Continuous or discrete attractors in neural circuits? A self-organized switch at maximal entropy

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A recent experiment suggests that neural circuits may alternatively implement continuous or discrete attractors, depending on the training setup. In recurrent neural network models, continuous and discrete attractors are separately modeled by distinct forms of synaptic prescriptions (learning rules). Here, we report a solvable network model, endowed with Hebbian synaptic plasticity, which is able to learn either discrete or continuous attractors, depending on the frequency of presentation of stimuli and on the structure of sensory coding. A continuous attractor is learned when experience matches sensory coding, i.e. when the distribution of experienced stimuli matches the distribution of preferred stimuli of neurons. In that case, there is no processing of sensory information and neural activity displays maximal entropy. If experience goes beyond sensory coding, processing is initiated and the continuous attractor is destabilized into a set of discrete attractors.

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Recurrent neural network models display persistent activity, i.e. stable attractor states, selective for the input stimuli ([1],[2],[3]). Discrete attractors are naturally generated by Hebbian plasticity ([4]), storing the correlations in the input, and have been widely used in modeling neural representations of learned objects. Continuous attractors, on the other hand, model neural representations of continuous variables, such as retinal angle of visual stimuli ([5]), eye position ([6]), or space coordinates ([7]). In order to build a continuous attractor, i.e. a subspace of marginally stable neural patterns, either homeostatic synaptic mechanisms are introduced ([8],[9]), or fine tuning of parameters is required ([10],[11]).

Recently, a series of experiments revealed that exposure of subjects to stimuli from a morphing sequence is able to generate, in the recorded neural activity, discrete attractors as well as continuous ones ([12],[13],[14]). In particular, in both [13] and [14], activity of hippocampal cells of rats is recorded while they move into boxes of morphing shapes. Varying the box shape, the former experiment revealed a sharp modulation (two discrete attractors) of neural activity, while the latter showed a gradual variation (a continuous attractor). Moreover, the well known continuous coding of space, given by the place fields of hippocampal cells ([12]), lays upon a discrete coding of shapes ([13]). Hence, discrete and continuous attractors coexist in the same neural module, and this raises the question of whether selection of the attractor type depend only on the training setup, and whether the same network can generate both, via the same synaptic plasticity mechanism.

In this letter, we present a binary neural network model, subject to Hebbian plasticity dynamics, which can be solved analytically (a similar model has been recently published in [16]). Previous solvable binary models consider plasticity as exclusively driven by the input stream, and treat recurrent neural dynamics only after learning. In our model, instead, the recurrent dynamics plays an active role in plasticity, giving rise to a surprisingly rich phenomenology. For rather typical choices of the form of the input tuning curve ([13]), the network autonomously develops either continuous or discrete attractors, depending on the frequency of occurrence of stimuli. If the distribution of presented stimuli equals the distribution of preferred stimuli of neurons, the emergent attractor is continuous. This corresponds to the case in which the occurrence of stimuli matches what is expected from sensory coding, there is no processing of sensory information, and neuronal activity displays maximal entropy. Conversely, if subsets of stimuli are presented more frequently, a discrete attractor appear for each highlighted set.

The model network consists of binary neurons, \( S_i = \pm 1 \), and binary synapses, \( J_{ij} = \pm 1 \) \((i, j = 1, \ldots, N)\). The efficacy of a synapse connecting neurons \( j \) to \( i \) follows a stochastic Hebb’s plasticity rule ([18]): if neurons \( i \) and \( j \) are in correlated states \((S_i = S_j)\) and \( J_{ij} = -1 \), then \( J_{ij} \rightarrow +1 \) with probability \( p \). If the neurons are in anti-correlated states \((S_i = -S_j)\) and \( J_{ij} = +1 \), then \( J_{ij} \rightarrow -1 \) with probability \( p \). Other configurations are unchanged. Mean-field dynamics, describing how the synaptic efficacies vary on average (denoted by angular brackets), is given by

\[
p^{-1} \frac{d \langle J_{ij}(t) \rangle}{dt} = -\langle J_{ij}(t) \rangle + S_i(t)S_j(t) \tag{1}
\]

Synapses store the memory of past correlations in neural activity, up to a timescale \( p^{-1} \), and regulate the recurrent currents received by neurons. The recurrent input to neuron \( i \) is equal to ([19])

\[
R_i(t) = \frac{1}{2N} \sum_{j=1}^{N} J_{ij}(t)S_j(t) \tag{2}
\]

Beside the recurrent current, representing the “memory trace”, each neuron \( i \) receives an external sensory signal,
determined by its "preferred stimulus" $\eta_t$. The external current to neuron $i$, upon presentation of stimulus $\alpha$, is defined by the "tuning curve" $E(\eta_t - \alpha)$, describing how the external current is modulated by changes in the presented stimulus. We assume that the tuning curve is monotonically increasing ($E' > 0$) and centered ($E(0) = 0$), and we define the space of stimuli as the unitary segment, $T = (-\frac{1}{2}, +\frac{1}{2})$, $\eta_t, \alpha \in T$. However, results can be generalized to a decreasing as well as to a periodic tuning curve (to be presented elsewhere). The preferred stimulus $\eta_t$ is randomly assigned to each neuron, following a distribution $\omega(\eta)$. The total current afferent to each neuron is the sum of the recurrent and the external currents, and neural activity is $+1$ or $-1$, respectively, if the total current is above or below threshold (set to zero), i.e. $\{1, 2\}$.

We present a theoretical analysis of the network dynamics, in the limit of an infinite number of neurons, and then we show computer simulations to corroborate the emerging picture.

It turns out that the dynamics of neural activity can be described by a label $\mu(t) \in T$, such that

$$S_i(t + dt) = \text{sign}\left(R_i(t) + E(\eta_t - \alpha)\right)$$

We hold trivially if the recurrent currents are negligible with respect to the external currents, and the activity label is just equal to the presented stimulus, $\mu = \alpha$. However, a self-consistent argument demonstrates that, under quite general conditions, Eq. (3) holds, for some $\mu$, even for large recurrent currents, after the synapses have "learned" the space of stimuli $T$. We know, from Eq. (1), that the average synaptic matrix $\langle J_{ij}(t) \rangle$ is a linear functional of the activity product $S_i(t)S_j(t)$. Then, since neural activities are mapped onto the space of stimuli ($\mu \in T$ in Eq. (1)), the synaptic matrix can be written as

$$\langle J_{ij}(t) \rangle = \int_T \psi(\mu, t) \text{sign}(\eta_t - \mu) \text{sign}(\eta_j - \mu) \ d\mu$$

where $\psi(\mu, t)$ is the "distribution of stored patterns", expressing the relative weight of different patterns, labeled by $\mu$, in the synaptic memory matrix. It is positive ($\psi(\mu, t) > 0$) and normalized ($\int_T \psi(\mu, t) d\mu = 1$). In the following, we study the stationary behaviour of $\mu$ and $\psi$, describing respectively the neural and synaptic states, and we discuss their physical interpretations.

We assume that the dynamics of neurons is much faster than that of synapses, which are essentially frozen on the neural timescale. Upon presentation of a given stimulus $\alpha$, neural activity reaches immediately a stationary state $\mu_s$, resulting from the competition of external and recurrent currents. Then, synaptic learning applies over the states $\mu_s$, until a new stimulus is presented and a new state $\mu_s$ is reached. By using Eqs. (2), (4), (5) with $\mu(t + dt) = \mu(t) = \mu_s$, and averaging over preferred stimuli, the equation for $\mu_s$ is found,

$$E(\mu_s - \alpha) + \Psi(\mu_s) - \Omega(\mu_s) = \text{const}$$

where $\Psi$ and $\Omega$ are the cumulative distribution functions of, respectively, the density distributions of the stored patterns $\psi$ and of the preferred stimuli $\omega$ (an example is given in Fig.1), i.e. $\Psi(\mu) = \int_{-\frac{1}{2}}^{\mu} \psi(\mu') d\mu'$, and $\Omega(\eta) = \int_{-\frac{1}{2}}^{\eta} \omega(\eta') d\eta'$, and $\text{const} = \int_{0}^{1} (\Psi - \Omega) d(\Psi + \Omega)/2$ (since synapses are frozen, the time dependence of $\psi$ is omitted). The stationary state $\mu_s$ is stable when $E'(\mu_s - \alpha) + \psi(\mu_s) - \omega(\mu_s) > 0$.

The neural dynamics is a trade-off between the external drive and the recurrent dynamics. In order to get a physical intuition of Eq. (6), we consider separately the recurrent and external contributions: the general solution will be somewhere in between the two cases. If the external input is strong, Eq. (6) reduces to $E(\mu_s - \alpha) = 0$, whose solution is $\mu_s = \alpha$. In that case, the strong input forces the neural pattern to match the stimulus. On the other hand, when the recurrent contribution dominates, Eq. (6) becomes $\Psi(\mu_s) - \Omega(\mu_s) = \text{const}$. The solutions of this equation are the attractors of the recurrent neural dynamics, in absence of the stimulus. If the distribution of stored patterns matches the distribution of preferred stimuli, i.e. if $\Psi = \Omega$ everywhere, then $\text{const} = 0$, and all values of $\mu_s \in T$ are solutions, all marginally stable: this corresponds to a continuous attractor. In general, if $\Psi \neq \Omega$, discrete attractors emerge. An illustrative example is given in Fig.1 where $\text{const}$ is neglected: two discrete attractors appear near the maxima of $\psi$. A continuous attractor would appear when the two curves superimpose, intersecting at all points.

The slow dynamics of $\psi$ depend on the sequence of input stimuli $\alpha$, through the sequence of the resulting stationary neural patterns $\mu_s$. We assume that each presentation of a stimulus $\alpha$ is drawn independently from a distribution $\phi(\alpha)$. Starting from the synaptic mean-field dynamics, Eq. (1), using Eqs. (4), (5) and averaging over the presented stimuli, the dynamics of $\psi$ is written as

$$p^{-1} \frac{d\psi}{dt}_{\mu, t} = -\psi(\mu, t) + \int \phi(\alpha) \delta(\mu - \mu_s) d\alpha$$

where $\delta$ is the Dirac pulse function, and $\mu_s$ depends, via Eq. (6), on the stimulus $\alpha$ and on the distribution $\psi$ itself. Eq. (7) implies that, from stimulus to stimulus, $\psi$ strengthens the memory of each activated pattern of neural activity $\mu_s$, and slightly weakens all the others. The external-recurrent trade-off play a crucial role in determining the stationary solution $\psi_s(\mu)$ of Eq. (7): when external currents dominate, $\mu_s = \alpha$, and the stationary...
solution simply replicates the distribution of presented stimuli, i.e. \( \psi_s = \phi \). In that case, the synapses store exactly the presented input patterns, weighted by their relative frequency of appearance. Then, a continuous attractor \((\psi = \omega)\) forms if the distribution of presented stimuli equals the distribution of preferred stimuli of neurons, i.e. if \( \phi = \omega \). Surprisingly, a continuous attractor stabilizes even if recurrent currents give a finite contribution, as demonstrated in the following.

In general, a stationary solution of Eq. (7) is difficult to find. Nevertheless, we can calculate self-consistently \( \psi_s(\mu) \) for stored patterns \( \mu \) which correspond to stationary states of the recurrent neural dynamics, i.e. those satisfying \( \Psi_s(\mu) - \Omega(\mu) = \text{const} \). The solution is

\[
\psi_s(\mu) = \phi(\mu) \left[ \frac{E'(0) - \omega(\mu)}{E'(0) - \phi(\mu)} \right]
\]

if positive, zero otherwise. This solution is stable if \( E'(0) > \phi(\mu) \). The contribution of the recurrent dynamics to plasticity is given by the term in square brackets, which disappears in the limit of large external input \( (E'(0) \to +\infty) \), for which we recover \( \psi_s = \phi \).

We stress that the solution (8) is not valid for all values of \( \mu \), but only at the fixed points of \( \Psi_s(\mu) - \Omega(\mu) = \text{const} \). However, if \( \phi = \omega \) the solution of Eq. (8) is \( \psi_s = \omega \), that corresponds to a continuous attractor, for which all points are fixed, and the solution (8) is valid everywhere. Hence, if the distribution of presented stimuli equals the distribution of preferred stimuli of neurons, a continuous attractor may stabilize, as a result of the combined synaptic and neural dynamics. The continuous attractor, in terms of plasticity dynamics, is stable if \( E'(0) > \text{Max}(\omega(\mu)) \), i.e. is favored by a strong external input and a homogeneous distribution of preferred stimuli.

If \( \phi \neq \omega \), only discrete attractors stabilize, and we can calculate the stationary solution \( \psi_s \) only at those points. However, we expect Eq. (8) to be a good approximation in the vicinity of a continuous attractor \((\phi \sim \omega)\), if it is stable and positive \((E'(0) > \phi, \omega)\). In that case, patterns are stored more efficiently if the corresponding stimuli are more experienced and less preferred by neurons (large \( \phi \) and small \( \omega \)). If the external input is weak \((E'(0) < \phi, \omega)\), the solution (8) is unstable: a continuous attractor is prohibited, while discrete attractors are still allowed, whose \( \psi_s(\mu) \) diverges. In that case, synaptic changes are driven by the recurrent synaptic structure itself, rather than by the external signal, and we expect that the initial synaptic structure strongly affects the dynamics.

In order to check to what extent the network processes sensorial information, we calculate the entropy of the distribution of the total neural activity, \( A = \frac{1}{N} \sum_i S_i \), which is a continuous variable in the limit of large \( N \), and whose distribution is denoted by \( \rho(A) \). In stationary conditions, using Eq. (4) and averaging over preferred stimuli, the entropy is calculated as

\[
H = - \int_{-\frac{1}{2}}^{\frac{1}{2}} \rho(A) \log \rho(A) dA = \int_0^1 \log \left( \frac{\Omega(\mu)}{\Psi(\mu)} \right) d\Psi
\]

which is negative, and corresponds to (minus) the information gained when using a code based on the distribution \( \Psi \) rather than on \( \Omega \) (if \( \Psi \) is the true distribution). If the two distributions are equal, the network is in a continuous attractor state, and the entropy of neural activity is maximal (zero, and \( A \) is uniformly distributed, \( \rho = 1 \)). Conversely, if \( \Psi \) is different from \( \Omega \), the information inside neural activity equals the information gained by using the synaptic matrix, structured by learning, instead of sensory coding. Once normalized, Eq. (8) is taken as an approximation of the stationary solution \( \psi_s \), whose cumulative \( \Psi_s \) is used for computing the theoretical entropy of Eq. (9).

We illustrate our predictions by 100 computer simulations of the dynamics of the network (Eqs. (1), (2) and (3)), which is composed of 1000 neurons. For each simulation, synapses and neurons are initialized at random, and distribution functions of preferred (\( \omega \)) and presented (\( \phi \)) stimuli are chosen randomly from the set of fourier series truncated at wave number 5 (i.e. \( 1 + \sum_{i=1}^{5} [a_i \sin(b_i \theta) + b_i \cos(b_i \theta)] \), where \( a_i, b_i \) are random in the interval \((-0.5, 0.5)\), and only positive series are taken). Then, 1000 preferred stimuli are drawn from \( \omega \), for the 1000 neurons, and 2000 stimuli, to be presented, are drawn from \( \phi \). The tuning curve is linear, and its angular coefficient \( E' \) is chosen, for each simulation, from a uniform distribution (in the interval \((0, 5)\)), to which is added the maximum of \( \phi \) and \( \omega \) (then (8) is stable and positive). Each stimulus is presented for 20 time steps,
and the learning timescale is set $p = 10^{-4}$. In order to analyse stationary conditions, neural activity is recorded only after presentation of the first 1000 stimuli, and entropy is evaluated by the neural activity (sampled in 50 bins) at the last step of each of the remaining stimuli, from 1001 to 2000.

Theoretical predictions are in good agreement with the simulation results, as shown in Fig. 2, where the measured entropy of neural activity is plotted against the prediction of Eq. (9), each point is one simulation. The agreement is especially good for large entropies, where the network is close to a continuous attractor state, and for which Eq. (8) is a better approximation. The observed contribution of recurrent dynamics to plasticity is an average 65% decrease in the entropy, with respect to the case of large external drive, separately studied.

In summary, we have shown that a simple plastic network can generate both discrete and continuous attractor states, depending on the statistics of experienced stimuli and the structure of sensory coding. The network provides a candidate explanation for the apparent discrepancy between the two experiments [13] and [14], in which similar experimental conditions result in the observation of the two different types of attractors. Here, the continuous attractor has been shown to be more stable when the distribution of preferred stimuli is homogeneous, such as commonly observed in the brain. We leave for a future work the study of the network finite-size effects, eventually wasting a perfect continuous attractor state. From the computational point of view, the network introduces a novel functionality: the network divides stimuli in clusters (discrete attractors) when subsets of stimuli occur more frequently than what is expected from sensory coding. In that case, neural activity expresses exactly the information gained by the learned synaptic matrix. If the statistics of presented and preferred stimuli match, neural activity displays maximal entropy (no additional information), and the network abandons any tentative to recognize clusters of stimuli, but it still provides their representation via the continuous attractor. The present network represents an effort to bridge high-level (memory) areas of the brain, which could be modeled by recurrent associative networks [3], and early sensory brain areas, in which continuously varying stimuli are represented by smooth tuning curves [17]. Here, the recurrent contribution to plasticity was found to decrease substantially the entropy of neural activity.

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