potential, in other words a maximal potential at junctional region, initiated by motor nerve stimulation, was intracellularly recorded, the difference in decaying time or in decaying curve was observed in these fibres (Fig. 1). The author analysed these differences from the point of view of temporal change of permeability and number of junction.

Figure 1. e.p.p., s.j.p., and i.j.p. (downwards).
Time mark: 60 c.p.s. Vertical lines
5mV.

METHODS

(1) Intrafusal muscle fibres were isolated from M. extensor dig. IV of Rana

nigromaculata by the method reported by Koketsu et al. (4, 5). This fibre was stimulated indirectly through N. peroneus lat. The junctional potential was obtained by microelectrode.

The electrotonic potential was recorded by use of a bridge of which one arm consisted of the electrode and the membrane resistance.

(2) The action potential of s.m.f. and t.m.f. of iliofibularis was recorded similarly to i.j.p.

Microelectrode used is less than 0.5μ in diameter, $10\sim 20M\Omega$ in resistance, and is made by boiling method, the distance from the electrode to input of amplifier being short as possible in order to lessen the stray capacity. The composition of Ringer's solution is NaCl 112mM, KCl 2mM, NaHCO_3 2.4 mM, CaCl_2 1.8mM.

The room temperature was $20^\circ\text{C}\sim 30^\circ\text{C}$.

RESULTS AND DISCUSSION

(1) The electrical characteristics of membrane

In analysing the junctional potential, it is necessary to obtain the electrical characteristics, for instance τ_m , λ , etc.

When V is the potential change across the membrane surface, the following equation was introduced by Hodgkin and Rushton (6).

$$-\lambda^2 \frac{\partial^2 V}{\partial x^2} + \tau_m \frac{\partial V}{\partial t} + V = 0 \dots\dots\dots [1]$$

where, $\lambda = \sqrt{r_m/(r_i + r_0)} \doteq \sqrt{r_m/r_i}$, $\tau_m = c_m r_m = C_m R_m$

r_m is the resistance $\times$ unit length of the membrane surface,

c_m is the capacity per unit length of the membrane surface,

r_i is the resistance per unit length of the axoplasm,

r_0 is the resistance per unit length of the external fluids,

R_m is the resistance $\times$ unit area of the membrane surface,

C_m is the capacity $\times$ unit area of the membrane surface.

When the distance between current electrode and recording electrode inserted into the same single fibre is x , the potential, V , across the membrane, at t after streaming, is shown as follows, from equation [1],

$$V = \frac{\sqrt{r_m r_i}}{4} \cdot I_0 \left[e^{\frac{x}{\lambda}} \left\{ 1 + \operatorname{erf} \left(\frac{x}{2\lambda} \sqrt{\frac{\tau_m}{t}} + \sqrt{\frac{t}{\tau_m}} \right) \right\} + e^{-\frac{x}{\lambda}} \left\{ 1 - \operatorname{erf} \left(\frac{x}{2\lambda} \sqrt{\frac{\tau_m}{t}} - \sqrt{\frac{t}{\tau_m}} \right) \right\} \right] \dots [2]$$

in cutting off,

$$V = \frac{\sqrt{r_m r_i}}{4} \cdot I_0 \left[e^{\frac{x}{\lambda}} \left\{ 1 + \operatorname{erf} \left(\frac{x}{2\lambda} \sqrt{\frac{\tau_m}{t}} - \sqrt{\frac{t}{\tau_m}} \right) \right\} - e^{-\frac{x}{\lambda}} \left\{ 1 - \operatorname{erf} \left(\frac{x}{2\lambda} \sqrt{\frac{\tau_m}{t}} + \sqrt{\frac{t}{\tau_m}} \right) \right\} \right] \dots [3]$$

where, t is the duration from cutting off moment, x is the distance as above,

$\text{erf } Z = \int_0^Z e^{-r^2} \cdot dr$, and I_0 : the streamed current.

By streaming or recording by a single electrode,

$$\text{equation [2]} \quad V = \frac{1}{2} \sqrt{r_m r_i} \cdot I_0 \text{erf} \sqrt{\frac{t}{\tau_m}} \dots \dots \dots [2]'$$

$$\text{equation [3]} \quad V = \frac{1}{2} \sqrt{r_m r_i} \cdot I_0 (1 - \text{erf} \sqrt{\frac{t}{\tau_m}}) \dots \dots \dots [3]'$$

(A) Method to obtain τ_m

τ_m is obtainable from an electrotonic potential curve by means of following method.

$$\lim_{t \rightarrow \infty} \text{erf} \sqrt{Z} = 1 \dots \dots \dots [4]$$

$$\text{erf} \sqrt{1} = 0.843 \dots \dots \dots [5]$$

So it is satisfactory to measure either the time that the electrotonic potential reaches 84.3% of terminal value ($t \rightarrow \infty$), from the onset of current, or the time reaching 15.7% of potential immediately before switching off, from [2]', [3]', [4], and [5]. The τ_m of every fibre, obtained by this way, is as follows.

t.m.f. = 16msec. s.m.f. = 40msec. i.m.f. = 10msec.

(B) Method to obtain R_m & λ

As already described, λ is shown by $\sqrt{r_m r_i}$, substituting by $R_m = 2\pi\rho r_m$, and $R_i = \pi\rho^2 r_i$.

$$\lambda = \sqrt{\rho R_m / 2R_i}$$

ρ (radius of fibre) is as follows.

t.m.f. = 50μ (1) s.m.f. = 22μ (2) i.m.f. = 8μ (5)

R_i of each fibre (specific resistance of axoplasm) was assumed by $250 \Omega\text{CM}$ (1).

In the terminal value ($t \rightarrow \infty$) of V , $V_0 = \frac{1}{2} \sqrt{r_m r_i} \cdot I_0$ is obtainable from R_m in equation [2]'. From this,

$$V_0 = \frac{1}{2} \sqrt{2\pi^2 \rho^3 R_m R_i} \cdot I_0$$

Since V_0 , I_0 , and ρ are measurable, R_m of each fibre, and hence λ of fibre is obtainable.

R_m , t.m.f. = $3600 \Omega\text{CM}^2$ s.m.f. = $4900 \Omega\text{CM}^2$ i.m.f. = $3480 \Omega\text{CM}^2$

λ , t.m.f. = 1.9mm s.m.f. = 1.47mm i.m.f. = 0.72mm

(2) *i. j. p. recorded by intracellular electrode*

The intrafusal fibre isolated from m. ext. dig. long IV of frog shows a specific junctional potential (i.j.p.) in the microelectrode recording, when that muscle is stimulated indirectly through n. peroneas lateralis (Fig. 3).

As shown in Fig. 3, i. j. p. similar to e. p. p. of twitch fibre, is (1) the rising and decaying time are somewhat longer than e. p. p., (2) the knob in rising and falling

Fig. 1.

Fig. 2.

Figure 2. Electrotonic potential curve of t.m.f. in the uppermost, s.m.f. in the middle and i.m.f. in the lowest trace. Time mark: 60 c.p.s.

Figure 3. Two intrafusal junctional potentials. Time mark: 60 c.p.s.

phase can be observed in the rapid record, and (3) i.j.p. is recordable from the whole length of the intrafusal fibre contrary to the end plate potential.

The property (1) suggests that the membrane characteristics and the nerve-muscle transmission of intrafusal fibre slightly differ from those of twitch fibre, and (2), (3) show a multiple innervation of intrafusal fibre as reported by Koketsu et al. (4), (5). The i.j.p., in general 8~10mV in size, shows the different times in reaching the peak of depolarization, such as 2~3msec. The rising time to a step varies from 0.8 to 1.5 msec., however, the half-time of decaying phase, which declines smoothly, is about 5 msec..

Fig. 4 is described by plotting the decaying time semi-logarithmically against time in a few i.m.f.'s. In Fig. 4, it is clear that intrafusal potential decrements exponentially in the decaying phase.

(a) Analysis of i. j. p.

- (i) Interrelation between decay time, t_0 , of i. j. p. and time constant, τ_m , in resting membrane.

Since the falling phase of i. j. p. decrements exponentially as written above, that potential should be written as

Figure 4. i. j. p. and its explanation. Ordinate is written in logarithmic scale. The number in () in each line shows the decay time.

$$V = V_0 \exp (-t/t_0),$$

if writes logarithmically

$$\ln V = \ln V_0 - t/t_0.$$

Substituting $\ln V = U$ and differentiating by t ,

$$dU/dt = -1/t_0.$$

Since dU/dt is a gradient in semilogarithmic scale, $-1/t_0$ in the right side corresponds to the gradient. Accordingly, t_0 is a reciprocal number of the gradient. When t_0 is considered as a decay time, t_0 is obtained from above Figure and is 6.5–7.8 msec. The ratio of decay time to time constant of resting membrane is 0.65–0.78, since τ_m of intrafusal fibre is 10 msec., when it is measured from an electrotonic potential curve. The reason which does not agree will be discussed in later. Though s.m.f. and i.m.f. are similarly supplied by a multiple innervation, the decay

time and the time constant of the former are equally ($t_0/\tau_m = 1$).

(ii) Interrelation between multiple innervation and decay time.

The size of i. j. p. varies by the position of recording electrode. This suggests that the distribution of intrafusal junction differs from that of slow fibre junction. The calculation to know the state of innervation of intrafusal fibre was made with following assumptions: (1) each junction distributes equidistantly, (2) the amount of depolarization in junctional membrane by a nerve impulse is equally, and (3) each junction is depolarized simultaneously.

In the intracellular recording of e.p.p., generally one in number, the potential across the membrane surface was given as below by Fatt and Katz (1),

$$V = \frac{q_0}{2C_m\lambda\sqrt{\pi t/\tau_m}} \exp\left(-\frac{x_i^2}{4\lambda^2} \cdot \frac{\tau_m}{t} - \frac{t}{\tau_m}\right) \dots\dots\dots [7]$$

where, q_0 is the initial charge on the membrane, x_i is the distance between the electrode and the end plate, and t is the time from the beginning of e.p.p.

In the junctional area of i.m.f., consisting probably of a few junctions, when the distance from an electrode to each junction is assumed as $x_1, x_2, x_3, x_4, \dots, x_n$, the spreading potential V is recorded as follows.

$$\begin{aligned} V &= \sum_i \frac{q_0}{2C_m\lambda\sqrt{\pi t/\tau_m}} \exp\left(-\frac{x_i^2}{4\lambda^2} \cdot \frac{\tau_m}{t} - \frac{t}{\tau_m}\right) \\ &= \frac{q_0}{2C_m\lambda\sqrt{\pi t/\tau_m}} e^{-\frac{t}{\tau_m}} \times \sum_i \exp\left(-\frac{x_i^2}{4\lambda^2} \cdot \frac{\tau_m}{t}\right) \end{aligned}$$

Change both sides into logarithmic scale, and differentiate by T ,

$$\frac{dU}{dT} = -\frac{1}{2T} + 1 + \frac{d}{dT} \ln\left\{\sum_i \exp\left(-\frac{x_i^2}{4\lambda^2} \cdot \frac{\tau_m}{t}\right)\right\}$$

where $\ln V = U$, and $t/\tau_m = T$

Because $dU/dT = \tau_m dU/dt$, and the right side shows the product of τ_m and a gradient, dU/dt , the elements of this gradient are T and x_i/λ .

(iii) Factors determining the ratio of decay time, t_0 , to time constant, τ_m

Because in the assumption interjunctional distance is equally,

$$x_i = y + kX$$

where k : a whole number, y : distance from the electrode to a proximal junction, and X : interjunctional distance.

If it is supposed that y is a function of X , that when the junction is an even number an electrode is inserted near the central junction ($y \doteq 0$), and that when an odd number, an electrode is laid at the middle of central two junctions ($y = X/2$), the former is $x_i = kX$, and the latter $x_i = (k+1/2)X$. From these facts, the factors determining t_0/τ_m are X/λ , N (number of junction), and $t/\tau_m = T$.

(iv) Interrelation among N , X/λ , and t_0/τ_m .

(A) The value of X/λ and N against t/τ_m is described from Figure 5 to 7, in which the number at right of each curve shows that of junction and from which the following can be thought.

(a) In large X/λ (for instance $X/\lambda = 1$), the curve is linear in less number ($N=3$) of junction, and dU/dT is constant without any relation to time. In $N=7$, there are $dU/dT = -1$ and $t_0/\tau_m = 1$ and a curve decays with time constant τ_m .

(b) In slightly smaller X/λ ($X/\lambda = 0.6$) and less N , a curve appears concave and becomes linear with progress of time. This is similar to e.p.p. of t.m.f. of which junction is one. When N is larger than 5 a curve is linear, and when N equals with or increases more than 7, t_0 coincides with τ_m ($dU/dT = -1$).

(c) In further smaller value of X/λ , ($X/\lambda = 0.2$) general aspect of curves in similar with (a) and (b). When N is larger than 15 a curve is linear, and when N equals with or increases more than 36 t_0 coincides with τ_m .

(d) From above fact, it is thought when there are many junctions the decay time becomes equal with τ_m . So that author attempts to write the number of junction which makes t_0 equal with τ_m , as follows.

Figure 5. Decaying phase in semi-logarithmic scale when distance of adjacent two junctions is λ . Number in each curve shows that of junction.

Figure 6. Decaying phase, in semi-logarithmic scale, in 0.6λ of interjunctional distance.

X/λ	0.1	0.2	0.4	0.6	0.8	1.0	1.6
N	72	36	18	12	9	more than 7	3

In this table, the product of each X/λ and the corresponding number of junction is constantly 7.2, namely, $(X/\lambda) \cdot N = 7.2$ can be written by $NX = 7.2\lambda$. In the latter equation, the left side is the product of the number of junction and the distance, and so is the extent of junctional region. This fact shows that when the junctional area is above 7.2λ the decay time, t_0 , becomes equal with the time constant of membrane, τ_m .

(e) t_0/τ_m of i. j. p. is 0.72, 0.75, and 0.78 respectively, as shown in Fig. 4. Further, X/λ , and N , can be introduced. When t_0/τ_m is 0.72, the relation between N and X/λ is as follows.

X/λ	0.1	0.2	0.4	0.6	0.8	1.0
N	24	12	6	4	3	more than 2

Accordingly $NX = 2.4\lambda$. Because, when the junctional area of focal potential is 2.4λ ,

Figure 7. Decaying phase, in semi-logarithmic scale, in 0.2λ , of interjunctional distance.

t_0/τ_m is 0.72. Similarly; when the junctional area of focal potential is 2.4λ , t_0/τ_m is 0.75 and when 3.2λ , 0.78.

(B) In the potential being not focally.

Above all results were obtained from a maximal focal potential that the recording electrode was laid just at the focus. When the electrode was moved far from very limited junction by the method described in below, the above curves in Fig. 8 were obtained.

(a) When the electrode was placed at the junctional area (P_A , P_B , P_C , & P_D) the decay time, t_0 , does not generally differ from that of focal potential.

(b) Even in that area, when the electrode was placed immediately near the junction, the curve first increases its gradient and then obtains the similar one (P_B , & P_D).

(c) When an electrode placed beside but immediately near the junction, (P_E ,

Figure 8. Change of decaying phase of junction potential and electrode position. Ordinate: potential height in logarithmic scale. Lower Figure shows the relative position of junction to electrode. Junction is shown semicircularly, and "p" shows the position of electrode. There are four junctions in 0.8λ of interjunctional distance.

P_F , P_C , & P_H), the gradient becomes smaller and the decay time does longer also.

(v) Comparison of theory with experiment.

Summary of experimental results is as follows.

i.j.p. number	decay time	t_0/τ_m	junctional area	time to peak
1	6.4 msec.	0.64		1.7 msec.
2	7.8 msec.	0.78	3.2λ	2.3 msec.
3	7.2 msec.	0.72	2.4λ	1.5 msec.
4	7.2 msec.	0.72	2.4λ	0.7 msec.
5	7.5 msec.	0.75	2.8λ	1.7 msec.

In this table, because No. 2 shows the longer time to peak it is thought that an electrode lays out of junctional area, and as shown in Fig. 8 t_0 may become longer

as its potential is a focal potential. In No. 3 and No. 4, an electrode places at junctional area, while in No. 5 it does relatively near a junction. No. 1 may not be a focal potential since the decay time in my few fibres is short and the rising time to peak is longer.

From above, if No. 3 and No. 4 may be a focal potential the multiple innervation of i.m.f. is not made on the whole length of fibre and may be limited at an area of 2.4λ which is 1.53 mm from a fact that λ is 0.72 mm.

(3) *s. j. p. recorded by intracellular microelectrode*

Fig. 9 shows a slow junction potential of m. iliofibularis of which rising or falling phase is relatively slow. The rapidly swept s.j.p. clearly discloses some steps which signify the multiple innervation, and it is found by Kuffler and Vaughan (2, 3) that s.j.p. can be recorded from whole length of fibre and there is no change in size and time. Ginsborg and Burke (7, 8) also obtained the same results.

(i) Falling phase of s. j. p.

When an electrode is inserted into the middle of junctional area of multiple-innervated s.m.f. above 7.2λ ,

$$\frac{d \ln V}{dt} = \frac{-1}{\tau_m}$$

When an electrode is little out of the place of junction, $d \ln V/dt = -1/\tau_m$ may be possible. Because the junctions of s.m.f. may lay along the whole length, potential recordable, V , is

$$\begin{aligned} V &= \sum \frac{q_0}{2C_m\lambda\sqrt{\pi T}} \exp\left(-\frac{X_i^2}{4T} - T\right) \\ &= \frac{q_0 e^{-T}}{2C_m\lambda\sqrt{\pi T}} \sum_i \exp\left(-\frac{X_i^2}{4T}\right) \\ &\doteq \frac{q_0 e^{-T}}{2C_m\lambda\sqrt{\pi T}} \sum_{-\infty}^{\infty} \exp\left(-\frac{X_i^2}{4T}\right) \\ &= \frac{q_0}{2C_m\lambda\sqrt{\pi T}} e^{-T} \cdot 2\sqrt{\pi T} \\ &= \frac{q_0 e^{-T}}{C_m\lambda} \end{aligned}$$

(ii) Analysis of s. j. p.

As Ginsborg and Burke (8), the height from the peak hyperpolarization was measured in each s.j.p.. The decay time, contrary to Ginsborg and Burke (8), is illustrated, from the beginning of decaying phase to the end, in Fig. 9 and 10, of which ordinate is potential height in logarithmic scale and abscissa is time, 2~5 msec. in interval, every 1 mm on C. R. T. In this curve, the reciprocal number of gradient of each curve corresponds to decay time.

(iii) s. j. p. without positive after potential.

As is clearly from Fig. 9, each curve shows a constant decay time except a short time after the beginning of recording, averaging by 41 msec. This coincided the value of τ_m of electrical properties in resting state. This fact shows the membrane behaves passively. In very steep gradient, since membrane time constant in resting membrane becomes different from decay time, some of all junctions may be depolarized.

Figure 9. s. j. p. without after-potential. Ordinate is logarithmic potential height from the resting level.

Abcissa: time in msec. Number in each curve shows decay time.

(iv) s. j. p. with positive after potential.

As shown in Fig. 10, a gradient changes stepwise at 40 msec., on the average, and the upper or the lower part of this point is linear. T_m , decay time in anterior half, is 41 msec. and T'_m decay time in posterior half, is 33 msec. on the average. T'_m/T_m of each fibre is nearly equally 0.8. That T_m equals with τ_m shows that membrane

acts passively. $\tau_m = C_m R_m$, so that R_m becomes smaller in a constant C_m , namely, the permeability of membrane may be increase.

Figure 10. s. j. p. with after-potential. Ordinate is potential height from hyperpolarization peak, in logarithmic scale. Denominator of number shows decay time in upper part, and numerator is in lower part.

(4) *e. p. p. of extrafusul fibre*

This is detailed by Fatt and Katz (1), however, the author compared this potential with other potentials. It is supposed that the junction in t. m. f. may be one (1). The rising time of this potential recorded by an electrode placing near the end plate is about 1.5 msec. (Fig. 11). This result is described simultaneously with other potential curve in a logarithmic scale, and shows the repolarization is more rapid than others.

The process of repolarization can be shown by Fatt and Katz's equation [7] on i. j. p.

Change the both sides in equation [7] into logarithmic scale,

Figure 11. e. p. p.

$$\ln V = \ln \frac{q_0}{2C_m\lambda} - \frac{1}{2} \ln \frac{\pi t}{\tau_m} - \frac{x^2}{4\lambda^2} \cdot \frac{\tau_m}{t} - \frac{t}{\tau_m} \dots \dots \dots [8]$$

Differentiate above equation by t , considering that q_0 , c_m , λ , and τ_m are independent of t ,

$$\frac{d \ln V}{dt} = -\frac{1}{2t} + \frac{x^2}{4\lambda^2} \cdot \frac{\tau_m}{t^2} - \frac{1}{\tau_m} \dots \dots \dots [9]$$

If an electrode is inserted near the end plate ($x \approx 0$),

$$\tau_m = \left(-\frac{1}{2t} - \frac{d \ln V}{dt} \right)^{-1} \dots \dots \dots [10]$$

From the equation [10], it may be probable to obtain τ_m . Searching for τ_m from Fig. 11 by equation [10], Fig. 12 is obtained. In Fig. 12, after 5 msec. τ_m is nearly constant, and the value of τ_m is 15 msec. and equals nearly time constant of resting membrane. So that, membrane may behave passively after 5 msec.

Figure 12. τ_m and duration in e. p. p. in Figure 11.

SUMMARY

(1) Time constant and length constant in resting membrane were obtained from t.m.f. i.m.f., and s.m.f.

(2) From the curve of falling phase of i.j.p., initiated by motor stimulation, the semilogarithmic plotting of potentials results in a line which shows that the decay time obtained from a gradient is smaller than time constant of resting membrane and is constant as 0.72 times of membrane time constant.

(3) The linear character of i.j.p. in semilogarithmic scale may be due to a multiple innervation. The junctional area is determined by the ratio of decay time to resting membrane time constant.

(4) Thus, the junctional area of i.m.f. is 2.4λ and is 1.5 mm.

(5) S.j.p. without positive after potential decays with resting membrane time constant, in semilogarithmic scale.

(6) S.j.p. with positive after potential shows a step in the decay time in its falling phase. The ratio of two part in decay time, T'_m/T_m , is 0.8. The anterior half of decay time, T_m , is equal with resting time constant, and the posterior half is due to increased permeability.

(7) S.m.f.'s membrane acts passively both in a case without positive after potential and in the anterior half of case with positive after potential.

(8) From the value in falling phase of the moment of e.p.p. recorded from t.m.f., the time constant of membrane after 5 msec is equal with that in resting membrane which behaves passively in falling phase.

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