A STOCHASTIC MODEL OF THE EARLY EVENTS OF THE TRANSDUCTION PROCESS IN A SINGLE OLFACTORY RECEPTOR NEURON SUBJECT TO PATHOLOGICAL ATTACKS

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5.1 Introduction

Mathematical modelling of coding of odour intensity has been a subject of intensive research in the recent past. The early events which take place in the transduction process of olfaction are (a) the binding of odor molecules with the olfactory receptor neurons (ORN’s) situated in the first layer of the olfactory system, (b) the electrophysiological processes that take place in these neurons and (c) the triggering of action potentials by the neurons. Experimental and modeling investigations have been carried out very extensively in the past to understand the implications of these events in the context of the coding of odor intensity in the pathways of the transduction process (see for example Van Drongelen [99], Sicard and Holley [81], Lancet [49], Anholt [9], Buck and Axel [19], Carlson [20], Lansky and Rospars [51], Lansky and Rospars [52], Kaissling [41], Rospars et al. [76], Bargman [13], Vermeulen et al. [100], and Lansky and Rospars [53]). These investigations aim primarily to explain the role of the family of ORN’s in enabling the olfactory system to recognize and discriminate thousands of odoriferous molecules. The experimental studies have succeeded in isolating the genes encoding odorant receptors which have expression restricted to the olfactory epithelium and also in recording intra-cellular events occurring in the first-layer of the olfactory system. On the other hand, the mathematical studies have provided models of the neuro-receptors based upon the experimental findings and these models account with greater satisfaction the odorant-dependent stimulation and concentration-dependent coding. Only a very few research articles have appeared in the literature on mathematical modeling and analysis of the transduction process in the olfactory receptor site (see Lansky and Rospars [51], Lansky and Rospars [52], Lansky and Rospars [53], Rospars et al. [76], Vermeulen et al. [100], Lansky and Getz [50], Rospars et al. [77], Belmabrouk et al. [15] and Grémiaux et al. [32]). Lansky and Getz [50] have obtained the steady-state characteristics of two basic models of signal processing in the olfactory receptor neurons under the assumption that the population of receptors is not homogenous and is characterized by different activation/deactivation rates. Rospars et al. [77] have modelled the early steps of transduction in insect olfactory receptor neurons taking into account the membrane cascade involving the interaction of receptors, G-proteins and effector enzymes. They have investigated the evolutions in time of these species in response to
single pulse stimulation of various intensities. Belmabrouk et al. [15] have studied, by using a computational modeling, the interaction of cellular and network mechanisms for efficient pheromone coding in moths and shown that they exhibit a multiphasic response of inhibition-excitation-inhibition to coding efficiency. Recently, Grémiaux et al. [32] have proposed a statistical model of the population of first-order olfactory receptor neurons and analyzed the peak firing rate and latency of the message sent to the brain by the whole ORN population at different stimulus intensities. In the above papers, the first events in the process of odorant-ORN interaction are identified as occupation and activation of the receptor sites by the odor molecules and the process of generation of action potential is studied by considering stochastic processes describing the occurrence of the first events and observing that the receptor potential depends on the number of activated receptor sites of the ORN. To be specific, in the paper of Lansky and Rospars [52], it has been assumed that an odor molecule can attach itself to an unoccupied receptor site rendering it an occupied site. If the attached odor molecule is strong enough, then the site becomes activated; otherwise the site becomes unoccupied. It is also assumed in their model that an activated site can become occupied site from the activation site. Besides all these events, one important feature which inhibits the transduction process is the olfactory impairment which is a common feature in several species. Turetsky et al. [97] have identified olfactory receptor neuron dysfunction in persons expressing Schizophrenia. It is also stated in their findings that impairments in odor detection and odor identification are present early in the course of illness and among those at risk for the disorder. To our knowledge, no mathematical models are available on the study of the early events that occur in the transduction process in olfactory system subject to pathological attacks. Accordingly, in this chapter, we extend the stochastic model of Lansky and Rospars [52] by including the possibility that some kind of pathological attacks occur as a stochastic point process whose events convert all occupied and activated sites of olfactory receptor neurons as unoccupied sites.

The organization of the chapter is as follows.

In section 5.2, we formulate the stochastic model of the transduction process in a single ORN. In section 5.3, we derive a system of differential-difference equations for
5.2. A two-stage Stochastic Model of Activation

We assume that there is only one odorant substance and the odor molecules interact with the receptor sites of the odorant-sensitive dendrite of a single ORN. Let there be a finite number \( n \) of receptor sites (receptor proteins) situated along the cylindrical dendrite. The olfactory receptor neuron suffers attacks at an exponential rate \( \eta \), each attack renders instantaneously all receptor sites as unoccupied sites. At time \( t \), each receptor site is exactly in one of the following states:

(i) **unoccupied** state with no odor molecule attached to it;

(ii) **occupied** state with an odor molecule attached to it;

(iii) **activated** state;

Let \( U(t) \) be the number of unoccupied receptor sites, \( O(t) \) be the number of occupied receptor sites and \( A(t) \) be the number of activated receptor sites on the ORN at time \( t \). The stochastic processes \( U(t), O(t) \) and \( A(t) \) evolve according to the following conditions:

(i) An unoccupied site existing at time \( t \) becomes occupied in the interval \( (t, t + \Delta) \) with probability \( \lambda \Delta + o(\Delta) \);

(ii) An occupied site existing at time \( t \) becomes activated in \( (t, t + \Delta) \) with probability
5.3 The Probability Structure of \((O(t), A(t))\)

Let the vector process \(\zeta(t)\) be defined by

\[
\zeta(t) = (O(t), A(t)).
\]  

(5.3.1)

We assume that the ORN is healthy at time \(t = 0\) and all the \(n\) sites are unoccupied at time \(t = 0\). Therefore, we have

\[
O(0) = 0, A(0) = 0.
\]  

(5.3.2)
5.3. **The Probability Structure of** \((O(t), A(t))\)

To study the transient behaviour of the ORN, we define the joint probability function of the vector stochastic process \(\zeta(t)\):

\[
p(i, j; t) = \mathbb{P}(O(t) = i, A(t) = j), i, j = 0, 1, 2, ..., n; i + j = n - U(t). \tag{5.3.3}
\]

Define

\[
Q(t) = \sum_{j=1}^{n} p(0, j, t) + \sum_{i=1}^{n} \sum_{j=0}^{n-i} p(i, j, t) = 1 - p(0, 0, t). \tag{5.3.4}
\]

Using the laws of probability, we obtain

**case (i):** \(i = 0, j = 0\)

\[
p(0, 0; t + \Delta) = p(0, 0; t)[1 - n\lambda\Delta] + p(1, 0; t)\mu\Delta + p(0, 1; t)\theta\Delta + \eta Q(t)\Delta + o(\Delta). \tag{5.3.5}
\]

**case (ii):** \(i = n, j = 0\)

\[
p(n, 0; t + \Delta) = p(n, 0; t)[1 - (n(\omega + \mu) + \eta)\Delta]
\]

\[
+ p(n - 1, 0; t)\lambda\Delta + p(n - 1, 1; t)\nu\Delta + o(\Delta); \tag{5.3.6}
\]

**case (iii):** \(i = 0, j = n\)

\[
p(0, n; t + \Delta) = p(0, n; t)[1 - (n\theta + \nu) + \eta]\Delta] + p(1, n - 1; t)\omega\Delta; \tag{5.3.7}
\]

**case (iv):** \(1 \leq i \leq n - 1, j = 0\)

\[
p(i, 0; t + \Delta) = p(i, 0; t)[1 - (n - i)\lambda + i(\omega + \mu) + \eta]\Delta]
\]

\[
+ p(i - 1, 0; t)(n - i + 1)\lambda\Delta
\]
\[ +p(i + 1, 0; t)(i + 1)\mu\Delta + p(i, 1; t)\theta\Delta + p(i - 1, 1; t)\nu\Delta + o(\Delta), \ i = 1, 2, ..., n - 1; \quad (5.3.8) \]

**case (v):** \( i = 0, 1 \leq j \leq n - 1 \)

\[ p(0, j; t + \Delta) = p(0, j; t)[1 - \{(n - j)\lambda + j(\theta + \nu) + \eta\eta\Delta] + p(1, j; t)\mu\Delta \]

\[ +p(1, j - 1; t)\omega\Delta + p(0, j + 1; t)(j + 1)\theta\Delta + o(\Delta), \ j = 1, 2, ..., n - 1; \quad (5.3.9) \]

**case (vi):** \( i \geq 1, j \geq 1, i + j = n \)

\[ p(i, j; t + \Delta) = p(i, j; t)[1 - \{i(\omega + \mu) + j(\theta + \nu) + \eta\eta\Delta] \]

\[ +p(i - 1, j; t)(n - i - j + 1)\lambda\Delta + p(i + 1, j - 1; t)(i + 1)\omega\Delta \]

\[ +p(i - 1, j + 1; t)(j + 1)\nu\Delta + o(\Delta), \ i, j = 1, 2, ..., n - 1; \ i + j = n; \quad (5.3.10) \]

**case (vii):** \( 1 \leq i \leq n - 2, 1 \leq j \leq n - 2, 2 \leq i + j \leq n - 1 \)

\[ p(i, j; t + \Delta) = p(i, j; t)[1 - \{(n - i - j)\lambda + i(\omega + \mu) + j(\theta + \nu) + \eta\eta\Delta] \]

\[ +p(i - 1, j; t)(n - i - j + 1)\lambda\Delta + p(i + 1, j - 1; t)(i + 1)\omega\Delta \]

\[ +p(i + 1, j; t)(i + 1)\mu\Delta + p(i, j + 1; t)(j + 1)\theta\Delta \]

\[ +p(i - 1, j + 1; t)(j + 1)\nu\Delta + o(\Delta), \ i, j = 1, 2, ..., n - 2; \ 2 \leq i + j \leq n - 1; \quad (5.3.11) \]

From (5.3.5) to (5.3.11), we obtain the following system of differential-difference equations:

\[ \frac{dp(i, j; t)}{dt} = -(n - i - j)\lambda + i(\omega + \mu) + j(\theta + \nu) + \eta)p(i, j; t) \]
5.3. The Probability Structure of \((O(t), A(t))\)

\[
+p(i - 1, j; t)(n - i - j + 1)\lambda + p(i + 1, j - 1; t)(i + 1)\omega \\
+p(i + 1, j; t)(i + 1)\mu + p(i, j + 1; t)(j + 1)\theta \\
+p(i - 1, j + 1; t)(j + 1)\nu, \ i, j = 1, 2, ..., n - 2; \ 2 \leq i + j \leq n - 1 ;
\]

\[
\frac{dp(i, n - i; t)}{dt} = -(\omega + \mu) + (n - i)(\theta + \nu) + \eta)p(i, n - i; t) \\
+p(i - 1, n - i; t)\lambda + p(i + 1, n - i - 1; t)(i + 1)\omega \\
+p(i - 1, n - i + 1; t)(n - i + 1)\nu, \ i = 1, 2, ..., n - 1 ;
\]

\[
\frac{dp(i, 0; t)}{dt} = -\eta\lambda + i(\omega + \mu) + \eta)p(i, 0; t) \\
+p(i - 1, 0; t)(n - i + 1)\lambda + p(i + 1, 0; t)(i + 1)\mu \\
+p(i, 1; t)\theta + p(i - 1, 1; t)\nu, \ i = 1, 2, ..., n - 1 ;
\]

\[
\frac{dp(0, j; t)}{dt} = -(n - j)\lambda + j(\theta + \nu) + \eta)p(0, j; t) + p(1, j; t)\mu \\
+p(1, j - 1; t)\omega + p(0, j + 1; t)(j + 1)\theta, \ j = 1, 2, ..., n - 1 ;
\]

\[
\frac{dp(n, 0; t)}{dt} = -\eta p(n, 0; t) + p(n - 1, 0; t)\lambda + p(n - 1, 1; t)\nu ;
\]

\[
\frac{dp(0, n; t)}{dt} = -(n\lambda + \eta)p(0, n; t) + p(1, n - 1; t)\omega ;
\]

\[
\frac{dp(0, 0; t)}{dt} = -(n\lambda + \eta)p(0, 0; t) + p(1, 0; t)\mu + p(0, 1; t)\theta + \eta.
\]

Using (5.3.12) to (5.3.18), we now proceed to obtain the time-dependent expression for the mean-structure of the process \(\zeta(t)\).
5.4 The Probability Generating Function $G(u, v, t)$

We define the probability generating function $G(u, v, t)$ as follows:

$$G(u, v, t) = e^{uO(t) + vA(t)} = \sum_{i=0}^{n} \sum_{j=0}^{n-i} u^i v^j p(i, j, t). \quad (5.4.1)$$

We have assumed that, at time $t = 0$, all the $n$ receptor sites are healthy and unoccupied (i.e., the ORN is in up state and $O(0) = 0, A(0) = 0$). Then, we have

$$G(u, v, 0) = \sum_{i=0}^{n} \sum_{j=0}^{n-i} u^i v^j p(i, j, 0) = p(0, 0, 0) = 1, \quad (5.4.2)$$

$$G(1, 1, t) = \sum_{i=0}^{n} \sum_{j=0}^{n-i} p(i, j, t) = 1. \quad (5.4.3)$$

Differentiating $G(u, v; t)$ partially with respect to $t$, we get

$$\frac{\partial G(u, v; t)}{\partial t} = \sum_{i=0}^{n} \sum_{j=0}^{n-i} u^i v^j \frac{dp(i, j; t)}{dt}$$

$$= u^n \frac{dp(n, 0; t)}{dt} + \sum_{j=0}^{n} v^j \frac{dp(0, j; t)}{dt} + \sum_{i=1}^{n-1} u^i \frac{dp(i, 0; t)}{dt} + \sum_{j=1}^{n-1} v^j \frac{dp(0, j; t)}{dt}$$

$$+ \sum_{i=1}^{n-1} u^i v^{n-i} \frac{dp(i, n - i; t)}{dt} + \sum_{i=1}^{n-2} n-1-i \frac{dp(i, j; t)}{dt}. \quad (5.4.4)$$

Using (5.3.12) to (5.3.18) in (5.4.4) and simplifying, we obtain

$$\frac{\partial G(u, v; t)}{\partial t} + \left[ \lambda(u^2 - u) + \mu(u - 1) + \omega(u - v) \right] \frac{\partial G(u, v; t)}{\partial u}$$
\[ +[\lambda(\nu - \nu) + \nu(\nu - \nu) + \theta(\nu - 1)] \frac{\partial G(u, v; t)}{\partial v} = [n\lambda(u - 1) - \eta]G(u, v; t) + \eta. \]  

(5.4.5)

Using (5.4.5), we can obtain the mean-structure of \( \zeta(t) \). This we do in the next section.

### 5.5 The Mean-Structure of \( \zeta(t) \)

The first-order moments of \( \zeta(t) \) can be found from (5.4.1). We define

\[
M_U(t) = \mathcal{E}[U(t)],
\]

(5.5.1)

\[
M_O(t) = \mathcal{E}[O(t)],
\]

(5.5.2)

\[
M_A(t) = \mathcal{E}[A(t)].
\]

(5.5.3)

The initial condition for these moments are given by

\[ M_U(0) = n, M_O(0) = 0, M_A(0) = 0. \]

(5.5.4)

Differentiating (5.4.5) with respect to \( u \) and setting \( u = 1, v = 1 \), we get

\[
\frac{dM_O(t)}{dt} + (\lambda + \omega + \mu + \eta)M_O(t) + (\lambda - \nu)M_A(t) = n\lambda.
\]

(5.5.5)

Differentiating (5.4.5) with respect to \( v \) and setting \( u = 1, v = 1 \), we get

\[
\frac{dM_A(t)}{dt} - \omega M_O(t) + (\theta + \nu + \eta)M_A(t) = 0.
\]

(5.5.6)

Denoting the Laplace Transforms of \( M_O(t) \) and \( M_A(t) \) by \( M_O^*(s) \) and \( M_A^*(s) \) respectively, we obtain from (5.5.5) and (5.5.6) the following:

\[
(s + \lambda + \omega + \mu + \eta)M_O^*(s) + (\lambda - \nu)M_A^*(s) = \frac{n\lambda}{s},
\]

(5.5.7)
\[ -\omega M'_O(s) + (s + \theta + \nu + \eta)M'_A(s) = 0. \] (5.5.8)

Solving (5.5.7) and (5.5.8), we get

\[ M'_O(s) = \frac{n\lambda(s + \theta + \nu + \eta)}{s[(s + \theta + \nu + \eta)(s + \lambda + \omega + \mu + \eta) + \omega(\lambda - \nu)]}, \] (5.5.9)

\[ M'_A(s) = \frac{n\lambda \omega}{s[(s + \theta + \nu + \eta)(s + \lambda + \omega + \mu + \eta) + \omega(\lambda - \nu)]}, \] (5.5.10)

Inversion of (5.5.9) and (5.5.10) yield explicitly

\[ M_O(t) = n\lambda \left[ \frac{\theta + \nu + \eta}{ab} + \frac{a + \theta + \nu + \eta}{a(a - b)} e^{at} - \frac{b + \theta + \nu + \eta}{b(a - b)} e^{bt} \right], \] (5.5.11)

\[ M_A(t) = n\lambda \omega \left[ \frac{1}{ab} + \frac{1}{a(a - b)} e^{at} - \frac{1}{b(a - b)} e^{bt} \right], \] (5.5.12)

where \( a \) and \( b \) are the roots of the quadratic equation:

\[ x^2 + (\lambda + \omega + \mu + \theta + \nu + 2\eta)x + (\theta + \nu + \eta)(\lambda + \omega + \mu + \eta) + \omega(\lambda - \nu) = 0. \] (5.5.13)

We obtain the steady-state means as follows:

\[ M_O(\infty) = \lim_{s \to 0} s M'_O(s) = \frac{n\lambda(\theta + \nu + \eta)}{\xi}, \] (5.5.14)

\[ M_A(\infty) = \lim_{s \to 0} s M'_A(s) = \frac{n\lambda \omega}{\xi}, \] (5.5.15)

where

\[ \xi = \lambda \nu + \lambda \omega + \mu \nu + \theta(\lambda + \mu + \omega) + \eta(\lambda + \mu + \omega + \nu + \theta + \eta). \]

Setting \( \theta = 0 \) and \( \eta = 0 \) in (5.5.14) and (5.5.15), we obtain

\[ M_O(\infty) = \frac{n\lambda \nu}{\lambda \nu + \lambda \omega + \mu \nu}, \] (5.5.16)
5.6. The Correlation Analysis

We denote the second moments as follows:

\[ M^{(2)}_O(t) = \mathcal{E}[O(t)[O(t) - 1]], \]
\[ M^{(2)}_{OA}(t) = \mathcal{E}[O(t)A(t)], \]
\[ M^{(2)}_A(t) = \mathcal{E}[A(t)[A(t) - 1]]. \]

Differentiating (5.4.5) partially with respect to \( u \), we get

\[
\frac{\partial^2 G}{\partial t \partial u} = [n\lambda(u - 1) - \eta] \frac{\partial G}{\partial u} + n\lambda G \\
-\left[ \omega(u - v) + (\lambda u + \mu)(u - 1) \right] \frac{\partial^2 G}{\partial u^2} - \left[ \omega + 2\lambda u - \lambda + \mu \right] \frac{\partial G}{\partial u} \\
-\left[ \lambda v(u - 1) + \theta(v - 1) + \nu(v - u) \right] \frac{\partial^2 G}{\partial u \partial v} - [\lambda v - \nu] \frac{\partial G}{\partial v}. \tag{5.6.1}
\]

Differentiating (5.4.5) partially with respect to \( v \), we get

\[
\frac{\partial^2 G}{\partial t \partial v} = [n\lambda(u - 1) - \eta] \frac{\partial G}{\partial v} \\
-\left[ \omega(u - v) + (\lambda u + \mu)(u - 1) \right] \frac{\partial G(u, v; t)}{\partial u \partial v} + \omega \frac{\partial G(u, v; t)}{\partial u} \\
-\left[ \lambda v(u - 1) + \theta(v - 1) + \nu(v - u) \right] \frac{\partial^2 G}{\partial v^2} - [\lambda(u - 1) + \theta + \nu] \frac{\partial G}{\partial v}. \tag{5.6.2}
\]
Differentiating (5.6.1) with respect to $u$ and putting $u = v = 1$, we obtain

$$M_O^{(2)}(t) = -(2\lambda + 2\mu + 2\omega + \eta)M_O^{(2)}(t) + 2(n - 1)\lambda M_O(t) - 2(\lambda - \nu)M_{OA}^{(2)}(t). \quad (5.6.3)$$

Differentiating (5.6.1) with respect to $v$ and putting $u = v = 1$, we obtain

$$M_{OA}^{(2)}(t) = -(\lambda + \mu + \omega + \nu + \theta + \eta)M_{OA}^{(2)}(t) + \omega M_O^{(2)}(t) - (\lambda - \nu)M_A^{(2)}(t) + (n - 1)\lambda M_A(t). \quad (5.6.4)$$

Differentiating (5.6.2) with respect to $v$ and putting $u = v = 1$, we obtain

$$M_A^{(2)}(t) = -(2\theta + 2\gamma + \eta)M_A^{(2)}(t) + 2\omega M_{OA}^{(2)}(t). \quad (5.6.5)$$

From (5.6.3)-(5.6.5), we obtain the steady-state equations

$$(2\lambda + 2\mu + 2\omega + \eta)M_O^{(2)}(\infty) + 2(\lambda - \nu)M_{OA}^{(2)}(\infty) = \frac{2n(n - 1)\lambda^2}{\xi}(\theta + \nu + \eta), \quad (5.6.6)$$

$$-2\omega M_{OA}^{(2)}(\infty) + (2\theta + 2\nu + \eta)M_A^{(2)}(\infty) = 0, \quad (5.6.7)$$

$$-\omega M_O^{(2)}(\infty) + (\lambda + \mu + \omega + \nu + \theta + \eta)M_{OA}^{(2)}(\infty) + (\lambda - \nu)M_A^{(2)}(\infty) = \frac{n(n - 1)\lambda^2}{\xi} \omega. \quad (5.6.8)$$

Solving (5.6.6)-(5.6.8), we get the steady-state second-order moments

$$M_O^{(2)}(\infty) = \frac{\Delta_1}{\Delta}, \quad (5.6.9)$$

$$M_{OA}^{(2)}(\infty) = \frac{\Delta_2}{\Delta}, \quad (5.6.10)$$

$$M_A^{(2)}(\infty) = \frac{\Delta_3}{\Delta}. \quad (5.6.11)$$
where

\[ \Delta = -(\lambda + \mu + \omega + \nu + \theta + \eta)[4(\lambda \nu + \lambda \omega + \mu \nu) + 4\theta(\lambda + \mu + \omega) + 2\eta(\lambda + \mu + \omega + \nu + \theta + \eta^2)], \]

\[ \Delta_1 = -\frac{2n(n-1)\lambda^2}{\xi}[\omega(\lambda - \nu) + (\lambda + \mu + \omega + \nu + \theta + \eta)(\theta + \nu + \eta)(2\theta + 2\nu + \eta)], \]

\[ \Delta_2 = -\frac{n(n-1)\omega^2}{\xi}(2\lambda + 2\mu + 2\omega + 2\nu + 2\theta + 3\eta)(2\nu + 2\theta + \eta), \]

\[ \Delta_3 = -\frac{2n(n-1)\omega^2}{\xi}(2\lambda + 2\mu + 2\omega + 2\nu + 2\theta + 3\eta). \]

Setting \( \theta = \eta = 0 \), we get

\[ M^{(2)}_O(\infty) = \frac{n(n-1)\lambda^2 \nu^2}{(\lambda \nu + \lambda \omega + \mu \nu)^2}, \quad (5.6.12) \]

\[ M^{(2)}_{OA}(\infty) = \frac{n(n-1)\lambda \nu}{(\lambda \nu + \lambda \omega + \mu \nu)^2}, \quad (5.6.13) \]

\[ M^{(2)}_A(\infty) = \frac{n(n-1)\lambda^2 \omega^2}{(\lambda \nu + \lambda \omega + \mu \nu)^2}. \quad (5.6.14) \]

From (5.6.12)-(5.6.14), we get

\[ \text{Var}[O(\infty)] = \frac{n\lambda \nu}{\lambda \nu + \lambda \omega + \mu \nu} \left[ 1 - \frac{\lambda \nu}{\lambda \nu + \lambda \omega + \mu \nu} \right], \quad (5.6.15) \]

\[ \text{Cov}[O(\infty)A(\infty)] = -\frac{n\lambda^2 \omega \nu}{(\lambda \nu + \lambda \omega + \mu \nu)^2}, \quad (5.6.16) \]

\[ \text{Var}[A(\infty)] = \frac{n\lambda \omega}{\lambda \nu + \lambda \omega + \mu \nu} \left[ 1 - \frac{\lambda \omega}{\lambda \nu + \lambda \omega + \mu \nu} \right]. \quad (5.6.17) \]

The results (5.6.15)-(5.6.17) are in agreement with that of Rospars and Lansky [52]. The steady-state coefficient of correlation between \( O(\infty) \) and \( A(\infty) \) is given by

\[ \rho(O(\infty), A(\infty)) = -\frac{\sqrt{\omega}(\lambda \nu + \lambda \omega + \mu \nu)}{\sqrt{(\lambda + \mu)(\lambda \omega + \mu \nu)}}. \quad (5.6.18) \]
5.7 A Numerical Illustration

In this section, we consider a numerical illustration to highlight the impact of the occurrence of pathological attacks on the coding of odour intensity. Let $s$ be the strength of the odour. Modelling the rate $\lambda$ of arrival of odour molecules in the form $\lambda = e^s - 1$, we get $\lambda = 1.6670$ when the strength $s = 0.511$. We assume the following values for the other parameters of the transduction process:

$$n = 100, \mu = 0.12, \nu = 0.3, \omega = 0.22, \theta = 0.1, \eta = 0.2.$$

We compute the mean values of $M_O(t)$ and $M_A(t)$ by varying $t$ and tabulate them in table 6.1. Fig. 6.1 and Fig. 6.2 provide the comparison between the process olfaction with and without pathological attacks. Both the figures 6.1 and 6.2 exhibit that the coding is delayed when pathological attacks are present.

Further to highlight the effect of pathological attacks on the mean number of activated sites, we increase the rate $\eta$ of occurrence of the pathological attacks from 0 to 1 and tabulate the mean number of the activated sites in table 6.2 for time points ranging from 0 to 2. For $\eta = 0, 0.2, 0.4, 0.6, 0.8, 1.0$, we plot $M_A(t)$ against $t$ in figure 6.3 and observe that as the rate of occurrence of the pathological attacks increases, the mean number of the activated sites decreases in value.
5.7. A Numerical Illustration

Table 5.1: Impact of pathological attacks on coding of odour intensity

<table>
<thead>
<tr>
<th>$t$</th>
<th>$M_O(t)$ $\eta = 0$</th>
<th>$M_O(t)$ $\eta = 0.2$</th>
<th>$M_A(t)$ $\eta = 0$</th>
<th>$M_A(t)$ $\eta = 0.2$</th>
</tr>
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Table 5.2: Effect of pathological attacks on activation

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Figure 5.1: Comparison of the mean number of occupied sites with and without pathological attacks during the time period 0 to 2

Figure 5.2: Comparison of the mean number of activated sites with and without pathological attacks during the time period 0 to 2
Figure 5.3: Effect of pathological attacks on activation