INFORMATION DYNAMICS IN NEURAL SYSTEMS: COMPUTING WITH SEPARATRICES

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Information processing in neural networks by computation with attractors (steady states, limit cycles, strange attractors) has been extensively discussed in application to many neural systems: central pattern generators, sensory systems (e.g. visual, olfactory), hippocampus, etc. Computation with attractors in a traditional way faces a fundamental contradiction between robustness and sensitivity. In this paper we discuss a new direction in information neurodynamics based on experiments performed in the locust olfactory system, the orientation sensory system of the marine mollusk Clione and the hippocampal place cell networks. This new concept uses the transformation of the incoming spatial or identity information into spatio-temporal output based on the intrinsic switching dynamics of neural networks with nonsymmetric inhibitory connections. This is called the Winner-Less Competition Principle (WLC). The key feature of a network that computes with separatrices is the robustness against noise and the simultaneous sensitivity of the sequence of switching to the incoming information. We present rigorous results about the stability of the sequential switching in the framework of the Lottka-Volterra model. Because of their fast reaction, the discussed neural networks are able to change their intrinsic dynamics to respond to new incoming information and solve many different functional tasks. Computation with separatrices can also be an optimal principle for the design of new paradigms of artificial neural networks.

Introduction

Plenty of experimental evidence show that information processing in neural systems, i.e. neurocomputation, can be modeled by dynamical systems. This is possible because two conditions are usually satisfied: (i) time is included in the computation, and (ii) the algorithm of the computation is a set of the deterministic rules. Operations such as associative pattern recognition, sequential learning, generation of spatio-temporal patterns that control behavior, and many others include time in the computation in a natural way. Some computation tasks, like encoding and presentation of sensory information (visual, olfactory, etc.) formally can be done «algebraically», without time, by using «identity» or «spatial» coding (e.g. spatial convergence and divergence and filtering of a spatial message). However, even if it is not necessary in principle, real sensory systems include time in the encoding space to solve non temporal problems such as the encoding and presentation of spatial images. This happens because the spatio-temporal encoding of sensory information has many privileges for the next steps of the information processing (recognition, association with messages from other sensory

systems, and decision making for the behavior). Including time in the information processing of spatial images provides such processing with robustness against noise and, at the same time, sensitiveness to the variation of the stimuli. In order to understand and model the process of computation in any neural system, we need to know how sensory signals (or other type of information) have to be fed into and how the result of the computation has to be read out. In the language of dynamical systems that means that we have to know what state of the system corresponds to the final result. It seems very natural to propose that the result of the computation has to be an attractor. Several models of neural systems that compute with attractors are well known. In such models the incoming information usually is a vector of initial conditions and the result of the computation is an attractor. It can be a stable fixed point corresponding to a minimum of the potential function like in the popular Hopfield model [1], a limit cycle [2], or a strange attractor [3].

It is important to emphasize that many models of computation that use the incoming information just as an initial condition for the dynamical system are not flexible and powerful enough. A more general computing approach would take advantage of the fact that the system can change its dynamics depending on the quality and the quantity of the incoming information. Such changing may follow the changing of the stimulus, which is also in many cases strongly time-dependent.

In this paper we discuss a new approach for neurocomputation: computation with separatrices that is based on the WLC principle [4]. According to this approach the computation is a non-stationary stimulus-dependent dynamics of the neural network: a sequential switching from one semi-stable state to another. The mathematical image of the semi-stable state is a saddle fixed point or a saddle limit cycle. For a stable computation with separatrices, each saddle state has to have a one-dimensional unstable separatrix. The sequence of switching is represented in the phase space of the dynamical system by a heteroclinic chain or a heteroclinic contour. Each stimulus has to build just one heteroclinic contour in the phase space of the dynamical system, and each heteroclinic contour corresponds to a specific stimulus. The heteroclinic chain can be open (non-closed).

The questions that we are going to discuss below are: (i) how a dynamical system that computes with separatrices sensitively responses to incoming signals, (ii) what are the conditions for the robustness of such computation, e.g. the topological similarity of the perturbed and original heteroclinic contour, and (iii) how subsystems with closed heteroclinic contours interact with each other. In fact we are going to show in this paper that WLC neural networks that compute with separatrices are able to solve the fundamental contradiction between robustness and sensitivity.

The Models

The activity of many different neural networks [4-7], can be implemented with the following dynamics:

$$\dot{a}_i = a_i(\sigma(H,S) - \Sigma_{j=1}^{N} \rho_{ij} a_j + H_i(t)) + S_i(t) \tag{1}$$

where $a_i > 0$ represents the instantaneous spiking rate of the principal neurons (PNs) that are making the computation, ρ_{ij}, represents the strength of inhibition in i by j, $H_i(t)$ represents the action from other neural ensembles, and $S_i(t)$ represents the stimuli from the sensors. In many neural networks, the inhibition among PNs is the result of the action of inhibitory local neurons (LNs). Usually LNs also receive an external input and because of this ρ_{ij} can depend on the stimuli.

The dynamical system (1) in the case $\sigma=1$, $H(t)=S(t)=0$ is the Lottka-Volterra model. The dynamics of the system is well known when the matrix ρ_{ij} is symmetric ($\rho_{ij}=\rho_{ji}$). In this case the autonomous system has a global Lyapunov function [6,1] and every trajectory approaches one of the numerous possible equilibrium points. For example, if the inhibitory connections are identical, $\rho_{ij}=\rho$, $\rho_{ii}=1$, this system has only one global attractor, e.g. $a_i=a_0=1/[1+\rho(N-1)]$ for $\rho<1$, and N attractors: $a_i=a_0=1$, $a_{j\neq i}=0$ if $\rho>1$. No other attractors, e.g. limit cycles, or strange attractors are present in the system. The situation is much more complex and interesting when the inhibition is non-symmetric: $\rho_{ij}\neq\rho_{ji}$. A detailed analysis is only possible in the case $N=3$ (see [8,9,4]). When $\rho_{ij}>1$, $\rho_{ji}<1$ there exists a heteroclinic contour in the phase space of the system that consists of saddle points and one-dimensional separatrices connecting them. In some regions of the parameter space ρ_{ij}, such heteroclinic contour (or limit cycle in its vicinity) is a global attractor. If ρ_{ij} depend on the stimulus, e.g. as a result of a learning mechanism, the system (1) can generate different heteroclinic contours for different stimuli [4].

Suppose

$$\rho_{ij} = \begin{pmatrix} 1 & \alpha_1 & \beta_1 \\ \beta_2 & 1 & \alpha_2 \\ \alpha_3 & \beta_3 & 1 \end{pmatrix}$$

and $0<\alpha_i<1<\beta_i$ and $\kappa_i=(\beta_i-1)/(1-\alpha_i)$. Then the heteroclinic contour is a global attractor if $\kappa_1\cdot\kappa_2\cdot\kappa_3>1$, and the nontrivial fixed point $A(a_1^0,a_2^0,a_3^0)$ is a saddle point. If $\kappa_1\cdot\kappa_2\cdot\kappa_3=1$, this fixed point becomes neutrally stable and there exists a family of neutrally stable periodic solutions in the phase space. When $\kappa_1\cdot\kappa_2\cdot\kappa_3<1$, A becomes a global attractor. The heteroclinic contour exists but loses its stability. It is important to emphasize that in the case $\kappa_1\cdot\kappa_2\cdot\kappa_3>1$ a small perturbation is able to destroy the heteroclinic contour and then a stable limit cycle appears in its vicinity. This limit cycle is characterized by a finite time period of switching among different states, in contrast with the infinite time of motion along the heteroclinic loop.

When $N>3$ the dynamics of system (1) can be very complex and even chaotic [5]. We are interested here in the existence and stability of the heteroclinic contours, which are the mathematical image of the winnerless competition behavior. Such contours may exist only in the nonsymmetric case e.g. $\rho_{ij}\neq\rho_{ji}$, when the saddle points (in the heteroclinic contours) satisfy certain conditions.

Existence and stability of the heteroclinic contour

In the autonomous case, the system (1) is the canonical Lottka-Volterra model:

$$\dot{a}_i = a_i[1 - (a_i+\Sigma_{i\neq j}^N\rho_{ij}a_j)]. \tag{2}$$

This model, in fact, is a normal form for a neural network with inhibitory connections. Suppose that the dynamics of a network of N inhibitory coupled neurons with M dynamical variables $y_i(t)=(y_i^{(1)}(t),...,y_i^{(M)}(t))$, $i=1,...,N$ can be described in the form of the following system of ODEs:

$$\dot{y}_i = F(y_i) - \Sigma_{j=1}^N G_{ij}(S)(y_i, y_j) + \tilde{S}_i(t) \tag{3}$$

where F is a nonlinear function that describes the dynamics of an individual neuron with M variables, $G_{ij}(S)(y_i,y_j)$ is a nonlinear operator describing an inhibitory action of the j-th neuron onto the i-th neuron, $S(t)=(S_1(t),...,S_N(t))$ and $(\tilde{S}_1(t),...,\tilde{S}_N(t))$ are the vectors representing stimuli to the network. The stimulus here acts in two ways: (i) it adds the

perturbation $\tilde{S}(t)$ into (3) as an external force, and (ii) it forms the matrix $G_{ij}(S)$. As a result of averaging, a simplified model that describes the firing rate of the neurons can be written in the form (1), where $\sigma=-1$ when there is no stimulus, and $\sigma=1$ when the stimulus has a component at neuron i [4]. In the absence of the external

force, $\tilde{S}(t)$ the system (2) is just a subsystem of (1) for which all $\sigma=+1$. Thus, we can formulate the stability conditions for the heteroclinic contours in the framework of this model.

«Codimension one» saddle points. A heteroclinic contour consists of finitely many saddle equilibria and finitely many heteroclinic orbits connecting this equilibria. Let's denote by A_1 the equilibrium point $(1,0,0,\ldots,0)$, by A_2 the point $(0,1,\ldots,0)$, and by A_N the point $(0,0,\ldots,1)$. For the sake of simplicity we assume that there is a heteroclinic orbit r_{ii+1} connecting the points A_i and A_{i+1}, $i=1,\ldots,N$ and $A_{N+1}\equiv A_1$. It is simple to see that every point A_i must have only one unstable direction. Otherwise the contour can not serve as an attracting set. By direct verification it can be shown that A_i satisfies this assumption provided that:

$$\rho_{ki} > 1, \quad k \neq i+1, \quad \text{and} \tag{4}$$

$$\rho_{i+1\,i} < 1. \tag{5}$$

(Here $i+1=i$ if $i=N$).

Moreover, if (4) and (5) are satisfied then the unstable direction at the point A_i is parallel (at that point) to the $\text{ort}(0\ldots010\ldots0)$, where 1 corresponds to the ith index.

An intersection of hyperplanes $P_{2i}=\cap_{j=1,j\neq i,i+1}^{N}a_j=0$ is a two-dimensional invariant manifold containing points A_i and A_{i+1} such that A_i is a saddle point on P_{2i} and A_{i+1} is a stable node on P_{2i}. The system (2) on P_{2i} has the form:

$$\dot{a}_i = a_i[1-(a_i+\rho_{ii+1}a_{i+1})], \qquad \dot{a}_{i+1} = a_{i+1}[1-(a_{i+1}+\rho_{i+1i}a_i)] \tag{6}$$

and, from (4) and (5), one has $\rho_{ii+1}>1$, $\rho_{i+1i}<1$.

This implies that there are no equilibrium points in the region $a_i>0$, $a_{i+1}>0$ and, since $\dot{a}_{i+1}<0$ if $a_{i+1}>>1$, then it is simple to see that the separatrix, say Γ_i, of the saddle point A_i must go to the attractor A_{i+1}, i.e. there is a heteroclinic connection between A_i and A_{i+1} on the plane P_{2i} (for the case $N=3$ see the proof in [8]).

Saddle values. The point A_i is a saddle point on P_{2i}. One can write a map from a transversal to the stable separatrix into a transversal to the unstable separatrix along the orbits going through a neighborhood of A_i. In suitable coordinates (ξ,η) it has the form:

$$\xi = c\eta^{\nu_i} \tag{7}$$

where η is a deviation from the stable manifold and ξ is the deviation from the unstable one, c is a constant and

$$\nu_i = -(1-\rho_{ii+1})/(1-\rho_{i+1i}) \equiv (\rho_{ii+1}-1)/(1-\rho_{i+1i}) \tag{8}$$

is the «saddle value» [10]. If $\nu_i >1$ then the map (7) is a local contraction and P_i is a dissipative saddle. If $\nu_i <1$ then (7) is a local expansion.

Stability of the heteroclinic contour. The following result tells us that the

contour $\Gamma=\cup_{i=1}^{N}\Gamma_i \vee A_i$ can be an attractor.

Theorem 1. *Assume that conditions (4), (5), (6) are satisfied and*

$$v = \prod_{i=1}^{N}[(\rho_{ii+1}-1)/(1-\rho_{i+1i})] > 1 \tag{9}$$

(here i+1=1 if i=N). Then there is a neighborhood U of the contour Γ such that for any initial condition $a^0=(a_1^0,\ldots,a_N^0)$ with $a^0_i>0$, one has $dist(a(t),\Gamma)\to 0$ as $t\to\infty$ where $a(t)$ is the orbit going through a^0.

The proof of the theorem is based on the construction of the Poincaré map along orbits in a neighborhood of the contour Γ (see [11]).

Birth of a stable limit cycle. Robustness

A direct corollary of Theorem 1 is the possibility of the birth of a stable limit cycle in an appropriately perturbed system. Consider the system

$$\dot{a}_i = a_i\left[1 - (a_i + \sum_{j\neq i}^{N} \rho_{ij} a_j)\right] + \varepsilon\Psi_i(a) \tag{10}$$

that coincides with (2) for $\varepsilon=0$, where $a=(a_1,\ldots,a_N)$ and Ψ_i is a smooth function, $i=1,\ldots,N$. For small $\varepsilon>0$ the system (10) has saddle equilibrium points $A_{i\varepsilon}$ and separatrices $\Gamma_{i\varepsilon}$ (the half of $W_{i\varepsilon}^N$ such that $A_{i\varepsilon}\to A_i$, as $\varepsilon\to 0$ and $lt_{\varepsilon\to 0}\Gamma_{i\varepsilon}\supset\Gamma_{ii+1}$, here *lt* means the topological limit, i.e. the set of the accumulation points).

Theorem 2. *Assume that the conditions of Theorem 1 are satisfied,*

$$lt_{\varepsilon\to 0}(\cup_{i=1}^{N} \Gamma_{i\varepsilon}) = \Gamma \tag{11}$$

and at least one of the separatrices $\Gamma_{i\varepsilon}$ is not a heteroclinic orbit. Then for any sufficiently small $\varepsilon>0$ the system (10) has a stable limit cycle L_ε (in a neighborhood of Γ) such that $lt_{\varepsilon\to 0}L_\varepsilon=\Gamma$.

The proof of this Theorem can be done in the standard way, i.e., by construction of the Poincaré map and by showing that this map is a contraction in an absorbing region. The condition (11) (or a similar condition) is necessary and sufficient for the existence of an absorbing region [11].

Numerical results show that the system (10) where $\Psi_i(a)\geq 0$ satisfy the condition (11) and has a stable limit cycle (see Fig. 1). In this example, the simulations were performed with the following equations:

$$\dot{a}_i = a_i(1-\sum_{j=1}^{N=6} \rho_{ij}a_j) + \varepsilon a_i a_{i+3} \tag{12}$$

where $i=1,2,\ldots,6$ and $i+3 \equiv i-3$ if $i>3$. We used the following values of the connection matrix $\rho_{ij}\neq 0$:

$$\rho_{1,3} = \rho_{3,5} = \rho_{5,1} = 5.0; \quad \rho_{4,6} = \rho_{2,4} = \rho_{6,2} = 2.0;$$

$$\rho_{1,6} = \rho_{2,1} = \rho_{3,2} = \rho_{4,3} = \rho_{5,4} = \rho_{6,5} = 1.5; \tag{13}$$

$$\rho_{1,1} = \rho_{2,2} = \rho_{3,3} = \rho_{4,4} = \rho_{5,5} = \rho_{6,6} = 1.0$$
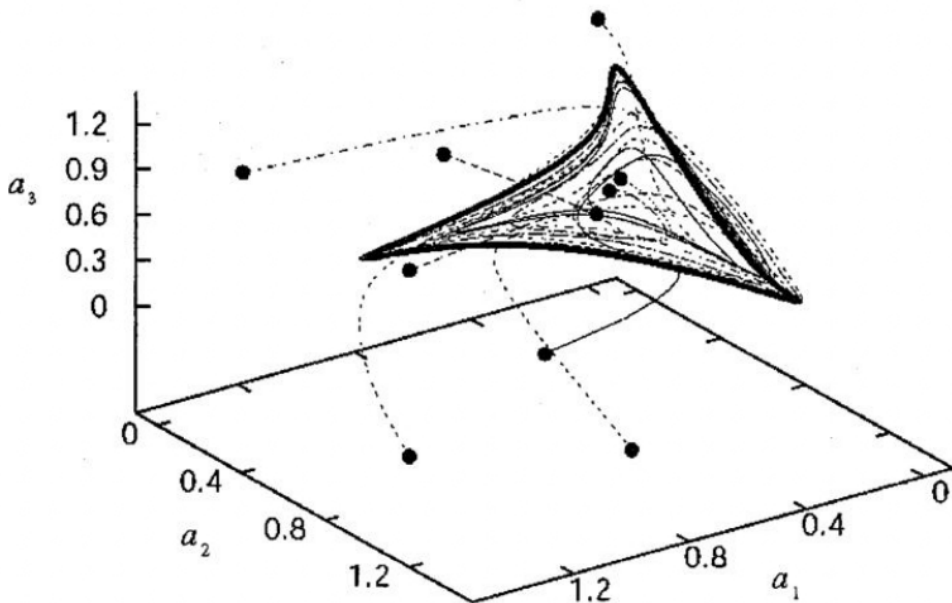
with $\varepsilon=0.01$.

Fig. 1. Small 3D projection of the 6-dimensional system (12) showing examples of trajectories falling into the limit cycle from different initial conditions. As the numerical results indicate, this limit cycle in the vicinity of the former heteroclinic contour is a global attractor

Computation with separatrices in the olfactory system

We have used observed features of olfactory processing networks [12] as a guide to the study of computation using competitive networks. In Figure 2 we show the simultaneously recorded activity of three different projection neurons (PNs) in the locust olfactory system, i.e. antennal lobe (AL), evoked by two different odors: despite similar PN activities before the stimulus onset (the result of the action of noise) each odor evokes a specific spatio-temporal activity pattern that results from interactions between these and other neurons in the network [12]. WLC networks produce identity-temporal or spatio-temporal coding in the form of deterministic trajectories moving along the heteroclinic contour. The saddle states in this case correspond to the activity of specific neurons or groups of neurons and the separatrices connecting these states correspond to sequential switching from one state to another.

From the experimental results we infer that a stimulus acts in two principal ways as we hypothesize above: (1) it excites a subset of projector neurons; (2) it modifies the effective inhibitory connections between the projector neurons as a result of the activation of the inhibitory interneurons that connect different PNs. The intrinsic dynamics of these neurons is governed by many variables corresponding to ion channels and intracellular processes. Such detailed description however is not needed to illustrate the principle of «coding with separatrices». We need only to capture the «firing» or «not-firing» state of the component neurons. We thus simplify the model to an equation for the firing rate $a_i(t)>0$ of neural activity, and thus we arrive to model 1.

When the inhibitory connections are not symmetric, the system with N competitive neurons has different heteroclinic contours depending on the stimulus. The heteroclinic contours are global attractors in the phase space and can be found for a range of values of $\rho_{ij}(S)$. This implies that if the stimulus is changed, another orbit in the vicinity of the heteroclinic contour becomes a global attractor for this stimulus, and guaranties a big capacity of the spatio-temporal representation of the odors [4].
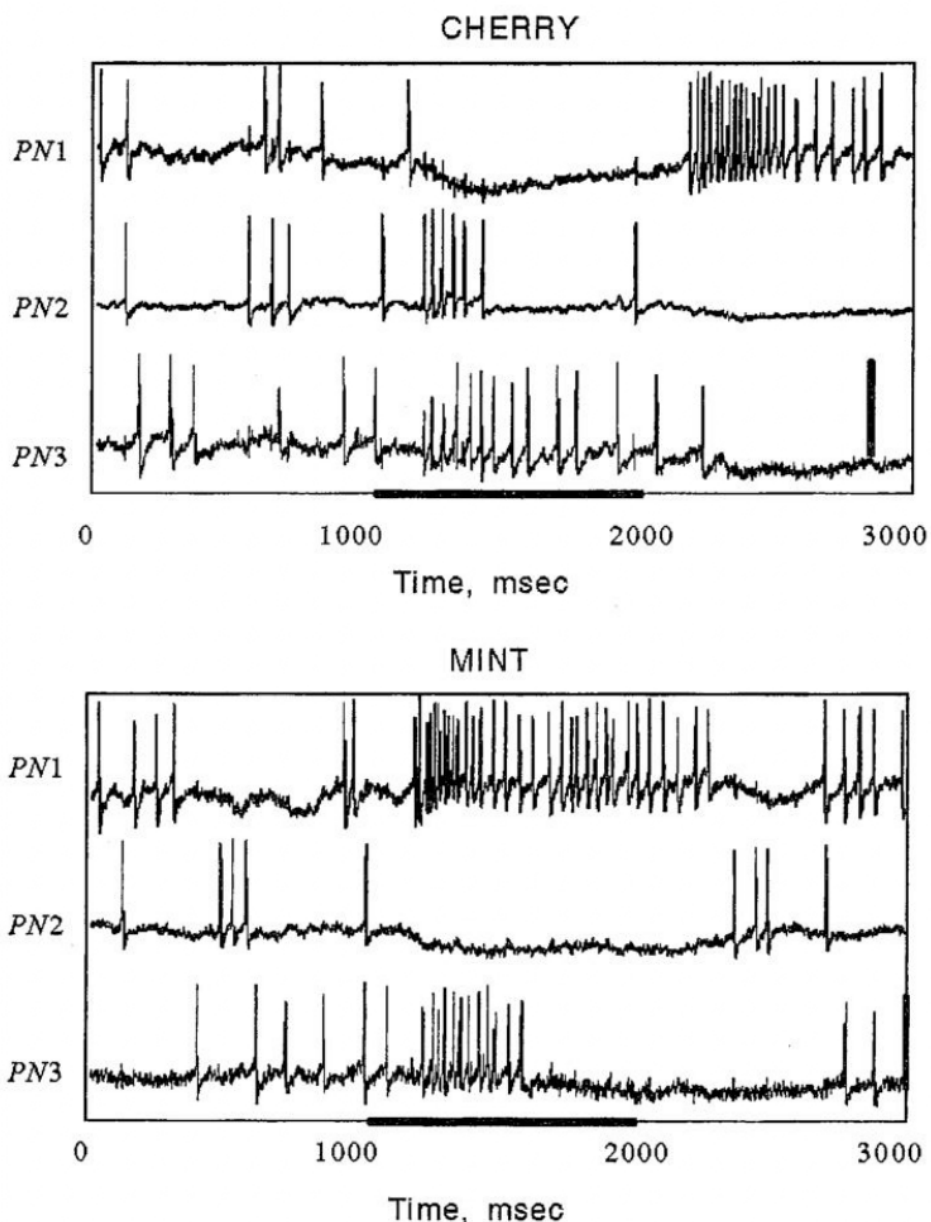
Fig. 2. The temporal patterns produced by three simultaneously sampled PNs in the locust antennal lobe when two different odors are presented during the time interval from 1000 to 2000 msec. The horizontal bar indicates the time interval when the stimulus was presented (see [12] for details)

Our numerical simulations [12] show that the network produces different spatio-temporal patterns in response to different stimuli and model the real data from the antennal lobe of the locust.

Chaotic dynamics of competitive patterns: hunting behavior of Clione

Neural networks with WLC dynamics are able to generate new information to answer a simple external signal. Such information can be used for the organization of

complex activity and, in particular, chaotic behavior of some animals. Let us consider the hunting activity of a marine mollusk *Clione*. This mollusk is a predator lacking a visual system. It feeds on a small mollusk, *Limacina*. The hunting behavior is a random search for prey: *Clione* «scans» the surrounding space in order to locate and catch the prey. Such behavior is turned on by the smell of the *Limacina*. The main role in the organization of such motion of *Clione* is played by a sensory neural network inside the statocyst (see Fig. 3). The statocyst is a special sensory organ responsible for the orientation in the gravitational field [13].

It is well known from the physiological data that the statocysts have up to 12 receptor neurons (SRNs) that are coupled with inhibitory synapses [13]. These neurons respond to the pressure exerted by the statolith, a stone located inside the statocyst. If no information about a prey (received by the chemical receptors) is present, the receptor neuron D (down, see Fig. 3) is excited by the statolith and it inhibits other SRNs. As a result, the information generated by D SRN arrives to the corresponding Central Pattern Generators (CPGs) that control the tail and wing movements. These CPGs establish the habitual «head up» position of *Clione*'s body. If the Hunting Central Neuron (HCN) receives a message from the chemo-sensors about the presence of a prey, HCN excites some SRNs and inhibits others. The behavior of the *Clione* in this case does not depend on the direction of the gravitational field and it moves in a random-like trajectory.

For the phenomenological modeling of the statocyst «hunting» dynamics we can neglect the statolith inertial dynamics and take into account the only key point: the position of the mollusk's body uniquely depends on the message that SRNs are sending to the central neurons that produce the commands to the CPGs. Thus, as a starting point, we consider just a SRN network under the action of the HCN excitation. We suppose that, as a result of the HCN stimulation, all SRNs («left», «right», «back», «front», «down», and «up») are in the same situation: they receive and send two inhibitory synapses (see Fig. 3, right panel).

The dynamics of the SRN's network can be described by model (1). In this case, $a_i > 0$ represents the instantaneous spiking rate of the receptor neuron i, $H_i(t)$ represents the stimulus from the hunting neuron to neuron i, and $S_i(t)$ represents the action of the statolith on the receptor that is pressing. When there is no stimulus from the hunting
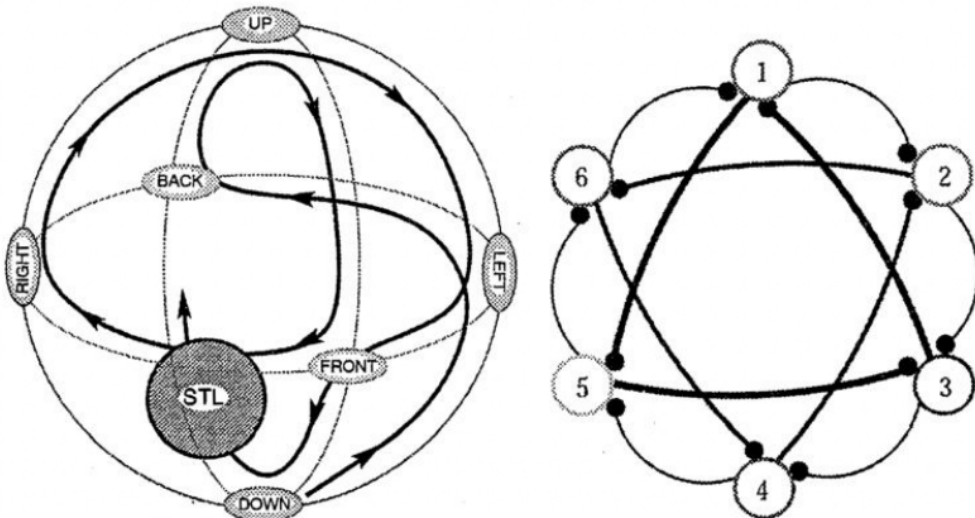

Fig. 3. Left panel: schematic representation of the statolith (STL) motion exciting different receptor neurons inside the statocyst. Right panel: inhibitory connections used in this network (thicker traces mean stronger inhibition)
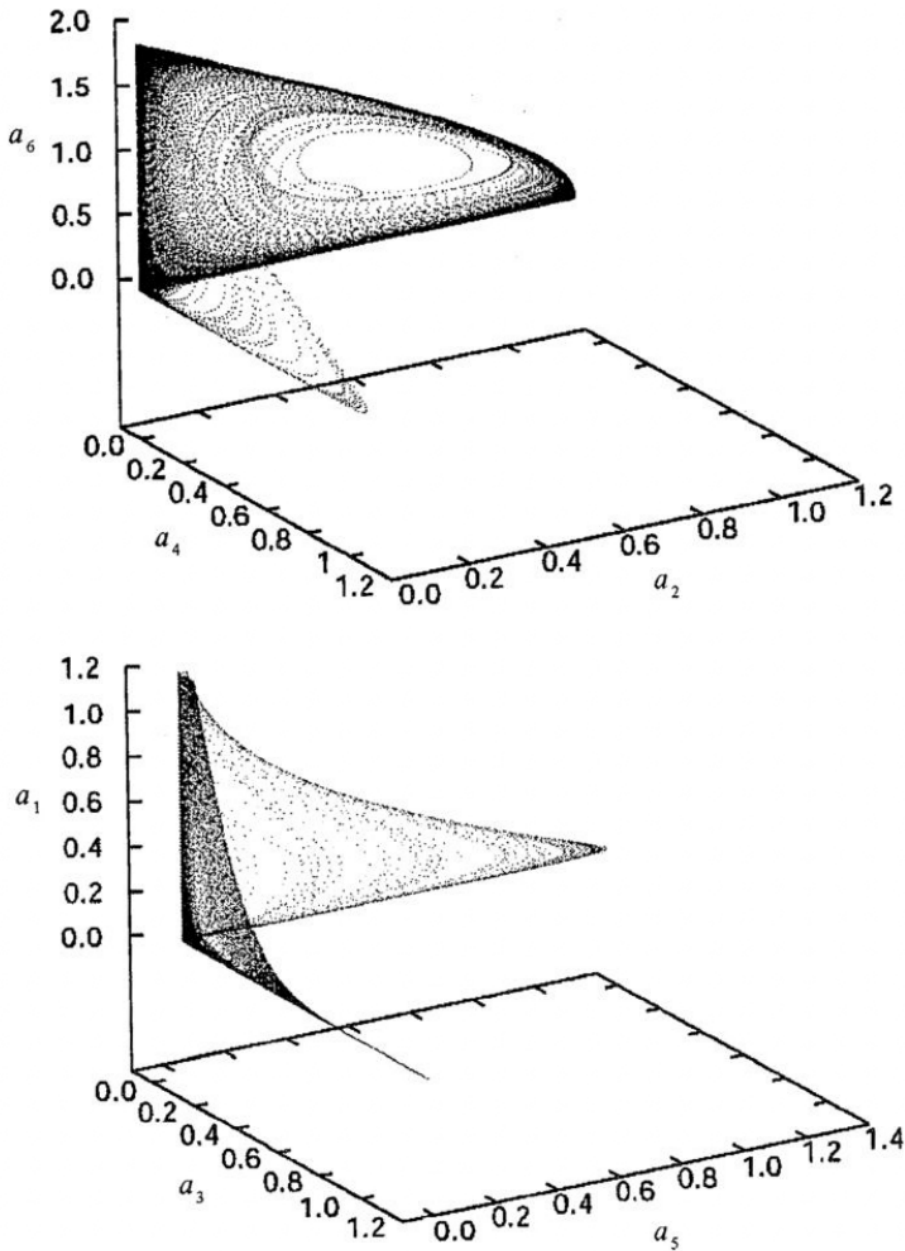
Fig. 4. Projections of the attractor from the six-dimenional phase space to two different three-dimensional spaces

neuron ($H_i=0,\forall i$) or the statolith ($S_i=0,\forall i$), then $\sigma(H,S)=-1$ and all neurons are silent; $\sigma(H,S)=1$ when the hunting neuron is active and/or the statolith is pressing one of the receptors. In our simulations, we have used the values $\rho_{ij}\neq0$ specified in (13).

When there is no activation of the sensory neurons from the hunting neuron, the effect of the statolith ($S_i\neq0$) in this model is to induce a higher rate of activity on one of the neurons (the neuron i where it rests for a big enough S_i value). We assume that this higher rate of activity affects the behavior of the motoneurons to organize the head up position. The other neurons are either silent or have a lower rate of activity and we can suppose that they do not influence the posture of *Clione*.

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When the hunting neuron is active a completely different behavior arises. We assume that the action of the hunting neuron overrides the effect of the statolith and thus $S_i \approx 0$, $\forall i$. The dynamical system (1) with the ρ_{ij} values specified above (see also Fig. 3) and with a stimuli from the hunting neuron given, for example, by $H_i = (0.730, 0.123, 0.301, 0.203, 0.458, 0.903)$ has a strange attractor in the phase space (see Fig. 4). This means that the SRN network generates new information (a chaotic signal with positive Kolmogorov-Sinai entropy) in the presence of the prey, which controls the CPGs and, in fact, organizes the random-like behavior of *Clione*.

The origin of the chaoticity in such dynamical system can be explained in the following manner [5]: due to the diversity in the strengths of the inhibitory connections we may consider the complete network as two weakly coupled WLC triangle networks. Independently each of them has a closed heteroclinic loop (see Fig. 1), which becomes a limit cycle under the action of a small perturbation (for example, a stimulus). The periodic oscillations corresponding to these limit cycles have, in general, different frequencies that are extremely sensitive to the distance to the heteroclinic loop in the non perturbed system (such oscillations are strongly non-synchronous). As we showed the weak interaction of these WLC triangles (nonlinear oscillators) generate chaos in wide regions of the control parameter space. New experiments have confirmed the validity of the model [14].

Discussion

We have tried to show that the computation with separatrices based on the WLC principle is a very natural and powerful strategy for information processing in real neural systems. Any kind of sequential activity can be programmed by a network with stimulus dependent nonsymmetric inhibitory connections. It can be the creation of spatio-temporal patterns of motor activity, the transformation of the spatial information into spatio temporal information for successful recognition and many other computations. In addition, we wish to mention that two important computational functions can be successfully implemented by computation with separatrices. These are: (i) sequential memory storage, and (ii) feature binding.

In reference [15] the authors suggest a new biologically-motivated model of sequential spatial memory which is based on the WLC principle. Each stimulus event (visual image, odor, etc...) is represented by a saddle point in the phase space of the system, and a network of one-dimensional separatrices leads the system along the sequence of events in the specific episode. After the learning process, such system is capable of an associative retrieval of the pre-recorded sequence of spatial patterns.

A binding problem occurs when two (or more) different events, e.g. scenes, features, or behaviors are represented by different neural ensembles simultaneously, and for some reason they are all connected with each other. Eventually, these coherent features are integrated by the nervous system of the animal onto a perceptual object, even if the features are dispersed among different sensory systems or subsystems. The binding is ubiquitous and occurs whenever a simultaneous remembrance or representation is important. The most common approach in the modeling of binding is to involve time in operation (von der Malsburg, Singer, and others). The idea is to use the coincidence of certain events in the dynamics of different neural units for binding. This is a dynamic binding. Usually, dynamic binding is represented by synchronous neurons or neurons that are in resonance with an external field. However, dynamical events like phase or frequency variations usually are not very reproducible and robust. It is reasonable to hypothesize that brain circuits that display sequential switching of neural activity [7] use the coincidence of this switching to implement dynamic binding of different WLC networks.

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