

A DYNAMIC MODEL OF KEY FEATURE EXTRACTION: THE EXAMPLE OF OLFACTION

II - Theoretical analysis by a Boltzmann-type distribution of attractors

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ABSTRACT

This paper presents theoretical results derived in the analysis of the model proposed in part I for the olfactory pathway. Some of these results are model-specific, others are of more generic interest. The latter include the description of the dynamics in the presence of noise as a two-step Markov process: this leads to the derivation of a Boltzmann-type distribution of the steady-state probabilities of attractors for a discrete-time dynamic systems with cycles of maximum length two. This leads to a clear understanding of the phenomena described from simulations in part I, including the emergence of three different noise regimes. More specific of the model is the description of the deterministic dynamics and the mathematical justification of the coding properties emerging from the prevalent lateral inhibition in the model.

1. INTRODUCTION

In this article, we report a generic result, which was established in the course of the theoretical analysis of the network described in part I of the paper: for a discrete-time network of binary neurons with fixed points or limit cycles of length 2, the steady-state probabilities of the attractors of the dynamics are governed by a Boltzmann-type distribution, where the traditional energy function is replaced by a two-step Lyapunov function. This approach allows us to analyze fully the limit behavior of the model in the presence of noise, and to understand the emergence of the noise regimes described in part I.

In addition, this article provides a comprehensive analysis of the dynamics of the model in the absence of noise.

For the convenience of the reader who is interested in the model itself, the organization of this article follows that of part I: in section 2, we first analyze the behavior of the model in the noise-free case, with emphasis on the determination of the stable glomerular images, i.e. the attractor of the dynamics; the basic tool that is used throughout the paper, the Lyapunov function of the model, is defined. The behavior in the presence of noise is subsequently analyzed in terms of Markov chains (section 3); the stationary probability distribution of pairs of consecutive states is derived, and the Boltzmann-type distribution of the attractors is established. The behavior of the model is also investigated as a function of the noise level, and the proof of the emergence of three different noise regimes is presented. The reader who is only interested in the derivation and application of the Boltzmann-type distribution of attractors may skip sections 2.2 to 2.5, which are essentially model-specific, and focus on section 3 and on the appendix.

2. DYNAMICS OF THE MODEL IN THE ABSENCE OF SYNAPTIC NOISE

2.1 Update rule and the Lyapunov function

As described in the previous paper, the model under investigation is a recurrent fully connected network of binary units, with unit delays and parallel (synchronous) discrete-time update scheme (Little dynamics). Each unit receives excitatory, time-varying inputs. In the absence of synaptic noise, the update rule is given by

$$g_i(t+1) = H[h_i(t)] = H\left[R_i(t) + \sum_{j=1}^N w_{ij} g_j(t) - \frac{1}{2}\right] \quad (1)$$

where w_{ij} are the synaptic weights, $R_i(t)$ are the inputs, and H is the Heaviside step. In the present model, all weights are equal to -1, and all inputs $R_i(t)$ are positive. Thus, the quantity $R_i(t)-1/2$ can be regarded as the (time-varying) threshold of unit i ; the term $1/2$ guarantees that the argument of the Heaviside distribution is always non-zero. Since the network is fully recurrent, the state vector of the model at time t is the vector $[g_1(t), g_2(t), \dots, g_N(t)]^T$. $h_i(t)$ is termed the "local field" at neuron i .

In order to get a better insight into the dynamics of the network, it is useful to introduce a Lyapunov function. A straightforward generalization of the Lyapunov function as introduced by Goles (Goles et al., 1985) is

$$L(t+1, t) = -\sum_{i,j} w_{ij} g_i(t+1) g_j(t) - \sum_i \left(R_i(t) - \frac{1}{2}\right) g_i(t+1) - \sum_i \left(R_i(t) - \frac{1}{2}\right) g_i(t)$$

where the states at times $t+1$ and t are connected by the update rule (1).

We prove in the following that, if the matrix of synaptic weights is symmetric, then the Lyapunov function is a non-increasing function of time if the inputs $\{R_i\}$ are constant: $L(t+2, t+1) \leq L(t+1, t)$.

The increment of the Lyapunov function with constant inputs can be put in the following form:

$$\Delta L = L(t+2, t+1) - L(t+1, t) = -\sum_i (g_i(t+2) - g_i(t)) (h_i(t+2))$$

$$\text{where } h_i(t) = R_i(t-1) - \frac{1}{2} + \sum_{j=1}^N w_{ij} g_j(t-1)$$

If $g_i(t+2)$ is equal to 1 then $h_i(t+2)$ is positive because of update rule (1) and, irrespective of the value of $g_i(t)$, the contribution of unit i to ΔL cannot be positive. Conversely, if $g_i(t+2)$ is equal to 0, then $h_i(t+2)$ is negative, and again the contribution of unit i to ΔL is nonpositive irrespective of the value of $g_i(t)$.

As a consequence, the only stable points of the deterministic dynamics of the model are either fixed points or two-step cycles: since the lower bound of the increment of the Lyapunov function is zero, the dynamics is bound to reach, after a finite number of steps, a situation where $\Delta L=0$, which is possible if and only if a fixed point ($g_i(t+1) = g_i(t)$) or a two-step cycle ($g_i(t+2) = g_i(t)$) is reached ($h_i(t+2)$ is never equal to zero because of the constant term $1/2$ in its definition).

2.2 Interpretation of the stable glomerular image in terms of dynamic thresholding of the stimulus

In the companion paper, we have taken advantage of the fact that the stable states of the model can be fixed points or cycles, by defining a ternary glomerular image whose elements are $G_i(t) = g_i(t-1) + g_i(t)$; $G_i(t)$ can take on the values 0, 1 or 2, and $G_i(t)$ is independent of time when a fixed point or a stable two-step cycle is reached. In the steady state, from the update rule (1), with $w_{ij} = -1$, G_i can be written as:

$$G_i = H\left(R_i - \frac{1}{2} - \sum_{j=1}^N g_j^1\right) + H\left(R_i - \frac{1}{2} - \sum_{j=1}^N g_j^2\right) \quad (2)$$

where $\{g_j^1\}$ and $\{g_j^2\}$ are the activities of glomerulus j during the two steps of the limit cycle. Since g_j^1 and g_j^2 are equal to 1 or zero, the sums on the right-hand side of relation 2 are simply the numbers of active glomeruli S_1 and S_2 at each step of the two-step cycle:

$$G_i = H\left(R_i - S_1 - \frac{1}{2}\right) + H\left(R_i - S_2 - \frac{1}{2}\right) .$$

Thus, the stable glomerular image can be derived from the input activity pattern $\{R_i\}$ by simply thresholding the latter with two thresholds $\theta_1 = S_1 + 1/2$ and $\theta_2 = S_2 + 1/2$, which are independent of i .

We now derive the following useful result: *all glomeruli that oscillate during a limit cycle do so in phase, i.e. they all undergo the same transition at the same time*: it is impossible that, at a given instant, some glomeruli become inactive whilst others become active. This can be proved as follows: consider step 1 of the cycle, with, for instance, $S_1 < S_2$; the only possibility for a glomerulus i to have an oscillatory activity is to have $R_i - S_1 - 1/2 > 0$ and to be inactive ($g_i^1 = 0$), since

- (i) if $R_i - S_1 - 1/2 > 0$ and $g_i^1 = 1$ then glomerulus i remains active,
- (ii) if $R_i - S_1 - 1/2 < 0$ and $g_i^1 = 0$ then glomerulus i remains inactive.
- (iii) if $R_i - S_1 - 1/2 < 0$ and $g_i^1 = 1$, then glomerulus i becomes inactive; since the limit cycle is of length 2, glomerulus i must become active at the next update, therefore one must have: $R_i - S_2 - 1/2 > 0$; thus, $R_i - S_2 - 1/2 > R_i - S_1 - 1/2$ which is inconsistent with the hypothesis that $S_1 < S_2$.

2.3 Derivation of the possible stable glomerular images in response to a given input signal

We have just shown that a stable state (fixed point or cycle) is related to the input signal $\{R_i\}$ by a simple thresholding operation. Therefore, given an input signal, each

possible stable state is uniquely determined by a pair of thresholds or, equivalently, by a pair of numbers of active glomeruli S_1 and S_2 . In the present section, we address the problem of finding the possible stable states in response to a given input. The brute-force solution, which consists, for a given input, in testing exhaustively all possible initial states and observing all the resulting stable states, is uninteresting and not practical. We present a simple graphical derivation of all possible stable states in response to a given input, which, in addition, allows us to estimate the size of the basins of attraction of the resulting stable glomerular images.

We first note that the model is symmetric under permutations : if $\{R_i\}_2$ is a permutation of $\{R_i\}_1$, then the various possible glomerular images $\{G_i\}_2$ are the result of the same permutation applied to $\{G_i\}_1$. Among a class of inputs which are equivalent under any permutation, we denote by $[R_k]$ the vector whose components are ranked in order of increasing value: $R_{k+1} \geq R_k$. We denote by $[G_k]$ a corresponding stable glomerular image, with $G_{k+1} \geq G_k$.

We have shown that the instantaneous glomerular activities can oscillate during the cycle, and that the glomeruli which oscillate do so in phase. Without loss of generality we assume that a pair (S_1, S_2) , corresponding to a ternary glomerular image $[G_k]$, has $S_1 \leq S_2$; then S_1 is the number of glomeruli which are active at both steps of the limit cycle, and S_2 is the number of glomeruli which are active at one of the two steps of the limit cycles; therefore, $S_2 - S_1$ is the number of glomeruli that oscillate, and $N - S_2$ glomeruli are inactive during the whole limit cycle. In other words, the first $N - S_2$ components of $[G_k]$ are equal to zero, the following

$S_2 - S_1$ components are equal to 1, and the last S_1 components are equal to 2. Thus, the pair (S_1, S_2) and the vector $[G_k]$ are biunivocally related.

If $[G_k]$ is a possible glomerular image of $[R_k]$, resulting from the thresholding of $[R_k]$ with the thresholds $(S_1 + 1/2, S_2 + 1/2)$, then the same pair (S_1, S_2) is one of the possible pairs determining stable images of all permutations of $[R_k]$. Figure 1 shows how it is possible to find graphically all the possible pairs (S_1, S_2) , that lead to different stable glomerular images, for a given input $[R_k]$. Since $R_{k+1} \geq R_k$, the input $[R_k]$ is represented as a stairlike line, shown as a thick black line on the above diagram. The second diagonal is also shown on the diagram (white line). We denote by S the number of active glomeruli at time t : any glomerulus i with input $R_i \geq S + 1/2$ will thus be active at time $t + 1$; therefore, by construction of the diagram, the number of active glomeruli at time $t + 1$ is equal to the number of rectangles to the right of the vertical thick black line on row S . The evolution at the next time step is obtained by finding the intersection of the vertical thick black line at row S with the second diagonal, and so on. The stable output cycles are found by recognizing that, for both rows of the cycle,

the numbers of rectangles between the black line and the diagonal are equal. In the example, there are four possible stable cycles defined by the pairs (0,17), (5,13), (8,11) and (10,10), the latter being a fixed point. The four corresponding images $[G_k]$ are readily derived: $[G_k]^1 = [1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1]$, $[G_k]^2 = [0\ 0\ 0\ 0\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 2\ 2\ 2\ 2]$, $[G_k]^3 = [0\ 0\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 2\ 2\ 2\ 2\ 2\ 2\ 2\ 2]$, and $[G_k]^4 = [0\ 0\ 0\ 0\ 0\ 0\ 0\ 2\ 2\ 2\ 2\ 2\ 2\ 2\ 2\ 2\ 2]$.

In addition, this construction allows us to compute the probability of occurrence of each of these states, if the initial state is a random variable whose probability distribution is known. The probability of each cycle is the sum of the probabilities of the initial number of active glomeruli that lead to this cycle. If this probability distribution is uniform, the probability for the model to have an initial total activity of S is $P(S) = \frac{1}{2^N \binom{N}{S}}$. In the example, initial values of S that lead the

deterministic system to $[G_k]^1$ are (0, 1, 2, 3, 15, 16, 17); those that lead to $[G_k]^2$ are (4, 5, 6, 13, 14); those which lead to $[G_k]^3$ are (7, 8, 11, 12) and those which lead to $[G_k]^4$ are (9, 10). The probabilities are thus respectively: 0.8%, 18.2%, 47.6% et 33.4%.

Thus, the dynamics of the model from a given initial state under a given input, in the absence of synaptic noise, can be fully predicted in a very simple graphical way, without resorting to heavy simulations. We now turn to the dual problem, namely, that of finding the stimuli which generate a given glomerular image.

2.4 Condition for a stimulus to generate a given glomerular image

Let us now examine the condition for an input $\{R_i\}$ to generate a given output $\{G_i\}$, which is a particular combination of n_0 0's, n_1 1's and n_2 2's, with $n_0 + n_1 + n_2 = N$. We have to calculate first the pair (S_1, S_2) such that:

$$\begin{cases} S_1 = n_2 \\ S_2 = n_1 + n_2 = N - n_0 \end{cases}$$

Then the condition for each value of the receptor activity can be expressed as follows as a function of the desired glomerular activity :

- (i) if $G_i = 0$, $R_i < S_1 + 1/2$,
- (ii) if $G_i = 1$, $S_1 + 1/2 < R_i < S_2 + 1/2$,
- (iii) if $G_i = 2$, $R_i > S_2 + 1/2$.

This is summarized by the following condition :

$$S_1 \delta(G_i, 1) + S_2 \delta(G_i, 2) - \delta(G_i, 0) + \frac{1}{2} < R_i < S_1 \delta(G_i, 0) + S_2 \delta(G_i, 1) + (N+1) \delta(G_i, 2) + \frac{1}{2}$$

where δ is the Kronecker symbol.

It is easy to see that the number of inputs that satisfy this condition, i.e. the size of the basin of attraction of the limit cycle defined by (S_1, S_2) is given by:

$$\binom{S_1+1}{S_1} \binom{N-S_2}{S_2-S_1} \binom{N+1-S_2}{S_2} .$$

This number is maximal for $S_1 = 0$ and $S_2 = N$, which corresponds to the 'garbage image' defined in the companion paper, i.e. the limit cycle in which all glomeruli oscillate. Thus, essentially 50 % of the possible input states *may* generate the garbage image, but will not always generate it since the final limit cycle depends on the initial state.

2.5 Conclusion

We have proved that, in the absence of noise other than input noise, the stable ternary glomerular image generated in response to a constant stimulus can be described as resulting from the application of two thresholds to the input image: this kind of "contrast enhancement" is typical of systems with lateral inhibition. We have also derived a geometrical construction of all possible glomerular images resulting from the application of a given stimulus, and we have derived the size of the basin of attraction of any given input.

Thus, in the absence of noise, the model is fully tractable analytically. The next section is devoted to an analysis of the behavior of the system when a model of "synaptic" noise is introduced.

3. LITTLE DYNAMICS WITH NOISE

3.1 Probabilistic transition rule

Instead of a deterministic dynamics as given by the transition rule (1) we consider now a probabilistic transition rule. The new state $g_i(t+1)$ of neuron i is no longer uniquely determined by the value of the local field $h_i(t)$. Instead, the local field will just determine the probabilities for the neuron to become active or inactive at time $t+1$. These probabilities are given by:

$$\begin{aligned} P[g_i(t+1) = 1] &= \sigma(h_i(t+1)) \\ P[g_i(t+1) = 0] &= 1 - \sigma(h_i(t+1)) \end{aligned}$$

where we introduce the sigmoid function

$$\sigma(x) = \frac{1}{1 + \exp(-x / \varepsilon)}$$

The parameter ε controls the steepness of the sigmoid function near $x = 0$, thus effectively controls the level of 'noise'. \square corresponds to the deterministic dynamics considered in the previous section.

The transition probabilities can be written in an equivalent, useful but less transparent way, as:

$$P[g_i(t+1)] = 1 - g_i(t+1) + (2g_i(t+1) - 1) \sigma(h_i(t+1))$$

The transition rules are again applied in parallel to all neurons. Therefore, as in the deterministic case, it is natural to describe the dynamics in terms of the states of the whole network. Given a network state $I = \{g_i^I\}$ at time t , the probability for the network to be in state $J = \{g_j^J\}$ at time $t+1$ is given by the product of the probabilities for each individual neuron i to be in state $g_j^J(t+1)$ at time $t+1$:

$$P(I \rightarrow J) = \prod_j P[g_j^J(t+1)]$$

3.2 Description of the transitions as a Markov process

The Little dynamics with noise is therefore a Markov process (see for instance Seneta 1981) described by the transition matrix

$$\begin{aligned} T(J, I) &= P(I \rightarrow J) \\ &= \prod_j P[g_j^J(t+1)] \\ &= \prod_j \left(1 - g_j^J(t+1) + (2g_j^J(t+1) - 1) \sigma(h_j(t+1)) \right) \end{aligned}$$

The Markov processes are usually studied in terms of probability distributions for the ensemble of equivalent Markov processes. Let $P(I)$ describe the ensemble probability that the network is in state I at a certain instant of time. Then the ensemble probability for the network to be in state J at the following time step is given by:

$$P_1(J) = \sum_I T(J, I)P(I)$$

and the ensemble probability after n time steps is:

$$P_n(J) = \sum_I T^n(J, I)P(I)$$

where $T^n(J, I)$ are the matrix elements of the n -th power of the transition matrix, defined by the recursion:

$$T^n(J, I) = \sum_K T(J, K) T^{n-1}(K, I)$$

$$T^1(J, I) = T(J, I)$$

Our aim is to investigate the limit behavior of the network as $\epsilon \rightarrow 0$. The problem has been studied for a slightly less general model by Peretto (Peretto, 1992). Here we suggest an alternative approach which leads to simpler and intuitively more transparent results. The idea is to study the probability distribution for the pairs of consecutive states instead of probability distributions for single states. This approach is suggested by the deterministic dynamics, where limit cycles of length 2 play an important role. Since we are going to deal with pairs of states, it is clear that we should look for a suitable two-state function which could describe the limit probability distribution. An obvious candidate is the Lyapunov function. In the following, we prove that it indeed controls the limit behavior of the network dynamics.

First we generalize the Lyapunov function (for constant input R_i) to be defined for any pair of states, not just for the states connected by the deterministic dynamic transition. So instead of a two-time function we introduce a *two-state* function defined as

$$L(J, I) = - \sum_{ij} w_{ij} g_i^I g_j^J - \sum_i \left(R_i - \frac{1}{2} \right) g_i^I - \sum_i \left(R_i - \frac{1}{2} \right) g_i^J$$

If the weight matrix w_{ij} is symmetric then the Lyapunov function is a symmetric function of its arguments I, J . As shown in the Appendix, the transition probability matrix can be described in terms of this two-state Lyapunov function as

$$T(J, I) = \frac{\exp(-L(J, I) / \epsilon)}{Z(I)} \tag{2}$$

$$Z(I) = \sum_J \exp(-L(J, I) / \epsilon)$$

This is a familiar Boltzmann-type law, except for the fact that the usual energy function is replaced by a Lyapunov function.

3.3 Introduction of a two-state Markov process

Now we have an appropriate tool for describing the dynamics in terms of the pairs of consecutive states. The basic idea is the following: consider some particular realization of the Markov process where the set of consecutive states is $\{ \dots I, J, K, L, \dots \}$.

M, \dots }; this sequence can be regarded as a sequence of pairs of consecutive states $\{(J, I), (K, J), (L, K), (M, L) \dots\}$. Our notation for the pair is the (out, in) type of notation, since we want to have the right multiplication of vectors by matrices. Note also, that for the consecutive pairs the 'out' state of the previous pair is equal to the 'in' state of the following pair. We denote by $\Pi(I, J)$ the ensemble probability that at some particular time instant the last observed pair of consecutive states is (J, I) : equivalently, it means that the last observed transition is from I to J .

In this way we define a new Markov process, related to the original one, namely, the 'pair to pair' process with the transition matrix $U(L, K ; J, I)$ given as

$$U(L, K ; J, I) = \begin{cases} T(L, K), & K = J \\ 0, & K \neq J \end{cases} \quad \text{where the notation } U(L, K ; J, I) \text{ means that the pair}$$

of states (J, I) is to be followed by the pair of states (L, K) . It is possible only if $K = J$ therefore $U(L, K ; J, I) = 0$ if state K is different from state J .

Using the Kronecker symbol one can write the above expression as $U(L, K ; J, I) = T(L, K) \delta(K, J)$.

The ensemble pair-distribution probabilities for consecutive time instants are then related by

$$\Pi(L, K) = \sum_{J, I} U(L, K ; J, I) \Pi(J, I)$$

The matrix $U(L, K ; J, I)$ is stochastic since it satisfies the conditions

$$U(L, K ; J, I) \geq 0, \quad \sum_{L, K} U(L, K ; J, I) = 1$$

Using the terminology of Otten and van Ginneken (Otten and van Ginneken, 1989) the 'pair to pair' Markov process is a chain, since one can get from a given pair to any pair with a nonzero probability within a finite number of steps, in particular within two steps. This can be seen by inspecting the square of the transition matrix $U(L, K ; J, I)$.

$$\begin{aligned} U^2(L, K ; J, I) &= \sum_{N, M} U(L, K ; N, M) U(N, M ; J, I) \\ &= \sum_{N, M} T(L, K) \delta(K, N) T(N, M) \delta(M, J) \\ &= T(L, K) T(K, J) \\ &= \frac{\exp(-L(L, K) / \epsilon)}{Z(K)} \frac{\exp(-L(K, J) / \epsilon)}{Z(J)} \end{aligned}$$

All matrix elements $U^2(L, K ; J, I)$ are positive, therefore the process is a chain.

It is also clear that it is theoretically easier to study still another Markov process with transition matrix

$$V(L, K ; J, I) = U^2(L, K ; J, I)$$

It is a 'pair to nonoverlapping pair' Markov process : from the original sequence of states $\{ \dots I, J, K, L, M, N \dots \}$ we construct the sequence of nonoverlapping pairs as $\{ \dots (J, I), (L, K), (N, M) \dots \}$. The 'pair to nonoverlapping pair' Markov process is a reflexive chain : all the elements of its transition matrix $V(L, K ; J, I)$ are positive, therefore all its diagonal elements are also positive. According to the chain limit theorem, the transition matrix of a reflexive chain has exactly one eigenvalue $\lambda_1 = 1$, and the absolute values of all the other eigenvalues are strictly smaller than one: $|\lambda_i| < 1$ for $i \neq 1$.

It means that the ensemble probability distributions corresponding to the 'pair to nonoverlapping pair' Markov process converges to a stationary distribution corresponding to the eigenvalue 1.

Denoting the 'pair to nonoverlapping pair' ensemble probability distributions as $\tilde{P}(J, I)$, the limiting distribution $\tilde{P}_\infty(J, I)$ satisfies the relation

$$\sum_{J, I} V(L, K ; J, I) \tilde{P}_\infty(J, I) = \tilde{P}_\infty(L, K) .$$

However it also means that the 'pair to pair' transition matrix $U(L, K ; J, I)$ also has just one eigenvalue whose magnitude is equal to 1. If there were more of them, their squares would be the eigenvalues of the matrix $V(L, K ; J, I)$. This in turn means that the 'pair to pair' process probability distributions also converge to a limiting distribution, which is the same as for the 'pair to nonoverlapping pair' limiting distribution : the eigenvectors corresponding to the eigenvalue 1 for the matrices $U(L, K ; J, I)$ and $V(L, K ; J, I)$ are the same.

So the last task is to find this limit distribution. An obvious Ansatz for a stationary distribution is :

$$P_\infty(J, I) = \frac{\exp(-L(J, I) / \epsilon)}{Z} \quad \text{with} \quad Z = \sum_{I, J} \exp(-L(J, I) / \epsilon) .$$

A simple calculation proves that the Ansatz is correct:

$$\begin{aligned}
\sum_{J,I} U(L, K ; J, I) P_{\infty}(J, I) &= \sum_{J, I} T(L, K) \delta(K, I) P_{\infty}(J, I) = \sum_I T(L, K) P_{\infty}(K, I) \\
&= \sum_I \frac{\exp(-L(L, K) / \varepsilon)}{Z(K)} \frac{\exp(-L(K, I)) / \varepsilon}{Z} \\
&= \frac{\exp(-L(L, K) / \varepsilon)}{Z} \sum_I \frac{\exp(-L(K, I)) / \varepsilon}{Z(K)} \\
&= \frac{\exp(-L(L, K) / \varepsilon)}{Z} = P_{\infty}(L, K)
\end{aligned}$$

where we used the symmetry of the Lyapunov function.

3.4 Comments and conclusions about the stationary probability distribution

We have proved that the 'pair to pair' Markov process converges and that the stationary probability distribution is given by

$$P_{\infty}(J, I) = \frac{\exp(-L(J, I) / \varepsilon)}{Z} \quad \text{with} \quad Z = \sum_{I, J} \exp(-L(J, I) / \varepsilon) \quad (3)$$

It is a Boltzmann type of distribution where, instead of one-state energy function, one has the two-state Lyapunov function. The low noise limit of the Markov process corresponds to the deterministic Little dynamics of the network, with the limit behavior of steady states which are either fixed points or two-step cycles.

There is a clear analogy with the simulated annealing (Cerny, 1985; Kirkpatrick et al., 1983) optimization algorithm. The deterministic case corresponds to the zero temperature regime where the system gets frozen into any of the local minima of the Lyapunov function, the latter being determined by the initial state of the network.

In the noisy system the boundaries between the basins of attraction of the different local minima can be overcome. If the system is annealed to the zero noise limit it ends in the absolute minimum of the Lyapunov function, which can be either a fixed point or a two-step cycle. In principle, the absolute minimum can be degenerate.

It is perhaps useful to stress that the 'pair to pair' Markov process does not satisfy the 'detailed balance' condition and so the process is not reversible. Of course, it satisfies the balance condition, which reads

$$\sum_{J, I} U(L, K ; J, I) P_{\infty}(J, I) - U(J, I ; L, K) P_{\infty}(L, K) = 0$$

The proof is by simple algebra

$$\begin{aligned}
& \sum_{J,I} U(L, K; J, I) P_{\infty}(J, I) - U(J, I; L, K) P_{\infty}(L, K) \\
&= \sum_{J,I} T(L, K) \delta(K, I) P_{\infty}(J, I) - T(J, I) \delta(I, L) P_{\infty}(L, K) \\
&= T(L, K) \sum_I P_{\infty}(K, I) - P_{\infty}(L, K) \sum_J T(J, L) \\
&= \frac{\exp(-L(L, K) / \varepsilon)}{Z(K)} \sum_I \frac{\exp(-L(K, I) / \varepsilon)}{Z} - \frac{\exp(-L(L, K) / \varepsilon)}{Z} \\
&= 0
\end{aligned}$$

3.5 Analysis of the evolution of the glomerular image as a function of the noise level

We have seen that the dynamics of the model with noise can be described by the transition matrix of the Markov process $T(J, I)$. The limit probability $P_{\infty}(J, I)$ of the pair of consecutive states (I, J) is given by equation (3). Each pair of consecutive states, or transitions, (I, J) is characterized by a vector $\{G_i^{(I, J)}\}$ of the glomerular activities (0, 1 or 2).

Thus, the limit probability for the glomerulus i to be active can be written as :

$$P_{\infty}(g_i = 1) = \frac{1}{2} \sum_{I, J} P_{\infty}(J, I) G_i^{(I, J)}$$

where the summation is over all possible transitions (I, J) .

We denote by $\bar{g}_i(\tau)$ the mean activity of glomerulus i measured during time τ , and $\bar{g}_i = \lim_{\tau \rightarrow \infty} \bar{g}_i(\tau)$, thus

$$\bar{g}_i = P_{\infty}(g_i = 1) = \frac{1}{2} \sum_{I, J} P_{\infty}(J, I) G_i^{(I, J)}$$

We denote by \bar{g}_i^0 the mean activity of glomerulus i when the Lyapunov function is minimum, i.e. in the limit of zero noise and infinite time: $\bar{g}_i^0 = \lim_{\varepsilon \rightarrow 0} \bar{g}_i$; one has:

$$\bar{g}_i^0 = \frac{1}{2} \frac{1}{\left(\sum_{(I, J)^0} (1) \right)} \sum_{(I, J)^0} G_i^{(I, J)^0}$$

where the summation is over the possible transitions (I, J) for which the Lyapunov function is minimum (the minimum can be degenerated).

In order to understand quantitatively the response of the system as a function of noise, we define a euclidean distance $D_0 = d(\bar{g}_i, \bar{g}_i^0)$ between vectors \bar{g}_i and \bar{g}_i^0 :

$$D_0 = \sqrt{\sum_{i=1}^N (\bar{g}_i - \bar{g}_i^0)^2} .$$

Similarly, one can define two distances of interest: (i) the distance D_1 between the mean glomerular activity and the receptor activity (normalized): $D_1 = d(\bar{g}_i, \bar{g}_i^1)$ with $\bar{g}_i^1 = \frac{R_i}{N+1}$, and (ii) the distance D_2 between the mean activity of the glomeruli and the 'garbage state' where all glomeruli oscillate in phase: $D_2 = d(\bar{g}_i, \bar{g}_i^2)$ where $\bar{g}_i^2 = 1/2 \forall i$. D_0 , D_1 and D_2 depend on the input $\{R_i\}$ and on the noise level ε . In order to understand the dynamics of the model as a function of the level of noise ε , we investigate these three distances as three functions of ε . These functions depend on the inputs, but it is possible for small systems to compute their values *averaged over all possible inputs* $\{R_i\}$ (for a model with N glomeruli, we consider $(N+2)^N$ different inputs):

$$\langle D_k(\varepsilon) \rangle = \frac{1}{(N+2)^N} \sum_{\{R_i\}} \sqrt{\sum_{i=1}^N (\bar{g}_i(\varepsilon, \{R_i\}) - g_i^k(\varepsilon, \{R_i\}))^2} ,$$

where $k=0, 1$ or 2 .

This has been computed for a system with $N = 5$ glomeruli, and . The results is shown on figure 2.

Interestingly, three noise regimes emerge. In a first regime, for small values of ε , the mean glomerular activity \bar{g}_i expresses essentially the image that codes for the input, since it is close to \bar{g}_i^0 . At higher noise levels, in a second regime, the mean glomerular activity tends to "copy" the receptor activities $\{R_i\}$; there is a value of the noise level ε for which the "copy" is optimal. Thus, the input-output mapping performed by the system is almost linear, although all the elements are non-linear. At the intersection between the curves $\langle D_1(\varepsilon) \rangle$ and $\langle D_2(\varepsilon) \rangle$ a third regime begins, where the noise blurs the input features: the mean glomerular activity becomes more and more independent of the inputs and closer to the 'garbage image'.

3.6 Analysis of the low-noise regime

The unexpected emergence of a 'quasi-linear' regime of noise, is worth investigating. The update rule in the noisy case is given by the following equations:

$$P[g_i(t) = 1] = \frac{1}{1 + \exp\left(\frac{-h_i(t)}{\varepsilon}\right)}$$

and $h_i(t) = R_i - \frac{1}{2} - S(t-1)$ with $S(t-1) = \sum_{j=1}^N g_j(t-1)$.

The first two equations can be summarized as:

$$P[g_i(t) = 1] = \frac{1}{1 + \exp\left(\frac{-\left(R_i - \frac{1}{2} - S(t-1)\right)}{\varepsilon}\right)}$$

When noise is present, g_i can be considered as a random variable; therefore the number of active glomeruli S is a random variable too. We denote by $P_\infty(S)$ the limit probability that the number of active glomeruli is equal to S ; it can be written as:

$$P_\infty(S) = \frac{1}{2} \sum_{(l, j)} \left[\delta\left(\sum_{i=1}^N g_{i,l}^l, S\right) + \delta\left(\sum_{i=1}^N g_{i,j}^j, S\right) \right] P_\infty(l, j)$$

We have seen in the previous section that:

$$\bar{g}_i = P_\infty(g_i = 1) .$$

Therefore we can write :

$$\bar{g}_i = \sum_{S=0}^N \frac{1}{1 + \exp\left(\frac{\left(S + \frac{1}{2} - R_i\right)}{\varepsilon}\right)} P_\infty(S)$$

If N is large, the summation can be approximated by an integral. Let us now assume that for a value (or range of values) of the noise parameter, $P_\infty(S)$ becomes close to the uniform distribution , then the mean activity of glomerulus i

becomes:

$$\bar{g}_i = \frac{1}{N+1} \int_0^N \frac{1}{1 + \exp\left(\frac{\left(S + \frac{1}{2} - R_i\right)}{\varepsilon}\right)} dS$$

which integrates to :

$$\bar{g}_i = \frac{1}{N+1} \left(N + \varepsilon \ln \left(\frac{1 + \exp\left(\frac{(1 - 2R_i)}{2\varepsilon}\right)}{1 + \exp\left(\frac{(1 + 2N - 2R_i)}{2\varepsilon}\right)} \right) \right) .$$

When \square , if $R_i > 0$, then \square ; conversely, if $R_i \leq N$, the

exponential term of the denominator is larger than 1. Taking these approximations into account, the mean glomerular activity can be written as :

$$\bar{g}_i \approx \frac{1}{N+1} \left(N + \varepsilon \ln \left(\exp \left(- \left(1 + 2N - 2R_i \right) / 2\varepsilon \right) \right) \right) \approx \frac{1}{N+1} \left(R_i - \frac{1}{2} \right).$$

Thus, the mean activity of each glomerulus is linear with respect to the corresponding stimulus, under the assumptions that (i) the probability distribution of the number of active glomeruli is uniform, that (ii) the noise level is small with respect to the input signal level, and that (iii) $0 < R_i \leq N$.

If $R_i = 0$, the limit of \square is 0. If $R_i = N+1$, the limit of \square is 1 if N is large.

To summarize: if the stationary probability distribution of the number of active glomeruli is close to uniform, the mean activity \square of glomerulus i is roughly affine with respect to the normalized input signal, in the low noise limit and if the number of glomeruli is large: the glomerular image "copies" (within a scaling factor) the stimulus. This is clearly apparent on Figure 15 of the companion paper, and is illustrated quantitatively on Figure 3.

The validity of this analysis relies on the assumption that there exists a range of noise levels for which the distribution of the total glomerular activity S , viewed as a random variable, becomes uniform. First consider two limit cases: (i) at high noise level, the probability for each glomerulus to be active approaches $1/2$; therefore, the distribution of S is close to gaussian (it is the limit of a binomial distribution when N is large) with a maximum at $N/2$; (ii) conversely, at very small noise levels the probability distribution of S depends on the most probable glomerular images, which in turn depends (in a non-linear fashion) on the receptor activities. Does there exist an intermediate regime where the distribution of S is close to uniform?

Some insight into this question can be gained in the following way: for small values of N , the euclidean distance $\Delta(\varepsilon)$ between the probability distribution of S and the uniform distribution can be computed numerically, as a function of ε , and averaged over all possible inputs:

$$\langle \Delta(\varepsilon) \rangle = \frac{1}{(N+2)^N} \sum_{\{R\}} \sqrt{\sum_{S=0}^N \left(P_{\infty}(S) - \frac{1}{N+1} \right)^2}$$

where $P_{\infty}(S)$ is a function of the inputs and of ε

$$P_{\infty}(S) = \frac{1}{2} \sum_{(I, J)} \left[\delta \left(\sum_{i=1}^N g_{i,S}^I \right) + \delta \left(\sum_{i=1}^N g_{i,S}^J \right) \right] P_{\infty}(I, J)$$

since $P_{\infty}(I, J)$ is a function of the inputs and of the noise level.

For a system of five glomeruli, the evolution of $\langle \Delta(\varepsilon) \rangle$ with ε is shown on Figure 4. This distance reaches a plateau for $\varepsilon \cong 1$, which indeed corresponds to the noise level for which the distance between the mean glomerular activity and the mean receptor activity is minimum: it is the smallest noise level for which the probability distribution of S is closest to the uniform distribution.

4. CONCLUSION

In the present article, we have developed a full analysis of a model proposed in the companion paper, using the tools of dynamic systems theory. We have shown that the model is fully tractable analytically, so that its coding properties can be understood and predicted in detail without having to resort to extensive simulations in order to explore the space of parameters of the model. The influence of intrinsic noise has been investigated by introducing a novel description of the dynamics of the model in terms of Markov processes. This has allowed us to show that the attractors of the dynamics of such a system obey a Boltzmann-type law, where the usual energy function is replaced by a two-step Lyapunov function.

The above theoretical results give an insight into the properties of a plausible, albeit very simple, dynamic model of the first two stages of the olfactory pathway, as proposed in the companion paper. The latter has presented the biological background and ingredients of the model, together with results of simulations. It was shown that the model has the ability of producing a stable glomerular image which codes for the key features of the input signal despite its fluctuations; this property is in agreement with behavioral data, and with the widely admitted idea that an "olfactory image" is generated and processed in the olfactory system. In the absence of synaptic noise, the fact that the dynamics of the model is fully understood allows us to analyze in depth the production of the glomerular image. The extraction of key features and image stabilization are robust not only to input noise, but also to synaptic noise in a range of low synaptic noise; for a higher level of noise, the model tends to "copy" the input stimulus at the glomerular level, without encoding it; at still higher noise levels, the behavior of the model becomes essentially independent of the

inputs. The biological interpretation of the first two noise regimes is not yet clear; they may be conjectured as being two different attentional regimes.

Thus, these results provide a firm theoretical foundation for further work in various directions in order to embody more biological ingredients in the model without sacrificing its legibility. The extensions of the model which are currently under investigation are (i) the introduction of a topology of glomerular organization, through the use of different synaptic delays corresponding to different distances between glomeruli, and (ii) the introduction of synaptic plasticity in the model.

APPENDIX

This appendix presents the algebra needed to derive the expression for the transition matrix elements $T(J, I)$. To simplify the notation we shall take here $\varepsilon = 1$. The generalization to arbitrary value is trivial.

Let us first consider the updating of a single neuron k . We denote by c_k the probability that this particular neuron will change its state during the update. Since

$$\begin{aligned} p[g_k(t) = 1] &= \sigma(h_k(t)) \\ p[g_k(t) = 0] &= 1 - \sigma(h_k(t)) = \sigma(-h_k(t)) \end{aligned}$$

one gets

$$\begin{aligned} c_k &= \sigma(h_k(t)) \quad \text{for } g_k(t-1) = 0 \\ c_k &= \sigma(-h_k(t)) \quad \text{for } g_k(t-1) = 1 \end{aligned}$$

These two relations can be equivalently written as

$$c_k = \sigma\left(\left(g_k(t) - g_k(t-1)\right) h_k(t)\right)$$

Now we denote by M the state of the network at time t and by M_k the state which differs from M just by flipping the changing of neuron k . Then it is easy to check that the following relation holds

$$\left(g_k(t) - g_k(t-1)\right) h_k(t) = -\left(L(M_k, M) - L(M, M)\right)$$

Indeed,

$$\begin{aligned} &\left(L(M_k, M) - L(M, M)\right) \\ &= -\sum_{ij} w_{ij} g_i^{M_k} g_j^M - \sum_i \left(R_i - \frac{1}{2}\right) g_i^{M_k} - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \\ &+ \sum_{ij} w_{ij} g_i^M g_j^M + \sum_i \left(R_i - \frac{1}{2}\right) g_i^M + \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \\ &= -\sum_{ij} w_{ij} g_i^{M_k} g_j^M + \sum_{ij} w_{ij} g_i^M g_j^M - \sum_i \left(R_i - \frac{1}{2}\right) g_i^{M_k} + \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \\ &= -\sum_j w_{kj} g_k^{M_k} g_j^M + \sum_j w_{kj} g_k^M g_j^M - \left(R_k - \frac{1}{2}\right) g_k^{M_k} + \left(R_k - \frac{1}{2}\right) g_k^M \\ &= \left(g_k^{M_k} - g_k^M\right) \left(-\sum_j w_{kj} g_j^M - \left(R_k - \frac{1}{2}\right)\right) \\ &= -\left(g_k(t) - g_k(t-1)\right) h_k(t) \end{aligned}$$

If we denote the variation of the Lyapunov function value due to changing one neuron state as

$$\Delta L_k = \left(L(M_{k'}, M) - L(M, M) \right)$$

we can express the probability of the single neuron flip as

$$c_k = \sigma(-\Delta L_k) = \frac{\exp(-\Delta L_k)}{1 + \exp(-\Delta L_k)} \quad (4)$$

The probability s_k for neuron k to stay unchanged is then

$$s_k = \frac{1}{1 + \exp(-\Delta L_k)} \quad (5)$$

Now we express the transition probability from state M to an arbitrary state N . Comparing the two states M and N we can find all the neurons which change their states during the transition $M \rightarrow N$ and so we can write

$$T(N, M) = \prod_{k, \text{ flips}} c_k \prod_{k', \text{ non flips}} s_{k'}$$

where the first product is over the neurons which change their state in the transition $M \rightarrow N$ and the second products is over the neurons which do not change their state during that transition. Using (4) and (5) we get

$$\begin{aligned} T(N, M) &= \prod_{k, \text{ flips}} \frac{\exp(-\Delta L_k)}{1 + \exp(-\Delta L_k)} \prod_{k', \text{ non flips}} \frac{1}{1 + \exp(-\Delta L_{k'})} \\ &= \prod_{k, \text{ flips}} \exp(-\Delta L_k) \prod_{k'} \frac{1}{1 + \exp(-\Delta L_{k'})} \end{aligned}$$

where the second product is over all the neurons. It means, however, that the second product does not depend on state N . It is just the normalization factor and we skip it for the moment.

$$T(N, M) \sim \prod_{k, \text{ flips}} \exp(-\Delta L_k)$$

The next step is to simplify the expression

$$\prod_{k, \text{ flips}} \exp(-\Delta L_k) = \exp\left(-\sum_{k, \text{ flips}} \Delta L_k\right)$$

Let us consider a state $M_{m,n}$ which differs from the state M by flipping the states of two neurons m and n . Then

$$\sum_{k, \text{ flips}} \Delta L_k = \Delta L_m + \Delta L_n = L(M_{m'}, M) + L(M_{n'}, M) - 2L(M, M)$$

and we shall show that

$$L(M_{m,n'} M) + L(M_{n'} M) - 2L(M, M) = L(M_{m,n'} M) - L(M, M) \quad (6)$$

We prove it by the following algebraic manipulations.

$$\begin{aligned} L(M_{m,n'} M) &= - \sum_{ij} w_{ij} g_i^{M_{m,n}} g_j^M - \sum_i \left(R_i - \frac{1}{2}\right) g_i^{M_{m,n}} - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \\ &= - \sum_{ij} w_{ij} g_i^M g_j^M + \sum_j w_{mj} g_m^M g_j^M + \sum_j w_{nj} g_n^M g_j^M - \sum_j w_{mj} g_m^{M_{m,n}} g_j^M - \\ &\quad \sum_j w_{nj} g_n^{M_{m,n}} g_j^M - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M + \left(R_m - \frac{1}{2}\right) g_m^M + \left(R_n - \frac{1}{2}\right) g_n^M - \left(R_m - \frac{1}{2}\right) g_m^{M_{m,n}} - \\ &\quad \left(R_n - \frac{1}{2}\right) g_n^{M_{m,n}} - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \end{aligned}$$

$$\begin{aligned} L(M_{m,n'} M) &= - \sum_{ij} w_{ij} g_i^M g_j^M + \sum_{ij} w_{ij} g_i^M g_j^M - \sum_{ij} w_{ij} g_i^M g_j^M + \sum_{mj} w_{mj} g_m^M g_j^M + \\ &\quad \sum_j w_{nj} g_n^M g_j^M - \sum_j w_{mj} g_m^{M_{m,n}} g_j^M - \sum_j w_{nj} g_n^{M_{m,n}} g_j^M - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M - \\ &\quad \sum_i \left(R_i - \frac{1}{2}\right) g_i^M + \sum_i \left(R_i - \frac{1}{2}\right) g_i^M + \left(R_m - \frac{1}{2}\right) g_m^M + \left(R_n - \frac{1}{2}\right) g_n^M - \left(R_m - \frac{1}{2}\right) g_m^{M_{m,n}} - \\ &\quad \left(R_n - \frac{1}{2}\right) g_n^{M_{m,n}} - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M + \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \\ &= - \sum_{ij} w_{ij} g_i^M g_j^M + \sum_j w_{mj} g_m^M g_j^M - \sum_j w_{mj} g_m^{M_{m,n}} g_j^M - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \\ &\quad + \left(R_m - \frac{1}{2}\right) g_m^M - \left(R_m - \frac{1}{2}\right) g_m^{M_{m,n}} - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \\ &\quad - \sum_{ij} w_{ij} g_i^M g_j^M + \sum_j w_{nj} g_n^M g_j^M - \sum_j w_{nj} g_n^{M_{m,n}} g_j^M - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \\ &\quad + \left(R_n - \frac{1}{2}\right) g_n^M - \left(R_n - \frac{1}{2}\right) g_n^{M_{m,n}} - \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \\ &\quad + \sum_{ij} w_{ij} g_i^M g_j^M + \sum_i \left(R_i - \frac{1}{2}\right) g_i^M + \sum_i \left(R_i - \frac{1}{2}\right) g_i^M \end{aligned}$$

This proves relation (6).

It is straightforward to generalize relation (6) to an arbitrary number of flipped neurons. Therefore the following relation holds, if state N differs from state M by all the neurons k which flip.

$$\sum_{k, \text{ flips}} \Delta L_k = \sum_{k, \text{ flips}} \left(L(M_k, M) - L(M, M) \right) = L(N, M) - L(M, M)$$

and therefore

$$T(N, M) \sim \exp\left(L(N, M) - L(M, M)\right)$$

Here again the factor $\exp(L(M, N))$ does not depend on N ; therefore it belongs to the normalization factor. Therefore one can write

$$T(N, M) \sim \exp\left(-L(N, M)\right)$$

or after normalization

$$T(N, M) \sim \frac{\exp\left(-L(N, M)\right)}{Z(M)}$$

$$Z(M) = \sum_N \exp\left(-L(N, M)\right)$$

which is relation (2).

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FIGURES

Figure 1

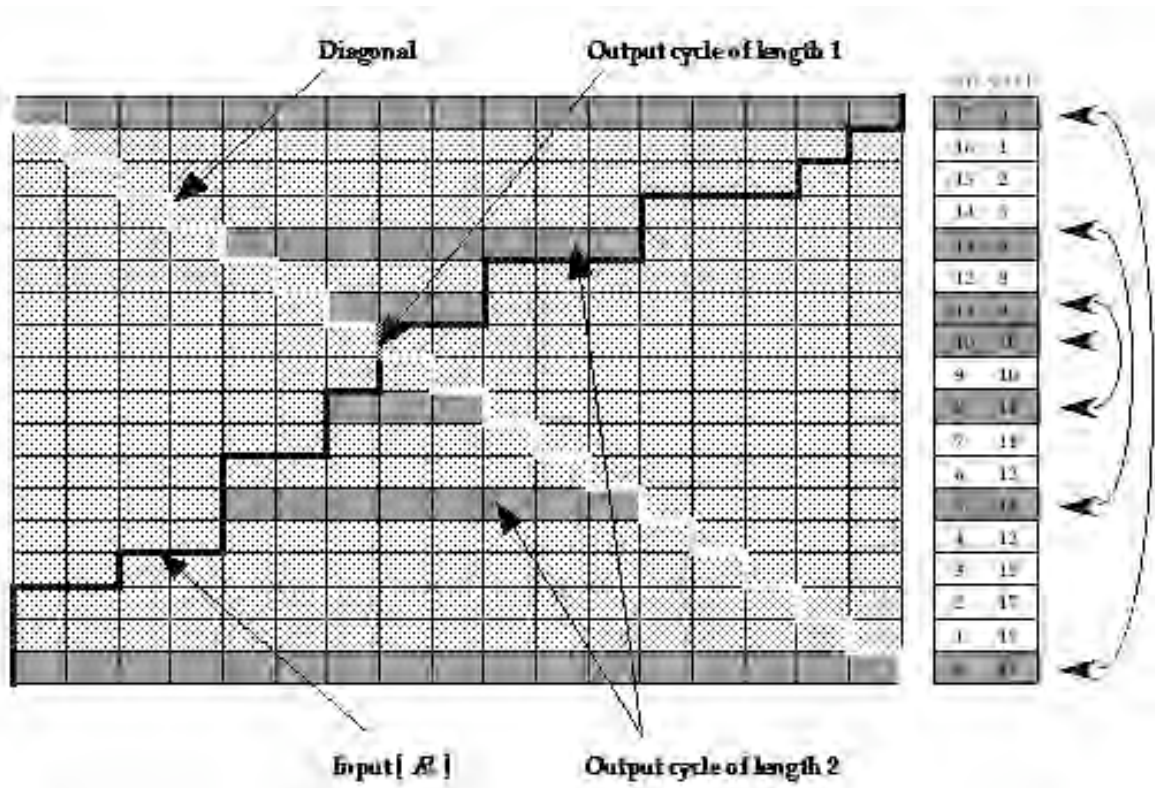


Figure 2

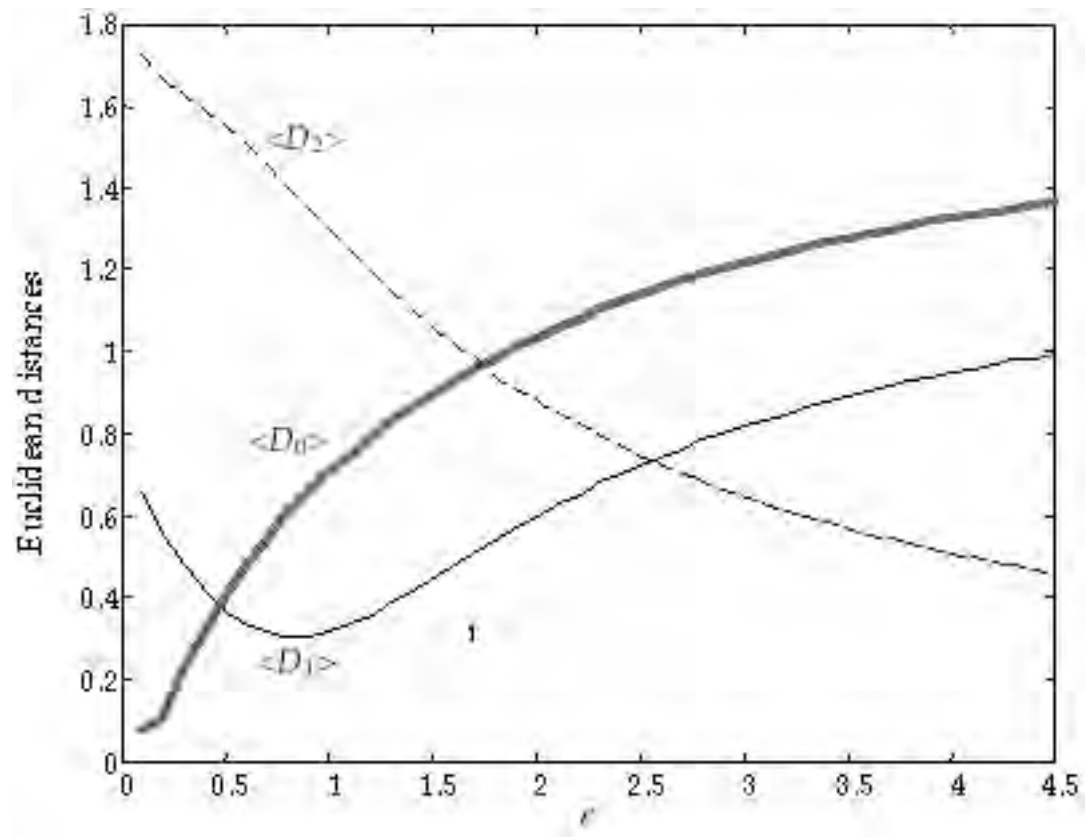


Figure 2

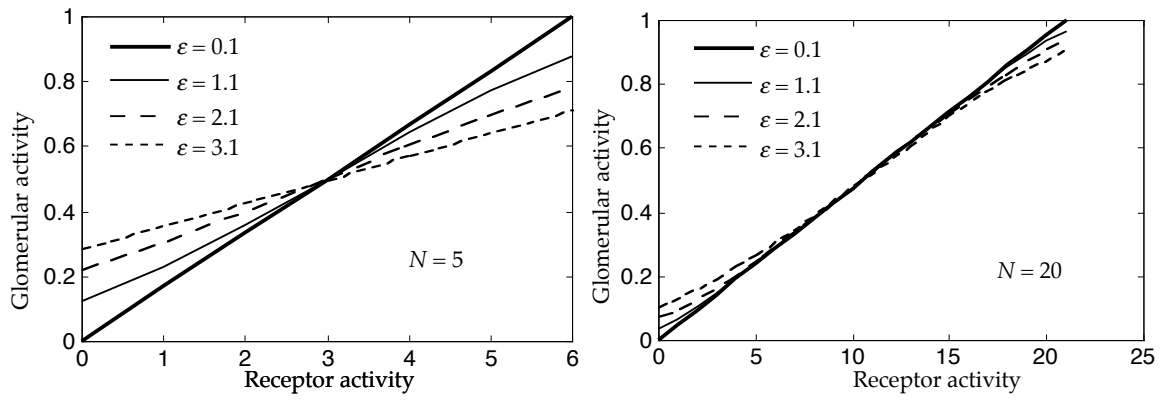


Figure 3

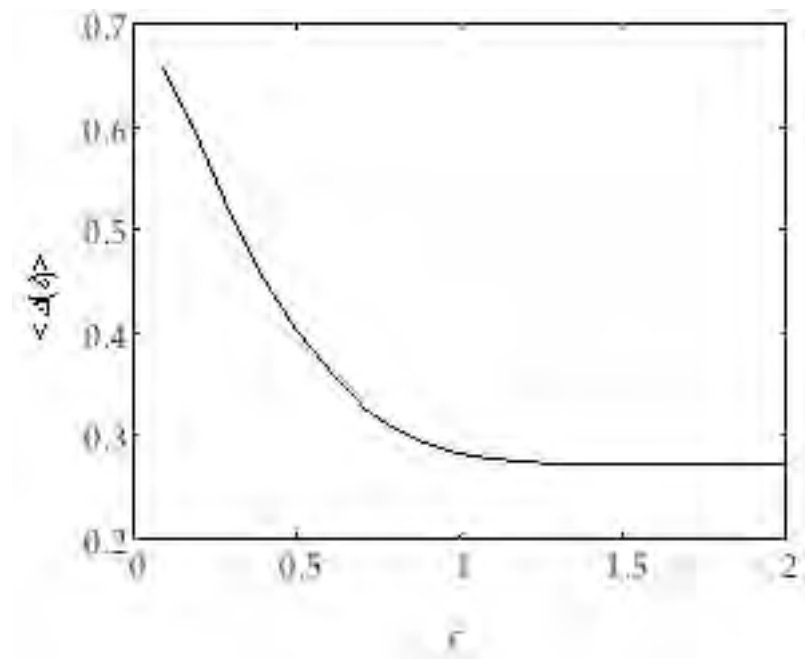


FIGURE CAPTIONS

Figure 1:

The graphical method for finding stable output states by finding the possible pairs (S_1, S_2) . For a system of N glomeruli, we construct a diagram with $N \times N+1$ rectangles. The glomeruli are numbered from 1 to N (horizontal axis), and the input activity is represented on the vertical axis (from 0 to $N+1$). As an example, we consider a system of $N = 17$ glomeruli. The specific input considered in this example is $[R_k] = [3 3 4 4 7 7 9 11 11 13 13 13 15 15 15 16 17]$. Four possible stable cycles are found, defined by the pairs $(0,17)$, $(5,13)$, $(8,11)$ and $(10,10)$, where the last one is a fixed point. The four corresponding images $[G_k]$ are readily derived: $[G_k]^1 = [1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1]$, $[G_k]^2 = [0 0 0 0 1 1 1 1 1 1 1 1 2 2 2 2 2]$, $[G_k]^3 = [0 0 0 0 0 0 1 1 1 2 2 2 2 2 2 2 2]$, and $[G_k]^4 = [0 0 0 0 0 0 0 2 2 2 2 2 2 2 2 2 2]$.

Figure 2:

The values (averaged over all possible inputs) of the three euclidean distances between the mean glomerular activities and (i) the image for which the Lyapunov function is minimum (i.e. the image that codes for the input), (ii) the receptor activities, (iii) the garbage image, are shown here as functions of the noise parameter ε , for a 5 glomeruli model. Different noise regimes emerge from this graph. Excluding the deterministic system, there is a first regime of noise, from 0 to 0.5, where the mean glomerular activity is closer to the coding image; in a second regime, from 0.5 to 2.5, the mean glomerular activity is closer to the input; the distance between the mean glomerular activity and the input is minimum for a value of ε close to 1. In the third regime, from $\varepsilon=2.5$ upwards, the glomerular image becomes closer to the garbage image. This is to be compared to Figure 13 of part I of this paper, which results from simulations performed with a single input, whereas the results of the present graph are averaged over all possible inputs.

Figure 3:

Plots of the mean glomerular activity $\bar{g}_i = \sum_{S=0}^N \frac{1}{\left(1 + \exp\left(\left(S + \frac{1}{2} - R_i\right) / \varepsilon\right)\right)} P_\infty(S)$ vs.

receptor activity, for models with 5 and 20 glomeruli and for four values of ε : (0.1, 1.1, 2.1 and 3.1), under the assumption that the probability distribution of the total glomerular activity is uniform. As ε increases, the slope decreases, but the relation is linear on a wide range of the receptor activities. In the low noise limit, the slope is

$1/N+1$ as expected, and it is almost independent of noise up to relatively high noise if N is large.

Figure 4:

Evolution of the euclidean distance $\langle \Delta(\varepsilon) \rangle$ between the probability distribution of S and the uniform distribution. A plateau is reached for \square . This corresponds roughly to the value of noise