Information Properties of a Neuron

By

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Two kinds of mathematical neural models, one simular to a sensory neuron and the other to a ganglion cell, are constructed and their properties in view of information theory are studied. Each of the models is essentially a threshold element, the output of which is a train of pulses emitted at the instants of the stored charge inside the neuron reaching the threshold. The interval of the pulses is a random variable, and a method to give its probability density function is derived. It is seen that the distributions of the output pulses of the models are very simular to the spike discharge patterns of actual neurons. For the sensory neuron model the channel capacity is obtained and thus the maximum capability for a neuron to transmit messages is clarified. The model can also be regarded as a sampling device which samples a continuous signal by firing a pulse every time the signal reaches the threshold. A method to recover the original signal from the intervals of the pulses thus emitted is given.

1. Introdution .

Conceptual or mathematical models of a neuron have been constructed and studied by various authers with the motive to clarify the neuaral behavior leaving the detailed complexity of the physiological neuron mechanism aside, and hoping to apply the results derived with the simplified models in communication, control, or some other engineering fields. In this paper, too, a neuron is regarded as an element of communication characterized by the emission of pulses, threshold and integration mechanism. The properties in view of the information theory are described.

One of the important aspects of the neural network as a communication system is that the messages are sent in the form of the pulse transmission rate, or, if we put it in a different way, of the intervals of the pulses, having a stochastic nature. Thus, in general, only one pulse or an interval has little meaning by itself, but a train of pulses is considered to be able to carry a message. Thus the emission of the pulses must be fast enough, for example, to follow the change of the external stimulus impressed on the neuron.

Two kinds of neural models are considered. The first one, a model of a sensory

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neuron, receives an external stimulus as its input and emits a train of pulses as its output. The intervals of the pulses are considered to carry the information about the stimulus. The second one, simular to a ganglion cell, receives trains of pulses as its input, which cause the emission of pulses at its output. The neuron is regarded as performing a kind of logic. The details of the models and their properties are described in the following sections.

2. Sensory Neuron Model And Its Properties

Description of the Model—The input stimulus x of this model is assumed to be a continuous function of time. The received input is accumulated in the neuron as the stored charge q, and when q reaches the threshold, the neuron emits an output pulse. At the same time q is set to a certain initial value, and the accumulation process starts again. It is also assumed that the level of the stored charge suffers random fluctuations, whose amplitude distribution density has a zero mean and variance σ^2, and is independent of the previous behavior of the neuron. Hence, except for the instants of the emission of the pulses, q is a random variable having the Markov property, the infinitesimal mean and variance of the change in q being x and σ^2, respectively.

The output of the neuron is a train of pulses, the interval of which is also a random variable. In order to obtain the probability desity function of the interval, the procedures to find the first passage time of a diffusion process can be made use of, provided that the input stimulus changes slowly. From the fact mentioned in section 1 we see that this condition is, in general, satisfied. The probability density of the interval is approximately that of the first passage time, if the effect arising from when the accumulation process starts, is negligible.

The Probability Density of the Interval—Let us consider only one interval, or one process of accumulation of the charge. The origins of time and charge q are chosen so that q reaches the threshold at $t=0$, and $q=0$ at the instant. The length of the interval is denoted τ, and thus the accumulation begins at $t=-\tau$. Let $q(-\tau) = -q_0$. Under the assumptions made above the probability density of the interval, denoted $g(\tau, q_0)$, satisfies the backward Kolmogorov equation. Hence,

$$\frac{\partial g(\tau, q_0)}{\partial \tau} = -x\frac{\partial g(\tau, q_0)}{\partial q_0} + \frac{\sigma^2}{2}\cdot\frac{\partial^2 g(\tau, q_0)}{\partial q_0^2}. \qquad (1)$$

The boundary and the initial conditions are $g(\tau, 0)=0$, $g(\tau, \infty)=0$; $\tau>0$, and $g(0, q_0) = 0$; $q_0>0$.

The solution of Eq. (1) with the specified conditions is

$$g(\tau, q_0) = q_0(2\pi\sigma^2\tau^3)^{-1/2} e^{-(q_0-x\tau)^2/2\sigma^2\tau} . \tag{2}$$

The input x is regarded as a positive constant. It can be seen that the probability density is very simular to that obtained from the spike discharge patterns of actual neurons[1)-4)].

The Channel Capacity of the Neuron—The output of the neuron model is the interval of the pulses and therefore the transmission of information requires time which is a function of the output message. Let the function be $l(\tau)$. Then the average rate of transmission of information is given by

$$R = I/L \tag{3}$$

where I is the amount of transmitted information (the average mutual information) and L is the average time required to send a message. In terms of the probability density, I and L are written as

$$I = -\int_0^\infty r(\tau) \log r(\tau)\, d\tau + \int_0^\infty \int_0^\infty p(x)p(\tau/x) \log p(\tau/x)\, dx\, d\tau \tag{4}$$

and

$$L = \int_0^\infty r(\tau)\, l(\tau)\, d\tau \tag{5}$$

respectively, where $p(x)$ is the probability density of x, $r(\tau)$ is the probability density of τ, and $p(\tau/x)$ is the conditional probability density of τ given x. As stated previously,

$$p(\tau/x) \sim g(\tau, q_0) = q_0(2\pi\sigma^2\tau^3)^{-1/2} e^{-(q_0-x\tau)^2/2\sigma^2\tau} . \tag{6}$$

By definition the channel capacity

$$C = \max_{p(x)} R \tag{7}$$

under the condition

$$\int_0^\infty p(x)\, dx = 1, \quad p(x) \geq 0 . \tag{8}$$

Since

$$r(\tau) = \int_0^\infty p(\tau/x) p(x)\, dx \tag{9}$$

and thus

$$\int_0^\infty r(\tau)\, d\tau = \int_0^\infty \int_0^\infty p(\tau/x)\, p(x)\, dx\, d\tau = \int_0^\infty p(x)\, dx , \tag{10}$$

$\int_0^\infty p(x)\, dx = 1$ if $\int_0^\infty r(\tau)\, dx = 1$. Likewise $\frac{\partial R}{\partial p} = 0$ if $\frac{\partial R}{\partial r} = 0$.

Hence, the maximization of R with respect to $r(\tau)$ includes that with respect to $p(x)$. Now let

$$U = R+\lambda\int_0^\infty r(\tau)\,d\tau \tag{11}$$

and introduce a function $h(\tau)$, which satisfies the following relation and is independent of x.

$$\int_0^\infty p(\tau/x)\,\log p(\tau/x)\,d\tau = \int_0^\infty p(\tau/x)\,h(\tau)\,d\tau \tag{12}$$

Then U is rewritten as

$$U = \left\{-\int_0^\infty r(\tau)\,\log r(\tau)\,d\tau+\int_0^\infty r(\tau)\,h(\tau)\,d\tau\right\}\Big/\int_0^\infty r(\tau)\,l(\tau)\,d\lambda+\lambda\int_0^\infty r(\tau)\,d\tau \tag{13}$$

Thus $dU=0$ if

$$\Big[-\{1+\log r(\tau)\}+r(\tau)\,h(\tau)\Big]L-Il(\tau)+\lambda L^2 = 0 \tag{14}$$

Multiplication of $r(\tau)$ to Eq. (14) and integration with respect to τ lead to

$$\lambda = \frac{1}{L}\,,\quad r(\tau) = e^{h(\tau)-Cl(\tau)} \tag{15}$$

From Eq. (15) channel capacity C can be obtained by noting that $\int_0^\infty r(\tau)\,d\tau=1$. It is necessary to check if C thus obtained is the maximum with respect to $p(x)$ as well as $r(\tau)$. Probability density $p(x)$ is the solution of the integral equation (9) with $r(\tau)$ given by Eq. (15). Note that the solution should be nonnegative; if not, the procedure described above is invalid.

For $p(\tau/x)$ given by Eq. (6), we obtain

$$h(\tau) = -\frac{1}{2}+\log\,(q_0/\sqrt{2\pi\sigma^2\tau^3})\,. \tag{16}$$

(See Appendix A.)

Finally in order to determine the channel capacity from Eq. (15), $l(\tau)$ should be given. It can easily be guessed that if $l(\tau)=\tau$, the interval of pulses itself, the channel capacity becomes infinity since the rate of information transmission can be made as large as desired by making x large. To suppress very short intervals which arise from a very strong input stimulus, it is reasonable to assume, for example,

$$l(\tau) = \tau+d^2/\tau \tag{17}$$

where d is a constant. The second term may be considered to signify the effect of refractory period during which the neuron hardly responds to the input stimulus. If Eq. (17) is assumed, then Eq. (15) gives

$$C\, e^{4dC} = q_0^2/2e\sigma^2 d^2\,, \tag{18}$$

from which C can be calculated.

It can also be derived that

$$r(\tau) = q_0(2\pi e\sigma^2\tau^3)^{-1/2}\, e^{-C(\tau^2+d^2)/\tau} \tag{19}$$

and

$$p(x) = 2x\, e^{-(1/2)-xq_0/\sigma^2}\Big[\{\beta/(x^2-\alpha)\}^{1/2} I_1(2\beta^{1/2}(x^2-\alpha)^{1/2})\, u(x^2-\alpha)+\delta(x^2-\alpha)\Big];$$
$$x\geq 0 \tag{20}$$

where

$$\alpha = 2\sigma^2 C\,, \quad \beta = (q_0^2-2\sigma^2 d^2 C)/4\sigma^4 \tag{21}$$

and

$\delta(t)$; delta function
$u(t)$; unit step function
$I_1(t)$; modified Bessel function of the first order.

(See Appendix B.) It can easily be seen that $p(x)$ is nonnegative.

In Fig. 1 C is plotted as a function of q_0/σ with d being a parameter. Small fluctuations in the stored charge level correspond to a small σ, and we see in

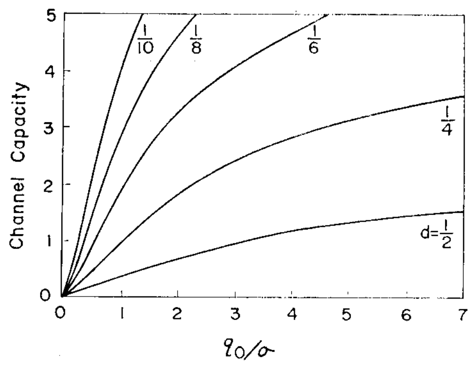

Fig. 1. Channel Capacity of Sensory Neuron Model.

Fig. 1 that C increases as σ decreases as is expected. The effect of d can also be seen in the figure.

The average of the input stimulus is

$$E[x] = q_0/d + 2\sigma^4\beta/Cd^2q_0 \tag{22}$$

and the average of the input power is

$$E[x^2] = q_0^2/d^2 + 3\alpha^4\beta(2Cd+1)/C^2d^2 \tag{23}$$

Thus the input power is automatically limited by the assumption (17).

Neuron as a Sampling Device—As described above the neuron emits an output pulse when stored charge q reaches the threshold. After a pulse is observed no message can be obtained at the output untill the next pulse appears, when the interval of the two pulses can be determined to give the output message. Thus the neuron can be regarded as a special kind of a sampling device, with the sampled value being always constant and equal to the threshold value, but with the sampling instants distributed nonuniformly. The question is whether it is possible to decide, from the intervals of the output pulses, about the stored charge q as a function of time.

Now, it has been assumed that q is set to the initial value just after the emission of a pulse, and therefore q is discontinuous at this instant. In other words, q does not have the band limited property which is essential in sampling theorems. This difficulty, however, can be avoided by introducing a new quantity defined by

$$q^*(t) = q(t) + nq_0\,, \quad (t_{n-1} \leq t < t_n)\,, \tag{24}$$

where n is the number of pulses emitted previously, and t_{n-1} is the instant when the n-th pulse is observed. We assume that the first pulse is emitted at $t=0$. Then

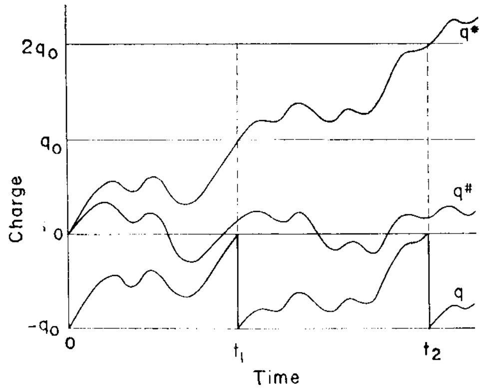

Fig. 2. Relation between q, q^* and $q\#$.

$q^*(0)=0$, $q^*(t_1)=q_0$, $q^*(t_2)=2q_0$, $\cdots$, $q^*(t_n)=nq_0$. The relation between q and q^* is illustrated in Fig. 2.

As seen in Fig. 2, q^* increases indefinitely. Therefore we introduce another quantity $q^\#(t)=q^*(t)-q_0kt$ (k will be properly chosen later.), and assume that $q^\#$ is band limited, that is, it has no frequency component above w cycle per second. Then, from the instants when the pulses are observed, we obtain

$$q^\#(t)\sim q_0\sum_{m=1}^{n}(m-kt_m)\left[\prod_{\substack{a=1\\ \neq m}}^{n}(t-t_m)\prod_{a=1}^{n}(t_m-a/2w)/\left(\prod_{a=1}^{n}(t-a/2w)\prod_{\substack{a=1\\ \neq m}}^{n}(t-t_a)\right]\right.$$
$$(\sin 2\pi wt/\sin 2\pi t_m) \tag{24}$$

if the average number of pulses observed per second is $2w$ or more;[5]

$$n/t_n\geq 2w\,. \tag{25}$$

The approximation (24) is valid in the interval of time when the effect of the finite number of sampling is negligible. If the equality in (25) holds, we see that it is reasonable to choose $k=2w$, since q^* increases $2wq_0$ average per second. If the neuron model is regarded as an integrating device, Ineq. (25) requires that the input had a d.c. level of at least $2wq_0$. The average interval derived from Eq. (6) also leads to that $x\geq 2wq_0$ under the modified interpretation of the condition (25).

3. Ganglion Cell Model And Its Properties

The second type of the model described in this paper is simular to a ganglion cell which acts as a relay station for transmitting signal in the neuronal circuit. As schematically shown in Fig. 3, the cell receives n input pulse trains. The probability density of the interval of the i-th input is denoted $f_i(\tau)$. Each pulse received by the cell is assumed to have a unit charge, which is stored in the cell.

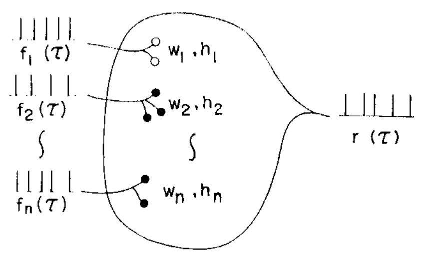

Fig. 3. Ganglion Cell Model.

When the stored charge reaches a certain threshold, a pulse is emitted as the output, and at the same time the stored charge becomes zero. The process is repeated, and thus a pulse train is observed at the output. Furthermore, the i-th input pulse train is assumed to have weight of w_i, or in other words, a pulse of the i-th input has the same effect as it has w_i units of charge. The pulse train may have an inhibitory property, in which case the weight becomes $-w_i$. We signify this property by h_i, that is, $h_i=1$ if the i-th input pulse train is inhibitory, and $h_i=0$ otherwise. The threshold value is denoted m. We are interested in getting the the probability density function, $r(\tau)$, of the output pulse interval of this model. From $r(\tau)$ the output uncertainty can be calculated and compared with the input uncertainty.

The steps to obtain $r(\tau)$ are as follows. As in section 2, only one interval of the output pulses is considered.

i) Find $p_i(k, \tau) \equiv$ the probability that k pulses are received at the i-th input during the time interval $(0, \tau)$. Since

$$p_i(k, \tau) = \int_0^\tau f_i(\tau_1)\, d\tau_1 \int_0^{\tau-\tau_1} f_i(\tau_2)\, d\tau_2 \cdots \int_0^{\tau-\tau_1-\cdots-\tau_{k-1}} f_i(\tau_k)\, d\tau_k \int_{\tau-\tau_1-\cdots-\tau_k}^{\infty} f_i(\tau_{k+1})\, d\tau_{k+1} \tag{26}$$

where τ_j is the length of the j-th interval, $p_i(k, \tau)$ is easily found by using the Laplace transform. Let $\mathcal{L}\{f\}$ denote the Laplace transform of f. From Eq. (26)

$$p_i(k, p) \equiv \mathcal{L}\{p_i(k, \tau)\} = \{f_i(p)\}^k\{1-f_i(p)\}/p\ , \tag{27}$$

where $f_i(p) \equiv \mathcal{L}\{f_i(\tau)\}$. Then

$$p_i(k, \tau) = \mathcal{L}^{-1}\{p_i(k, p)\}\ . \tag{28}$$

ii) Find $g(m, \tau)\, d\tau \equiv$ the probability that the total stored charge is m in the time interval $(\tau, \tau+d\tau)$. It is convenient to use the z transform to get $g(m, \tau)$.

$$g(z, \tau) \equiv z\{g(m, \tau)\} = \prod_{i=1}^{n} p_i(z^{w_i(-1)^{h_i}}, \tau)\ , \tag{29}$$

where $p_i(z, \tau) \equiv z\{p_i(k, \tau)\}$. Hence,

$$g(m, \tau) = z^{-1}\{g(z, \tau)\}\ . \tag{30}$$

iii) Finally $r(m, \tau)\, d\tau \equiv$ the probability of emission of a pulse during the time interval $(\tau, \tau+d\tau)$, can be found from the relation

$$\int_0^\tau r(m, t)\, g(o, \tau-t)\, dt = g(m, \tau)\ . \tag{31}$$

Therefore

$$r(m, p) \equiv \mathcal{L}\{r(m, \tau)\} = g(m, p)/g(o, p) \tag{32}$$

where $g(k, p) \equiv \mathcal{L}\{g(k, \tau)\}$; $k = m, o$. Then the probability density of the output pulse interval

$$r(\tau) \sim r(m, \tau) = \mathcal{L}^{-1}\{r(m, p)\}\ . \tag{33}$$

If there is no inhibitory input, and thus the stored charge is monotonously increasing, step iii) can be bypassed by

$$r(m, \tau) = z^{-1}\left\{\frac{\partial}{\partial \tau} q(z, \tau)/(1-z)\right\} \tag{34}$$

The relative uncertainty of the i-th input and the output is defined as

$$H_i = -\int_0^\infty f_i(\tau) \log f_i(\tau)\, d\tau \tag{35}$$

and

$$H_0 = -\int_0^\infty r(\tau) \log r(\tau)\, d\tau\ , \tag{36}$$

respectively.

Example 1. $f_i(\tau) = \lambda_i\, e^{-\lambda_i \tau} \qquad i = 1, 2, \cdots, n$

For these input pulse trains,

$$g(z, \tau) = e^{(-\mu + \sum_{i=1}^{n} \lambda_i s_i)\tau} \tag{37}$$

where $\mu = \sum_{i=1}^{n} \lambda_i$ and $s_i = z^{-w_i(-1)^{h_i}}$.

If $w_i = 1$ and $h_i = 0$ for all i, we obtain

$$r(m, \tau) = e^{-\mu\tau}\mu(\mu\tau)^{m-1}/(m-1)!\ , \tag{38}$$

$$H_i = -\log \lambda_i + 1\ , \tag{39}$$

$$H_0 = -\log \mu + a(m)\ , \tag{40}$$

where

$$a(1) = 1.0, a(m) = m + \log (m-1)! - \{1/(m-2)!\}\int_0^\infty x^{m-1} \log x \cdot e^{-x} dx;\ m \geq 2, \tag{41}$$

and $a(m)$ can be easily calculated sequentially, for example, $a(2) = 1.577$, $a(3) = 1.848$, $a(4) = 2.023$. Since $\mu = \sum_{i=1}^{n} \lambda_i$ the output uncertainty can be less than the input uncertainty, signifying the effect of the summation and intensifying function of a neuron.

Example 2. $f_i(\tau) = \lambda_i^2 \tau\, e^{-\lambda_i \tau}$

For these input pulse trains

$$g(z, \tau) = \prod_{i=1}^{n} (s_i^{-1/2} \sinh \lambda_i \tau s_i^{1/2} + \cosh \lambda_i \tau s_i^{1/2})\, e^{-\lambda_i \tau}\ . \tag{42}$$

In case $w_i=1$, $h_i=0$ and $\lambda_i=\lambda$ for all i,

$$r(z,\tau) = \lambda n\, e^{-\lambda n\tau} z^{1/2} \sinh \lambda\tau z^{1/2}(z^{-1/2}\sinh \lambda\tau z^{1/2} + \cosh \lambda\tau z^{1/2})^{n-1} . \tag{43}$$

If n is small $r(m,\tau)$ can be derived as given in Appendix C.

Appendix A

Substituting Eq. (6) into Eq. (12), we get the following integral equation.

$$\int_0^\infty p(\tau/x) \log \{q_0(2\pi\sigma^2\tau^3)^{-1/2} e^{-(q_0-x\tau)^2/2\sigma^2\tau}\} d\tau = \int_0^\infty p(\tau/x)\, h(\tau)\, d\tau \tag{A1}$$

The left-hand side of the equation can be rewritten as

$$\int_0^\infty p(\tau/x) \log \{q_0(2\pi\sigma^2\tau^3)^{-1/2}\} d\tau - (q_0^2/2\sigma^2)\int_0^\infty (1/\tau)\, p(\tau/x)\, d\tau$$
$$+ xq_0/\sigma^2 - (x^2/2\sigma^2)\int_0^\infty \tau p(\tau/x)\, d\tau$$
$$= \int_0^\infty p(\tau/x) \log \{q_0(2\pi\sigma^2\tau^3)^{-1/2}\} d\tau - \frac{1}{2} = \int_0^\infty p(\tau/x) \left\{\log q_0(2\pi\sigma^2\tau^3)^{-1/2} - \frac{1}{2}\right\} d\tau \tag{A2}$$

Thus Eq. (16) follows.

Appendix B

From Eq. (9) and Eq. (19) we obtain

$$\int_0^\infty p(x)\, e^{-(q_0-x\tau)^2/2\sigma^2\tau} dx = e^{-(1/2)-C(\tau^2+d^2)/\tau} \tag{A3}$$

Rewriting,

$$\int_0^\infty p(x)\, e^{q_0 x/\sigma^2} e^{-\tau x^2/2\sigma^2} dx = e^{-(1/2)-C(\tau^2+d^2)/\tau + q_0^2/2\sigma^2\tau} \tag{A4}$$

This integral equation can be conveniently solved by utilizing a Laplace transform pair as follows. Let a Laplace transform pair be given by

$$\int_0^\infty f(t)\, e^{-st} dt = F(s) . \tag{A5}$$

Putting $t=x^2$ and $s=\tau/2\sigma^2$, we obtain

$$\int_0^\infty 2xf(x^2)\, e^{-\tau x^2/2\sigma^2} dx = F(\tau/2\sigma^2) . \tag{A6}$$

Comparing Eq. (A6) with Eq. (A4), we see that, if we decide $F(\tau/2\sigma^2)$ from the right-hand side of Eq. (A4) and then $F(s)$, we can get $f(t)$ by using a Laplace transform table. Once $f(t)$ is obtained,

$$p(x) = 2xf(x^2)\, e^{-q_0 x/\sigma^2}; \qquad x \geq 0\,. \tag{A7}$$

From Eq. (A4) we get

$$F(s) = e^{-(1/2)-2\sigma^2 Cs-(2\sigma^2 d^2 C-q_0^2)/4\sigma^4 s} \tag{A8}$$

and then

$$f(t) = e^{-1/2}\Big[\{\beta/(t-\alpha)\}^{1/2} I_1(2\beta^{1/2}(t-\alpha)^{1/2})\, u(t-\alpha) + \delta(t-\alpha)\Big]. \tag{A9}$$

Thus Eq. (20) follows.

Appendix C

$n = 1;$

$$r(m,\, \tau) = \lambda\, e^{-\lambda\tau} (\lambda\tau)^{2m-1}/(2m-1)\,!$$

$n = 2;$

$$r(m,\, \tau) = \lambda\, e^{-2\lambda\tau} \frac{(2\lambda\tau)^{2m-1}}{(2m-1)\,!}\left(1+\frac{\lambda\tau}{2m}\right)$$

$n = 3;$

$$r(m,\, \tau) = \frac{3\lambda}{4}\, e^{-3\lambda\tau} \frac{(\lambda\tau)^{2m-1}}{(2m-1)\,!}\left\{3^{2m-1}+1+\frac{2(3^{2m}-1)\,\lambda\tau}{2m} + \frac{3(3^{2m}-1)(\lambda\tau)^2}{2m(2m+1)}\right\}$$

$n = 4;$

$$r(m,\, \tau) = \frac{\lambda}{2}\, e^{-4\lambda\tau} \frac{(\lambda\tau)^{2m-1}}{(2m-1)\,!}\left\{4^{2m-1}+2^{2m}+\frac{3\cdot 4^{2m}\lambda\tau}{2m} + \frac{3(4^{2m+1}-2^{2m+2})(\lambda\tau)^2}{2m(2m+1)} + \frac{(4^{2m+2}-2^{2m+4})(\lambda\tau)^3}{2m(2m+1)(2m+2)}\right\}$$

$n = 5;$

$$r(m,\, \tau) = \frac{5\lambda}{16}\, e^{-5\lambda\tau} \frac{(\lambda\tau)^{2m-1}}{(2m-1)\,!}\left\{5^{2m-1}+3^{2m}+2 + \frac{4(5^{2m}+3^{2m}-2)\,\lambda\tau}{2m} + \frac{6(5^{2m+1}-3^{2m+1}-2)(\lambda\tau)^2}{2m(2m+1)} + \frac{4(5^{2m+2}-3^{2m+3}+2)(\lambda\tau)^3}{2m(2m+1)(2m+2)} + \frac{5(5^{2m+2}-3^{2m+3}+2)(\lambda\tau)^4}{2m(2m+1)(2m+2)(2m+3)}\right\}$$

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