Sensory Coding with Dynamically Competitive Networks

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Abstract

Studies of insect olfactory processing indicate that odors are represented by rich spatio-temporal patterns of neural activity. These patterns are very difficult to predict a priori, yet they are stimulus specific and reliable upon repeated stimulation with the same input. We formulate here a theoretical framework in which we can interpret these experimental results. We propose a paradigm of “dynamic competition” in which inputs (odors) are represented by internally competing neural assemblies. Each pattern is the result of dynamical motion within the network and does not involve a “winner” among competing possibilities. The model produces spatio-temporal patterns with strong resemblance to those observed experimentally and possesses many of the general features one desires for pattern classifiers: large information capacity, reliability, specific responses to specific inputs, and reduced sensitivity to initial conditions or influence of noise. This form of neural processing may thus describe the organizational principles of neural information processing in sensory systems and go well beyond the observations on insect olfactory processing which motivated its development.

Sensory networks in the brain effortlessly solve very complex pattern learning, pattern storage, and pattern recognition problems. These problems are complex because the natural environments in which animals live are noisy and nonstationary and because natural patterns such as faces, animal calls or odors are multidimensional, unpredictable by the animal, and remarkably numerous. This ease of computation and striking reliability is perhaps perplexing as the computing elements of the brain, our neurons, are often considered to be unreliable electrical devices. Just how the brain represents, stores, and recalls complex sensory inputs using these neurons remains a major challenge in neuroscience.

Many agree that the brain uses distributed and combinatorial codes for sensory representations: codes in which input-specific information is contained across populations of coarsely tuned neurons [1],[2]. However, the possibility that the dynamics of neural circuits, that is the temporal behavior exhibited by groups of interconnected neurons[3],[4],[5],[6],[7],[8] are also centrally important in sensory coding is not yet widely accepted. There appear to be two reasons for this reluctance. First, while stimulus or behavior-specific temporal patterns of neural activity have been observed in a few systems, their relevance for perception or action has so far been difficult to establish directly. Second, in the few cases where information theory has been applied to the analysis of single neuron responses, the temporal features of those responses accounted for only a small fraction of their variance [9],[10],[11],[12],[13]. As applied to single neurons, then, average firing rate measurements appeared to convey most of the information that could be theoretically extracted from sensory spike trains\textsuperscript{1}.

Dynamical Odor Representation: Experimental Data

Experiments conducted in our laboratory and elsewhere directly address these two objections. The observations show that (1) temporal and relational features of neural activity contain

\textsuperscript{1}We do not consider here the case in which the timing of spikes represents the time variations of the stimulus. Rather, we focus on neural dynamics as an intrinsic component of a stimulus representation and not on its time evolution alone.
information which is not captured in firing rates and cannot be found by considering single neurons alone [14], [15] and (2) such temporal/relational features are required for certain sensory discrimination tasks [16] as well as for optimal decoding by downstream neurons [17]. Circuit dynamics thus appear relevant not only for an observer deciphering brain codes but also, and more importantly, for the animal’s own sensory performance.

What form do these temporal patterns take? Our observations focused on olfactory processing in locust and bees. The insect antennal lobes, the analog of the vertebrate olfactory bulb [18], contain two classes of neurons: (1) the excitatory projection neurons (PN), the analog of mitral cells in vertebrates, which send signals downstream to other brain structures, and (2) inhibitory local neurons (LN), the analog to granule cells in vertebrates, whose projections are within the antennal lobe only. In locust all odor related information is carried by 830 PNs from each antennal lobe [19]. Each odor, regardless of its complexity, evokes synchronized and oscillatory activity in the 20-30 Hz range, but only in a specific subset of these PNs [20]. Probably no more than 20% are excited by any particular odor. Individual PNs, however, display slower odor and PN-specific response patterns superimposed on their fast global oscillatory coordination. Consequently, pairwise synchronization of PNs is usually transient [14], [15]. An odor representation can thus be thought of as an evolving PN assembly whose members are progressively updated throughout the duration of a stimulus. Although PN update is orchestrated at an overall rate of 20-30 Hz, the slower aspects of individual PN responses do not appear to contain periodic motifs.

If an odor stimulus is sustained for several seconds, olfactory receptor adaptation diminishes the PN/LN network activation. We can thus experimentally study the spatio-temporal evolution of this system for a limited time during each presentation of the stimulus. Nonetheless, we observe that this evolution remains stable over repeated, identical stimulations. This leads us to the central question of this paper: What advantages, if any, could this rich, distributed spatio-temporal behavior present for stimulus representation or classification?

To answer this question, we must first understand the origin of the dynamical aspects of this representation. Only then will we be able to construct models which embody these dynamical rules. Two of the main experimental features we want to capture are (1) stimulus-evoked nonstationary and irregular spatio-temporal waveforms, or patterns, and (2) stability of these patterns in time and neuron space over repeated presentations of the stimulus, despite the natural fluctuations in the stimuli and in the neural system. To achieve these observed biological features, we cannot use the now familiar strategy for representing odors and other sensory inputs which seeks to associate a basin of attraction - more particularly the attractor in that basin - with each specific input. We have developed a different strategy.

**Dynamical Competition: Principles**

We hypothesize, guided by our experiments, that the transient dynamics of the system embodied in its state space trajectory is dictated by the input itself. The state space of the autonomous (nonstimulated) system is enlarged by the degrees of freedom contained in the stimulus upon reception of the input, and dynamical evolution within that space occurs in an input dependent way. The trajectory followed by the system then defines the only
global attractor associated with the particular input. In other words the system does not seek attractors in pre-existing basins of attraction defined by the network alone.

We describe below a set of simplified, biologically realistic mathematical models which realize this idea. They produce a dynamical evolution which does not go to an attractor of the stimulus free system but rather realizes a rich set of input-dependent trajectories.

The basic principle relies on a dynamical competition between evolving groups of PNs interconnected by inhibition through the LNs. In state space this continuing competition is embodied in trajectories in the neighborhood of heteroclinic orbits, appearing as a sequence of “ribs” in state space, connecting unstable fixed points or limit cycles of the system. In this view of sensory information processing, the solution to the decoding/recognition problem lies not in the attractors of the autonomous dynamical systems but in the orbits themselves. A state space representation of this kind of trajectory is displayed in Figure 1a.

As observed in experiments, specific odors are represented not only by specific groups of excited neurons but also by the temporal sequence of their activation. To reproduce the very specific stimulus dependent transient behaviors seen in biology the system must be strongly dissipative. Under such conditions, a trajectory, initiated by a given input, rapidly converges to the heteroclinic sequence associated with the particular stimulus. This rapid convergence is essential for the reliability of this mode of representation.

There are surely many possible implementations of this general idea. We provide here examples which are appealing because of their biological underpinnings, their relative simplicity and their potential generality.

**Dynamical Models: Architecture**

The main features of our model are

- The network can be described as a set of neural ensembles or layers coupled by inhibition and excitation.

- Each ensemble contains two types of neurons: excitatory PNs and inhibitory LNs. In our model the PNs and LNs are in one to one proportion for reasons of simplicity. In the locust antennal lobe the ratio is more like 3/1 [19]. The exact ratios are not important.

- The PN/LN pairs are not reciprocally connected. An excited PN does not directly excite the LN which inhibits it. This is supported by antennal lobe data [19], [21].

- Excitatory connections between PNs can be random, sparse dense, or “all to all” without altering the basic properties.

- Each ensemble is part of a lattice with internal inhibitory connections. In the simplified models considered here all PNs receive the same number of inhibitory inputs.
• The inhibitory connections within ensembles have characteristic time scales different from those between ensembles. Fast and slow inhibition with different pharmacological properties have been demonstrated in the locust system [14], [21].

• Spiking activity in PNs is very low in the absence of sensory input. Upon receiving an input, a PN rises above threshold and one or more action potentials result.

To demonstrate how dynamical competition works, we neglect many important points about real biological neural assemblies. These include the action of the sensory inputs on the LNs [18] and the variation of synaptic weights over time, perhaps reflecting adaptation or short-term plasticity in the network. These processes are probably essential for the subsequent steps of neural processing including learning and recognition, which we do not address directly here.

A simple realization of our proposed architecture is seen in Figure 1b where the lateral inhibitory connections form hexagons. We assume that the groups of neurons excited by different receptors through a glomerulus are not overlapping and the inhibition between the groups is cyclic. Despite its symmetry each of these networks exhibits rich transient dynamics upon stimulation. The critical feature of each network is the absence of reciprocal inhibition of the PNs or of the families of PNs that form a closed network. Such a connection scheme could turn off the excitatory output from one glomerulus and turn on another. It is crucial to realize that these connectivity schemes represent functional, and not simply anatomical connections. In other words, many anatomical connectivity schemes can be equated to this functional matrix.

The simplified model presented in Figure 1b with high symmetry and no random connections is still quite complex. To allow analysis we further simplify the model. We take all neurons with the same “color” within the same ensemble to be tightly synchronized, and we treat them as a single neuron. The circuit is then reduced to the cyclic model in Figure 1c consisting of nine groups of neurons.

We have investigated several implementations of this simplified model: (1) “averaged neurons” with smoothed voltage responses to a stimulus, and (2) two dimensional FitzHugh-Nagumo oscillators with periodic spiking. We will first describe an “averaged” model to provide some insight into the underlying dynamics of this circuit. We will then examine networks constructed from FitzHugh-Nagumo neurons.

**Averaged Dynamics**

We begin by considering one triplet of coupled neurons from the nine neuron model seen in Figure 1c. We characterize each neuron by its “activity” $Y_i(t) \geq 0$. The interaction among neurons is quadratic in $Y_i(t)$ reflecting simplified inhibitory synaptic connections acting without the usual threshold and time delay. These $Y_i(t)$ are taken to satisfy dynamical equations of the form

$$\frac{dY_i(t)}{dt} = Y_i(t)\left\{\sigma(E_i(t) + S_i(t)) - \sum_{k=1}^{3} \rho_{ik} Y_k(t)\right\}, \quad (1)$$
where \( \sigma(x) \) is the threshold function
\[
\sigma(x) = 1 - \frac{2}{1 + e^{10(x-0.4)}},
\]
and
\[
E_i(t) = g_e \sum_{k \neq i} Y_k(t),
\]
\( g_e \) is the strength of excitatory connection, \( S_i(t) \) is the input sensory stimulus arriving at neuron \( I \), \( E_i(t) \) is the excitatory input from other neurons in the ensemble or triplet, and the \( \rho_{ik} \) are the strengths of inhibitory synapses within the same ensemble.

When there is no input, \( S_I = 0 \), the threshold function is \( \sigma(x) \approx -1 \), each activity is strongly damped and all \( Y_i \rightarrow 0 \). When an input activates neuron \( I \), \( \sigma(x) \approx +1 \), the dynamics of that neuron near \((0,0,0)\)—the rest state—becomes unstable and its activity grows exponentially rapidly towards one of the unstable fixed points \((1,0,0)\), \((0,1,0)\), or \((0,0,1)\). Because these fixed points are also unstable, the trajectory approaches one of them, for example, \((0,0,1)\), and never quite reaches it before the instability of that fixed point drives it towards another, for example \((0,1,0)\). The activity \( Y_3 \approx 1 \) enters the equation for both \( Y_1 \) and \( Y_2 \) through \( E_1 \) and \( E_2 \) and further destabilizes motion near the other fixed points. The trajectory, determined in detail by the stimulus pattern \((S_1, S_2, S_3)\), continues to traverse the heteroclinic region until the stimulus is removed at which time the system returns to the rest state.

An input pattern (for example, a spike train from afferents integrated to provide a pulse of some longer duration) produces a well determined, reproducible pattern of firing both in space (neuron identity) and time. Different input patterns will give rise to different sequences of waveforms in each individual neuron.

In Figure 2a we show the sequence of waveforms in one of these triplets arising from the input choice \( S_I = (0.721, 0.089, 0.737) \) over a fixed time interval (zero otherwise). Its phase space portrait \((Y_1(t), Y_2(t), Y_3(t))\) is displayed in Figure 2b. One can see the elements of sequential firing observed experimentally as well as the basic dynamical idea which is a trajectory transformation along the “ribs” of the heteroclinic connections between the unstable fixed points of our system. If we change the stimulus to \( S_I = (0.189, 0.037, 0.342) \) representing a different “odor”, the pattern changes markedly as also observed experimentally (Figure 2c,d).

The next level of complexity introduces a network of three ensembles of such triplets interconnected by inhibition. This structure resembles that within a triplet but we have increased the spatial scale on which the dynamics operates. We now have the following equations for the activity of the \( I^{th} \) neuron in the \( \alpha^{th} \) triplet \( Y_I^\alpha(t) \)
\[
\frac{dY_I^\alpha(t)}{dt} = Y_I^\alpha(t) \left\{ \sigma(E_I^\alpha(t) + G_I^\alpha(t) + S_I^\alpha(t)) - \sum_{k=1}^{3} \rho_{ik} Y_k^\alpha(t) - g_i \sum_{k} Y_{k(\alpha+1) \mod 3} \right\},
\]
where \( E_I^\alpha(t) = g_e \sum_{k \neq i} Y_k^\alpha(t) \) is the PN excitatory input from other neurons within the triplet, \( G_I^\alpha(t) \) are excitatory inputs from the other triplets to element \( Y_I^\alpha(t) \), and \( g_i \) is the
strength of inter-ensemble inhibition. $S^\alpha_I(t)$ is the externally imposed sensory input to neural

element $I$ found within neural triplet $\alpha$.

This network of triplets with constituent averaged neurons evolves as described earlier. No single ensemble can remain excited as the stable state of the dynamics. Each one is active only transiently, intermittently or possibly not at all, depending in detail on the input configuration (see Figure 3). Each input evokes, and is therefore represented by, a specific trajectory in the state space of the system as a whole.

**Spiking Neurons**

We next add spiking behavior of the simplest sort to these “averaged” neurons by using a FitzHugh-Nagumo model for each PN in the network. This provides a limit cycle at each neural node. While this addition falls short of a conductance-based description, it captures another essential feature of the neural dynamics.

The basic triplet of the dynamically competitive network is now described by a membrane voltage $U_i(t)$, a slow current $I_i(t)$ and a postsynaptic variable $v_i(t)$ satisfying

\[ \epsilon \frac{dU_i(t)}{dt} = f(U_i(t)) - I_i(t) - \gamma_1(U_i(t) - \bar{U}_I)v_{I-1}(t) + S_i(t), \]
\[ \frac{dI_i(t)}{dt} = U_i(t) - bI_i(t) + a, \]
\[ \alpha_1 \frac{dv_i(t)}{dt} = \sigma(U_i(t)) - v_i(t), \]

in which the three FitzHugh-Nagumo neurons are connected by the inhibitory coupling $-\gamma_1(U_i(t) - \bar{U}_I)v_{I-1}(t)$. $v_0(t) = v_3(t)$, $\bar{U}_I = \min(U_I(t)) \simeq -1.5$, $f(U) = U - U^3/3$ and $\sigma(U)$ is a step function. When a stimulus $S_I \geq 0.4$ is provided to this triplet, one or more of the $v_i$ is driven into activity by the increase in membrane voltages. This in turn drives the network, via the inhibitory couplings from neighboring neurons, along separatrix-like orbits. Our results are shown in Figure 4. One can clearly see the dynamical competition among unstable regions of the state space. Each unstable region is now characterized by nearly periodic behavior associated with the limit cycle or periodic spiking activity.

The final embodiment of our dynamical competition network combines three of these spiking triplets in a fashion similar to that for the averaged neurons above. We associate a fast membrane potential $U^\alpha_I(t)$ with the $I^{th}$ neuron in the $\alpha^{th}$ ensemble along with a slow current $I^\alpha_I(t)$ and two postsynaptic variables $v^\alpha_I(t)$ and $w^\alpha_I(t)$ corresponding to fast and slow inhibition respectively.

The dynamics are now specified by equations:

\[ \epsilon \frac{dU^\alpha_I(t)}{dt} = f(U^\alpha_I(t)) - I^\alpha_I(t) - \gamma_1(U^\alpha_I(t) - \bar{U}^\alpha_I)v^\alpha_{I-1}(t) \]
\[- \gamma_2(U^\alpha_I(t) - \bar{U}^\alpha_I) \sum_i w^{\alpha-1}_i(t) + S^\alpha_I(t), \]
\[ \frac{dI^\alpha_I(t)}{dt} = U^\alpha_I(t) - bI^\alpha_I(t) + a, \]
\[ \begin{align*}
\alpha_1 \frac{dv_1^\alpha(t)}{dt} &= \sigma(U_1^\alpha(t)) - v_1^\alpha(t), \\
\alpha_2 \frac{dw_1^\alpha(t)}{dt} &= \sigma(U_1^\alpha(t)) - w_1^\alpha(t).
\end{align*} \]

\[ w_1^0(t) = w_3^0(t) \text{ and } v_1^0(t) = v_3^0(t). \]

In Figure 5a we show the time courses for a network composed of three triplets of FitzHugh-Nagumo neurons connected as displayed in Figure 1c. This is now a set of nine membrane voltages in which the evolving firing patterns associated with dynamical competition are clearly visible. The global spiking activity resembles the global spatio-temporal activity observed in our experiments in the antennal lobe. The time series of two simultaneously recorded PNs are presented in Figure 5b.

**Dynamical Competition in the Presence of Error and Noise**

To be useful our dynamical model must exhibit both the reliability and the noise tolerance observed in the biological system. Since any network is subject to internal and external fluctuations, our model must produce very similar orbits when noise is present in the network and the stimulus. These features are part of the dynamics of our networks.

**Insensitivity of Patterns to Initial Conditions**

Using our “averaged neurons” we investigated the critical question of reproducibility of the spatio-temporal patterns when the initial conditions for the network were varied. We selected initial conditions uniformly distributed within a sphere of radius \( R \) around the origin of \( Y_1^\alpha \) space. This captures the idea that the network can be in a set of states near the “rest state” when the stimulus arrives. For each \( R \) we calculated the orbits starting in this sphere, and then we evaluated the cross-correlation function \( C_\tau(R) \) between orbits at \( R > 0 \), representing uncertain initial conditions, and orbits at \( R = 0 \), representing well specified initial conditions.

\[ C_\tau(R) = \frac{\langle (Y_1^\alpha(t) - < Y_1^\alpha(t) >_t)(Y_1^\alpha(t+\tau) - < Y_1^\alpha(t+\tau) >_t) \rangle_{R=0}}{(\text{Variance at } R=0)} \frac{\text{Variance at } R \neq 0}{(\text{Variance at } R \neq 0)} . \]

The averages were made looking at a window of time \( t \) thus allowing us to determine quantitatively how sections of the whole time series “stay together” for this time. Using the whole time period of 3000 to 5000 time units during which the stimulus was presented, we are thus able to examine many windows of potential coherence. We evaluated \( C_\tau(R) \) for \( t = 200 \) and \( t = 400 \) time units. The orbits for \( R \geq 0 \) were time-delayed relative to one another by an amount \( \tau \) selected to minimize cross-correlation. This emphasizes the worst possible case of overlap between orbits starting from different initial conditions. Selecting the initial conditions uniformly in a finite sphere around the origin in \( Y_1^\alpha \) space gives added weight to larger changes in initial conditions than would a Gaussian distribution, also contributing
to minimizing cross-correlation. Finally these averages for each $Y_l^\alpha$ were averaged over all neurons in the network.

In Figure 6 we plot $C_T(R)$ for all inhibitory couplings $g_i = 0.5$ over an averaging window of 200 time steps and for all $g_i = 0.1$ over averaging windows of 200 and 400 time units. When the inhibition responsible for trajectories along the heteroclinic orbits is strong ($g_i = 0.5$), $C_T(R)$ drops from a maximum at $R = 0$ to a plateau of about 0.84 for $R \geq 0.05$. This indicates an 84% reproducibility of the trajectories of our system, namely a remarkable insensitivity to the initial state of the system at the time of stimulation.

With weaker inhibitory coupling ($g_i = 0.1$), the cross-correlation drops only to 0.75, indicating the still enormously high reliability of spatio-temporal trajectories in $Y_l^\alpha$ space. This small dependence on or “forgetting” of the initial conditions relies on the exponentially fast departure from rest as the neural assembly is stimulated. The precise, quantitative rate of that exponential departure depends directly on $g_i$. In the last curve we show $C_T(R)$ calculated over 400 time units. Because of intrinsic instabilities in the nonlinear system and the spread of initial conditions this value is further reduced to about 0.5.

**Robustness of Patterns to Noisy Stimuli**

We now examine the performance of our competitive networks in the presence of internal and stimulus noise, using spiking FitzHugh-Nagumo neurons at each of the nine nodes in the network. Noise was added to each stimulus so that

$$S_l^\alpha(t) = 0.3 + s_l^\alpha g(t) + \eta_l^\alpha + \delta_l^\alpha,$$

where the $s_l^\alpha$ were chosen in the range 0.1 to 0.5; the function $g(t)$ simulates time-dependence of stimulus: it smoothly rises from 0 to 1 and then falls to 0.1 during the presentation of the stimulus. The noise terms $\eta_l^\alpha$ were uniformly distributed variables with maximum values ranging from 1% to 20% of the stimulus $s_l^\alpha$. The terms $\delta_l^\alpha$ with $|\delta_l^\alpha| = \delta \in [0, 0.1]$ represent the “offset” of the stimulus. Noise with a maximum level close to the firing threshold was added to each dynamical variable, the $U_l^\alpha, I_l^\alpha$, etc of the Fitzhugh-Nagumo equations.

Figures 7a and 7b plot spatio-temporal patterns obtained with respectively 1% and 15% stimulus noise $\eta_l^\alpha$. at $\delta = 0$. In Figure 7a the noise level in the system was below threshold and no spikes were generated in the absence of a stimulus. In Figure 7b, we raised the noise level above threshold, and spikes were generated randomly even in the absence of a stimulus.

Can the dynamical competitive network reproduce the patterns associated with a particular stimulus even in the presence of noise? We estimated the topological similarity of patterns produced with different levels of noise by calculating the overlap $G_l^\alpha(\delta, \tau, \eta)$ of their spike envelopes with and without stimulus noise $\eta_l^\alpha = 0$, for each neuron. This overlap is a function of the variance in the stimulus $\delta$ and the time scale of the dynamics $\tau$. The time scale is important because noise keeps the orbit from approaching the heteroclinic orbits and changes the response time scale for spiking.
To characterize reproducibility over the whole network, we evaluated the product of these functions $G(\delta, \tau, \eta) = \prod_{I, \alpha}(G^\alpha_I(\delta, \tau, \eta))$ over all the neurons. The normalized functions $G/G_{\text{max}}$ for noise levels $\eta = 0.01$ and $\eta = 0.15$ are shown in Figures 7c and 7d. Even in the presence of substantial noise, the peak in the overlap function is very sharp and appears near the original stimulus at $\delta = 0$, indicating that the competitive network can reliably “recognize” the stimulus in the presence of noise.

**Discussion**

We have proposed an innovative class of neural network models whose dynamics reproduce the rich spatiotemporal features observed in insect olfactory networks. Our goal was to determine whether this seemingly complex form of information coding, whose biological relevance has been shown experimentally [15], [16], [17] presents clear and possibly general advantages for pattern classification, memory and recognition. We found that stimulus-dependent activity of this type, though indeed spatially and temporally complex, has underlying dynamical order and stability. The physical principles of this mode of representation rely on transient orbits moving between unstable regions of state space (fixed points or limit cycles in our models). Each orbit is defined by an input and has rich structure only as long as the input lasts. This is in strong contrast with the behavior of familiar competitive network structures. In the pioneering work of Hopfield, Cohen and Grossberg [22], [23] for example, input patterns play the role of initial conditions which lead the network to store information or represent stimuli as attractors. These attractors might be fixed points, limit cycles or even strange attractors [24].

Besides this attractor based storage, we propose that the brain uses “winnerless” networks, in which dynamical competition between groups of interconnected neurons produces stimulus-specific orbits in their phase space. In these neural networks, the selection of the system orbit is strongly influenced by network parameters and by nonstationary external inputs as found in a realistic environment. As we have shown here one essential feature of this dynamical mode of representation is that it is remarkably resistant to noise and to wide variations in initial conditions. This conclusion holds even though the trajectories in phase space are not directed towards traditional attractors while the input is present. The fact that stimulus-specific trajectories depend continuously on the input is also a crucial feature of these networks. This continuous dependence means that stationary states of the system, as found naturally between activations by sensory inputs, do not represent stimulus memory traces. In other words, the network resets itself “for free” as soon as stimulation ceases. A fundamental advantage of this mode of representation is that memory capacity is enlarged. Assuming that input memories incorporate these dynamical features, interferences between stored patterns will be reduced-each pattern “traverses” the network’s phase space along a different skeleton-and the probability of a “superposition catastrophe”, familiar to classical attractor networks [25], will be reduced.

The idea that the transient, stimulus-dependent (non-autonomous) behavior of a dynamical system can be used to encode information is, to our knowledge, not found directly in the dynamical systems literature. Nothing that we know suggests that such behavior has
singular or unacceptable mathematical properties. Fortunately, the systems we have used to explore and illustrate our ideas are simple, which should allow mathematical analyses in the future. Our ideas can be linked to a class of control algorithms whose key features rest on selecting a time-dependent input to stabilize an unstable periodic orbit of the autonomous dynamical system (see [26]). Our goal, however, is fundamentally different: we (or nature) exploit(s) the rich properties of the stimulus-driven system instead of stabilizing the autonomous (resting) system, whose state is stable.

It is also interesting to note that the “non-potential” behavior of the trajectories which traverse state-space close to heteroclinic structures has precursors in the dynamical theory of pattern formation. Busse and Heikes (1980) [27] proposed a model for the description of convection in rotating fluids which consisted of three variables representing three sets of fluid rolls oriented at $\frac{2\pi}{3}$ relative to each other. Their model has no stable fixed point, as in our simplified triplet model with stimulus, and evolves along the heteroclinic orbits connecting the three unstable fixed points.

Our dynamical encoding scheme raises a number of important biological questions. For example, if the brain uses such strategies to represent sensory stimuli [28], [29], [30], how are such dynamical patterns decoded? Although this is ultimately an empirical question, it is useful to examine the implications of our proposal. First, we note that temporal decoding algorithms may not pose fundamental theoretical problems ([31], [32], [33]). Second, physiological and behavioral experiments carried out with the insect olfactory system (and which motivated this study) already indicate that time is a relevant parameter for stimulus representation and decoding ([34], [15], [16], [17]). Third, note that even if a decoder of spatio-temporal patterns had a long time constant, i.e., compressed a spatio-temporal representation into a spatial one, our representation would have still gained in precision, because of the intrinsic stability of the dynamical encoding.

The properties of these simplified model networks may also emerge from more realistic circuits having the same general character of dominance by unidirectional inhibitory connections. In particular, if the system is large, it is not necessary to demand that the network architecture be cyclic. A network with sparse, random connections will exhibit the same essential features as our simple, example networks. Indeed, we anticipate that more complex and more realistic networks of neurons and synapses will make dynamical competition behavior even more advantageous and natural for representation, and possibly learning, storage and recognition of sensory inputs. The fundamental scheme we propose is not linked to the nature of the stimulus, though it was clearly suggested by our analysis of odor inputs, nor is it linked to the size of the brain processing the stimulus. The strategy we have described may thus apply to many other brain circuits in insects and other animals, including mammals and constitute a fundamental feature of sensory networks in the brain.

\footnote{It is important to note that such a mode of representation will work best if the time scale of the stimulus is slower than those of the networks representing it}
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**Figure Captions**

**Figure 1** (1a.) The general scheme of dynamically competitive neural models. This is a single triplet of neurons in \((Y_1, Y_2, Y_3)\) space. The unstable fixed points (saddles) at \((1,0,0)\), \((0,1,0)\) and \((0,0,1)\) are connected by three separatrices, the “ribs” in our description. When the network receives a stimulus, an orbit in this space visits the neighborhood of these “ribs” as it move from fixed point to fixed point. (1b) An example of a neural network architecture with “no winner” competition. We portray a set of three groups of PN/LN neurons each organized into a hexagonal lattice. There is unidirectional inhibition between the lattices causing activation of this network to proceed from lattice to lattice in a “no winner” fashion. (1c) Reduction of three lattices of neurons to simplified ensembles of three PNs (red circles) and three LNs (blue circles) coupled with unidirectional inhibition shown by blue arrows and excitatory connections shown by red arrows.

**Figure 2** (2a) Time series of a single triplet of averaged neurons, Equations (1)–(3), with inputs \(S_i = (0.721, 0.089, 0.737)\). (2b) The state space orbit \((Y_1(t), Y_2(t), Y_3(t))\) for the times series shown in Figure 2a. (2c) Time series of a single triplet of averaged neurons, Equations (1)–(3), with inputs \(S_i = (0.189, 0.037089, 0.342)\) (another “odor”). (2d) The state space orbit \((Y_1(t), Y_2(t), Y_3(t))\) for the times series shown in Figure 2c. We chose \(\rho_{11} = \rho_{22} = \rho_{33} = 1\), \(\rho_{12} = \rho_{23} = \rho_{31} = 5\) and \(\rho_{21} = \rho_{32} = \rho_{13} = 0.2\) along with \(g_e = 4\).

**Figure 3** The time series of neurons 1, 4, 8 from three different triplets of averaged neurons from equation (4) with \(g_I = 0.1\), \(S^3_1 = 1.0\), and the same parameters \(\rho_{ij}\) as in figure (2). In spite of the stimulus was applied only to one neuron, all neurons are firing.

**Figure 4** Three dimensional phase portrait of the dynamical competition for a network of three FitzHugh-Nagumo neurons, Equation (5). Note the “winnerless” movement between the spiking behavior (unstable limit cycles) of the neurons as the orbits traverse the network upon stimulation. Here we have taken \(\epsilon = 0.08, a = 0.7, b = 0.8, \alpha_1 = 10.1, \gamma_1 = 2.0, S_i = (0.39, 0.4, 0.399)\). This figure uses state space coordinates which are linear combinations of the FitzHugh-Nagumo variables: \(\xi_1 = 15v_1 + I_1 + U_3, \xi_2 = 15v_2 + I_2 + U_1\), and \(\xi_3 = 15v_3 + I_3 + U_2\).

**Figure 5a** Time series of nine noisy FitzHugh-Nagumo neurons organized into three families connected by unidirectional inhibition, Equation (6). We chose \(\epsilon = 0.08, a = 0.7, b = 0.8, \alpha_1 = 5.1, \alpha_2 = 50.1, \gamma_1 = \gamma_2 = 2.0\). \(S^3_1 = (0.5, 0.5, 0.6, 0.5, 0.5, 0.5, 0.5, 0.5, 0.9)\). The stimulus strength \((S_I - 0.3)\) is shown in green bars on the right of each time course. The stimuli were on for times \(1000 \leq t \leq 3000\), and independent, identically distributed noise uniform in \([0.0, 0.015]\) was added to each stimulus. The “magnifying glass” shows individual spikes generated by one neuron.

**Figure 5b** Simultaneous intracellular recordings from two PNs in the locust antennal lobe. Here the time is in ms; the stimulus was applied for time \([1000,2000]\). body. Note the
complex response patterns of these two neurons, comprising fast, transient oscillatory activity (also seen in the local field potential) as well as slower and neuron-specific modulation of firing rate, in response to the presentation of the odor heptanone. Methods as in [14].

Figure 6 The cross correlation $C_r(R)$ for the model in Equation (4) as a function of R, the radius within which initial conditions for the dynamical competition network were uniformly distributed. The cross correlation functions were normalized to $C_r(R = 0) = 1$.

Figure 7 Response of orbits to stimulus noise. Spiking activity of the nine neuron model of dynamical competition using FitzHugh-Nagumo neurons at each node (Equation (6)) with 1% and 15% noise (a, b). We used the stimulus $s_1^1 = 0.1$, $s_2^1 = 0.1$, $s_3^1 = 0.2$, $s_1^2 = 0.2$, $s_2^2 = 0.3$, $s_3^2 = 0.2$, $s_1^3 = 0.2$, $s_2^3 = 0.1$, and $s_3^3 = 0.1$, applied during $1000 \leq t \leq 3000$. It was slowly increased from 0 to 1 over $1000 \leq t \leq 1500$ and then slowly decreased from 1 to 0.1 during $1500 \leq t \leq 3000$ as shown in the top traces. The noise level was $\eta_1^\alpha = 0.01$ (a) and $\eta_1^\alpha = 0.15$ (b). The stimulus offset was $\delta = 0$. c,d Overlap between the neural firing patterns with and without noise. $\eta_1^\alpha = 0.01$ in (c) and $\eta_1^\alpha = 0.15$ (d). The stimulus “offset” was $\delta_1^1 = \delta$, $\delta_1^2 = -\delta$, $\delta_1^3 = -\delta$, $\delta_2^1 = \delta$, $\delta_2^2 = -\delta$, $\delta_2^3 = \delta$, $\delta_3^1 = \delta$, $\delta_3^2 = -\delta$, $\delta_3^3 = \delta$. 
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