

DIGRAPHS VS. DYNAMICS IN DISCRETE MODELS OF NEURONAL NETWORKS

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ABSTRACT. It has recently been shown that discrete-time finite-state models can reliably reproduce the ordinary differential equation (ODE) dynamics of certain neuronal networks. We study which dynamics are possible in these discrete models for certain types of network connectivities. In particular we are interested in the number of different attractors and bounds on the lengths of attractors and transients. We completely characterize these properties for cyclic connectivities and derive additional results on the lengths of attractors in more general classes of networks.

1. Introduction. Many neuronal networks exhibit dynamics where time appears to progress in distinct episodes. During each episode, subpopulations, or clusters, of cells fire in near synchrony, while cells from different clusters are at rest. However, the membership of clusters may change so that two cells may fire together during one episode but not during some other subsequent episode. This type of phenomenon is called *transient synchrony* or *dynamic clustering* [3] and has been observed for example in the thalamocortical system responsible for the generation of sleep rhythms [7, 12, 24], networks within the basal ganglia that have been implicated in the generation of Parkinsonian tremor [4, 5], and networks within the olfactory bulb of mammals, or antennal lobe of insects [2, 3, 18, 19].

A fundamental issue in neuroscience is to understand how the network dynamics depend on the underlying network architecture. In particular, it is a matter of active debate in the neuroscience community whether neural coding of perceptions (e.g. odors) corresponds to different attractors or to distinct transients of the network dynamics. The former requires the existence of sufficiently many different attractors, while the latter would require at least sufficiently long transients [9, 10, 18, 19]. For example, in the insect antennal lobe, odor can be represented as trajectories of the neuronal state space that eventually move into distinct regions that are specific to each odor [9, 19]. Neural activity patterns that represent odorants in the antennal lobe are statistically most separable at some point during the transient phase, well

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before reaching the target region [10, 19] and this time constraint is consistent with the behavioral data [10]. If animals use information in either the transient or attractor phase of any proposed dynamic process, the behavior data can set important time constraints for that process to produce discriminable patterns.

In [23] it was shown that the dynamics in a general class of ODE models of excitatory-inhibitory networks, with a general class of architectures, can be rigorously reduced to a class of discrete-time finite-state models of neuronal networks. In the latter type of model, time is inherently partitioned into subsequent episodes and thus the result of [23] provides a possible explanation for the phenomenon of dynamic clustering. The discrete models proposed in [23] provide a simpler framework for studying the relationship between network connectivity and network dynamics than the more detailed ODE models. In this paper we continue the study, begun in [13], of this dependence for the discrete models. Motivated by the findings described in the previous paragraph, our focus here is on the lengths of attractors, of the transients, and on the number of different attractors.

An important theme in study of discrete-time finite-state dynamical systems that goes back at least to 1969 when Kauffman first proposed Boolean networks as models for gene regulation [15, 16] is what kind of dynamics is to be *expected* for what kind of connectivities. In these investigations the network is randomly drawn from a probability distribution with specified parameters and features of the dynamics for randomly chosen initial conditions are studied either analytically or empirically with computer simulations.

Our paper [13] follows this line of research for the neuronal network models under consideration here, with the parameter representing the average indegree of each node. Both analytic and numeric results in [13] indicate that for generic neuronal networks with relatively dense connectivities, most initial conditions will already belong to attractors of the shortest possible lengths among all non-steady state attractors. Thus, in these networks the transients generically have length zero and every neuron fires as soon as it reaches the end of its refractory period. For *very* sparse connectivities, the (unique) steady-state attractor becomes generic. This makes such networks with either dense or very sparse connectivities unlikely candidates for neural coding either in terms of attractors or transients. Further numerical explorations indicate that there exists a small range of connection probabilities for which longer attractors and transients become generic [2, 14], which corresponds to biologically more realistic scenarios. Therefore it is important to understand which structural properties of the network connectivity enable this kind of dynamics. This question is the starting point of the research we report here.

Our approach here is different from the one in [13] in that we study what kind of dynamics *are possible in principle* for a given connectivity. This type of question has been studied for other networks of biological relevance, (see e.g. [6, 11, 20, 21, 22, 25, 26]), but not previously for the models of neuronal networks considered here.

In Section 3 we will start with the investigation of the important base case of networks whose connectivity is given by one directed Hamiltonian cycle of length n . In this case the length of all attractors is bounded by the number n of nodes in the network. The number of different attractors is equal to the number of possible necklaces of a certain kind with n beads, a well-studied problem in combinatorics. This number grows exponentially in n . The maximal length of the transients is $n + 2p^* - 3$, where p^* is the maximal refractory period (see Section 2 for the definition).

For broader classes of digraphs D the problem of deriving bounds on the possible number of different attractors, and the possible lengths of attractors and transients leads to challenging mathematical problems. In Section 4 we will illustrate what kind of results can be expected along those lines by focusing on the problem of attractor lengths. We will demonstrate that the length of an attractor is closely related to its dynamics on sets of directed cycles in D , which underscores the importance of having characterized the possible dynamics for the base case that was considered in Section 3. In particular, we will prove the existence of a structure that we call a *core* for periodic attractors in certain types of networks (Theorem 5) and derive consequences for the attractor length under some additional assumptions. We believe that these results open up a promising area of further mathematical exploration, and we pose several open and apparently quite challenging mathematical problems.

In Section 5 we discuss the relevance of our results to neuroscience, in particular, how they relate to the potential of neural coding in terms of attractors or transients. We also suggest more directions of further research.

The results reported in this paper were either first obtained in the first author's Ph.D. thesis [1], or generalize results obtained therein. [1] also contains many additional results on possible dynamics for these networks.

2. Basic definitions. The discrete-time finite-state models of neuronal networks in [23] are based on the following assumptions: At any given time, an individual neuron either fires or is at rest. After a neuron has fired, it needs to go through a certain refractory period during which it cannot fire. After it has gone through its refractory period, a neuron will fire again when it receives sufficient firing input from other neurons. Formally,

1. A neuronal network N is modeled by a loop-free digraph $D = \langle V_D, A_D \rangle$ together with two vectors $\vec{p} = [p_1, \dots, p_n]$ and $\vec{th} = [th_1, \dots, th_n]$ of positive integers. The number p_i is called the refractory period of the i -th neuron, and the threshold th_i indicates how many other neurons are needed to cause firing of the i -th neuron. For convenience of notation, we will henceforth always assume that $V_D = [n] = \{1, \dots, n\}$ for some positive integer n and use the letter n exclusively for the number of nodes in the connectivity digraph of the network that is being considered. Each vertex $i \in [n]$ is interpreted as a neuron and an arc $\langle j, i \rangle$ is interpreted as neuron j sending synaptic input to neuron i .
2. With any given network $N = \langle D, \vec{p}, \vec{th} \rangle$ we associate a discrete-time finite-state dynamical system that for convenience also will be denoted by N . A state \vec{s} of the system at time t is a vector $\vec{s}(t) = [s_1(t), \dots, s_n(t)]$, where $s_i(t) \in \{0, 1, \dots, p_i\}$ for all $i \in [n]$. The state space of N will be denoted by St_N . The state $s_i(t) = 0$ of neuron number i is interpreted as firing at time t .
3. The dynamics of N is defined as follows:
 - (a) If $s_i(t) < p_i$, then $s_i(t+1) = s_i(t) + 1$.
 - (b) If $s_i(t) = p_i$, then $s_i(t+1) = 0$ if there exist at least th_i different $j \in [n]$ with $s_j(t) = 0$ and $\langle j, i \rangle \in A_D$, and $s_i(t+1) = p_i$ otherwise.

Let us now formally define the properties of the dynamics that we are interested in. The *trajectory* of an initial state $\vec{s}(0)$ is the sequence $\vec{s}(0), \vec{s}(1), \vec{s}(2), \dots$ as determined by 3 above. Since the state space St_N is finite, we must eventually have $\vec{s}(t_0) = \vec{s}(t_1)$ for some $0 \leq t_0 < t_1$, and from time t_0 , the trajectory becomes

cyclical. Let t_0 and t_1 be the smallest times with this property. Then the set of states $\{\vec{s}(t_0), \vec{s}(t_0 + 1), \dots, \vec{s}(t_1 - 1)\}$ is called the *attractor* of $\vec{s}(0)$; its length is equal to $t_1 - t_0$. The set $\{\vec{s}(0), \vec{s}(1), \dots, \vec{s}(t_0 - 1)\}$ is called the *transient* of $\vec{s}(0)$; its length is equal to t_0 . Note that a transient of length zero occurs whenever the initial state is in an attractor.

For example, in the state $\vec{s}_{\vec{p}} = [p_1, \dots, p_n]$ each neuron has reached the end of its refractory period and since no neuron fires in this state, no firing will occur at any future time. Thus $\vec{s}_{\vec{p}}$ is a *steady state* of N , which means that $\{\vec{s}_{\vec{p}}\}$ is an attractor of length one. It is not hard to see that $\vec{s}_{\vec{p}}$ is the only steady state attractor of N . All other attractors exhibit periodic firing patterns and we will refer to them as *periodic attractors*.

If $\vec{p} = [p_1, \dots, p_n]$ is the vector of refractory periods, then we will write p^* instead of $\max \vec{p}$. Note that the size of the state space of a network N with n nodes is bounded by $|St_N| = \prod_{i=1}^n (p_i + 1) \leq (p^* + 1)^n$. Since attractors are pairwise disjoint subsets of the state space, for fixed p^* both the maximum lengths (of transients and of attractors) and the maximum number of different attractors can grow at most exponentially in n . We are interested in investigating the growth of these numbers relative to the size n of the network under the standing assumption that p^* is fixed. This assumption reflects the empirical observation that while neuronal networks in real organisms may consist of a huge number of neurons, these will be of a bounded number of distinct types, thus in particular, of relatively few distinct refractory periods.

Finally, let us introduce some notation that will be used throughout the remainder of this paper. For a given positive integer n , let $D_c(n)$ be the cyclic digraph on $[n]$ with arc set $A_c(n) = \{< i, i + 1 > : i \in [n - 1]\} \cup \{< n, 1 >\}$. The symbol $j \% n$ denotes $((j - 1) \bmod n) + 1$. For a given trajectory $\vec{s}(0), \vec{s}(1), \vec{s}(2), \dots$ let us define the *active set at time t* as $Act_t = \{i \in [n] : s_i(t) = 0\}$ for each $t \geq 0$.

The symbol \mathbb{N} will denote the set of nonnegative integers. For every node i , define the *period* T_i of i (in an attractor A) as the smallest positive integer T such that $s_i(t) = s_i(t + T)$ for all $t \in \mathbb{N}$ with $\vec{s}(t) \in A$. Note that $T_i \leq |A|$ and $T_i = 1$ if and only if node i never fires in A .

3. Cyclic digraph $D_c(n)$. In this section, we will consider neuronal networks with underlying digraph $D_c(n)$. Some proofs will only be sketched; for more details see [1].

In such networks, node i gets input *only* from node $(i - 1) \% n$. Thus, if $i \in [n]$ is such that $th_i > 1$, then $s_i(t) \neq 0$ for all $t > 0$ and the system will eventually reach the steady state attractor $\vec{s}_{\vec{p}}$. Therefore we will focus here exclusively on the case $\vec{th} = \vec{1} = [1, \dots, 1]$ which allows for more interesting dynamics.

Moreover, a firing of node i at time t can induce at most one firing at time $t + 1$, and it follows that $|Act_t| \geq |Act_{t+1}|$ along any trajectory, which in turn implies that $|Act_t|$ is constant on any attractor. Thus throughout any attractor a firing of node i at time t *always will* induce a firing of node $(i + 1) \% n$ at time $t + 1$. If t_0 is such that $|Act_{t+t_0}| = |Act_{t_0}|$ for all $t \geq 0$, then for all $t \geq 0$ we have

$$Act_{t+t_0} = \{(i + t) \% n : i \in Act_{t_0}\}. \quad (1)$$

Thus if t_0 is as above, there exists a divisor m of n such that $Act_{t+m} = Act_t$ for all $t \geq t_0$. For node i to fire at time t , the rules of the dynamics require that it must be in state p_i at time $t - 1$. After node i has fired at time t (formally:

$s_i(t) = 0$), its state will increase until it reaches the end of its refractory period: $s_i(t + 1) = 1, \dots, s_i(t + p_i) = p_i$. It follows that along any attractor the state $s_i(t)$ of any node will be uniquely determined by its refractory period and the set Act_t . These observations prove the following.

Proposition 1. *Let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network with $D = D_c(n)$. Then the length $|A|$ of any attractor is a divisor of n . Moreover, the period T_i in A of any node i is equal to $|A|$.*

The following theorem gives the exact number of different attractors.

Theorem 1. *Let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network with $D = D_c(n)$. Then the number of different attractors is*

$$1 + \sum_{k=1}^{\lfloor \frac{n}{p^*+1} \rfloor} \frac{1}{n - kp^*} \sum_{a \in \{\text{divisors of } \gcd(k, n - k(p^*+1))\}} \phi(a) \binom{\frac{n-kp^*}{a}}{\frac{k}{a}}, \tag{2}$$

where ϕ is Euler’s phi function and $\lfloor \frac{n}{p^*+1} \rfloor$ is the largest integer less than or equal to $\frac{n}{p^*+1}$.

Proof. Let $D = D_c(n)$. Let us count the number of the attractors in N .

There is exactly one steady state attractor.

Now consider a periodic attractor and the smallest m such that for some t some node i fires both at times t and $t + m$, that is, $i \in Act_{t+m} \cap Act_t$. It follows from Equation 1 that each node j will fire both at times t^* and $t^* + m$ for some t^* , so we may assume wlog that $p_i = p^*$. After it has fired, node i needs to go through states $1, 2, \dots, p_i, \dots, p_i$ before firing again. This implies that $m \geq p_i + 1 = p^* + 1$, that is, the distance between two firing nodes is at least $p^* + 1$. In particular, $|Act_t| \leq \lfloor \frac{n}{p^*+1} \rfloor$.

As we already mentioned above, the state $\vec{s}(t)$ in an attractor is uniquely determined by the location of the set Act_t .

We may consider each attractor with fixed $|Act_t| = k$ as a necklace with k red beads and $n - k(p^* + 1)$ black beads. Pick a state \vec{s} in the attractor. Each red bead corresponds to a block of $p^* + 1$ positions of \vec{s} of the form $[*, \dots, *, 0]$, where the wildcards $*$ correspond to the stages in the refractory period of the corresponding neuron, but not to firing. This type of block represents one firing together with the mandatory waiting period that must precede the next firing. Black beads correspond to optional extensions of the minimal waiting period between two consecutive elements of Act_t .

There is a one-to-one correspondence between periodic attractors in N and this type of necklaces. Now the theorem follows from the well-known formula for the number of different such necklaces (e.g. Theorem 1 in [8]). \square

Corollary 2. *Let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network with $D = D_c(n)$. Then the number of different attractors grows exponentially in n .*

Proof. The number of different attractors is bounded by $|St_N| = \prod_{i=1}^n (p_i + 1) \leq (p^* + 1)^n$. So, it grows at most exponentially in n under our standing assumption that p^* is fixed. But here this assumption is not even needed, since the number of distinct necklaces with two types of beads is trivially bounded by 2^n .

To see that the number grows at least exponentially in n for fixed p^* , let $k = \lfloor \frac{n}{3(p^*+1)} \rfloor$ and consider all necklaces with k red beads such that with at most one

possible exception each pair of consecutive red beads is separated by either one or two black beads. There are 2^{k-1} distinct necklaces with this property. Thus, the number of possible attractors is at least 2^{k-1} . \square

Now let us derive an upper bound for the lengths of the transients.

Recall that $|Act_t|$ is a nonincreasing function of $t \geq 0$. Thus, $|Act_{t+1}| < |Act_t|$ for some $t \geq 0$ implies that the length of the transient is at least $t + 1$. Moreover, if the length of the transient is $\tau_0 \geq 0$, then $|Act_t| = |Act_{\tau_0}|$ for all $t > \tau_0$.

Lemma 3. *Let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network with $D = D_c(n)$. Consider a trajectory that starts in state $\vec{s}(0)$ and let t_0 be the smallest time such that $|Act_t| = |Act_{t_0}|$ for all $t \geq t_0$. Then*

- (i) *The length of the transient is at most $t_0 + p^* - 1$.*
- (ii) *If $t_0 > 0$, then there exists a node i with $s_i(t_0 - 1) = 0$ and $s_{(i+1)\%n}(t_0) > 0$.*
- (iii) *If $t_0 > p^*$, then for all nodes i as in (ii) we must have $p_i < p_{(i+1)\%n}$.*
- (iv) *If $t_0 > p^*$, then the length of the transient is at most $t_0 + p^* - 2$.*

Proof. Note that Equation 1 will hold for all $t \geq t_0$, and the set Act_t will be completely determined by the location of the set Act_{t_0} and $t - t_0$. Thus the only way in which $\vec{s}(t_0)$ may fail to be in the attractor is if there is a node i where $s_i(t_0) < s_i(t)$ for some t with $Act_t = Act_{t_0}$ and $\vec{s}(t)$ in the attractor. But then $s_i(t_0) \geq 1$, and it will take at most $p^* - 1$ additional time steps before each such node i reaches the end of its refractory period. This proves part (i).

Part (ii) is obvious.

For the proof of (iii), assume node i is such that $s_i(t_0 - 1) = 0$ and $s_{(i+1)\%n}(t_0) > 0$. Then we must have $s_{(i+1)\%n}(t_0 - 1) < p_{(i+1)\%n}$, and node $(i + 1)\%n$ must have fired at some time $t_0 - p > 0$, where $p \leq p_{(i+1)\%n}$. It follows that $s_i(t_0 - p - 1) = 0 = s_i(t_0 - 1)$, which implies $p_i < p \leq p_{(i+1)\%n}$.

For the proof of (iv), let $t > t_0$ be such that $Act_t = Act_{t_0}$. As in the proof of part (i), it suffices to show that if $s_i(t_0) < s_i(t)$, then it takes at most $p^* - 2$ steps after t_0 for node i to reach the end of its refractory period. As before, we must have $s_i(t_0) > 0$. If also $s_i(t_0 - 1) > 0$, then $s_i(t_0) > 1$ and it takes at most $p_i - 2 \leq p^* - 2$ steps until node i reaches the end of its refractory period. On the other hand, if $s_i(t_0 - 1) = 0$ and $s_{(i+1)\%n}(t_0) = 0$, then $(i + 1)\%n \in Act_{t_0} = Act_t$. It follows that $i \in Act_{t-1}$ and $s_i(t_0) = 1 = s_i(t)$, which contradicts our choice of i . Thus $s_{(i+1)\%n}(t_0) > 0$, which in view of part (iii) implies that $p_i < p^*$. Again, it will take at most $p^* - 2$ steps for node i to reach the end of its refractory period. \square

If all nodes have the same refractory period, then the scenario in point (iii) of Lemma 3 cannot occur, and point (ii) implies that $t_0 \leq p^*$. In view of point (i), this in turn implies the following result.

Theorem 2. *Let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network with $D = D_c(n)$, and $\vec{p} = [p, \dots, p]$ is constant. Then the length of any transient is at most $2p - 1$.*

The upper bound given by Theorem 2 is optimal (see Example 3.6.11 of [1]).

For nonconstant \vec{p} , the optimal upper bound on the length of the transients depends both on n and p^* .

Theorem 3. Let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network with $D = D_c(n)$. Then
 (i) The length of any transient is at most $n + 2p^* - 3$.
 (ii) If $p^* < n$, then the length of any transient is at most $3n - 5$.
 (iii) If $p^* \geq n$, then the length of any transient is at most $\max\{n + p^* - 1, 3(n - 1)\}$.

Proof. We first derive an upper bound for t_0 of Lemma 3.

Lemma 4. Let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network with $D = D_c(n)$. Then $|\text{Act}_{n+p^*-t}| = |\text{Act}_{n+p^*-1+t}|$ for all $t \geq 0$.

Proof. Let $D = D_c(n)$, $\vec{s}(0) \in St_N$, and let $t_0 = n + p^* - 1$.

First note that since node i receives firing input only from node $(i-1)\%n$, if $t > 0$ and $s_i(t) = 0$, then $s_{(i-1)\%n}(t-1) = 0$. By induction it follows that if $t_1 \geq t \geq 0$ and $s_i(t_1) = 0$, then $s_{(i-t)\%n}(t_1 - t) = 0$. In particular, if $t_1 \geq n$ and $s_i(t_1) = 0$, then $s_i(t_1 - n) = 0$.

Now assume towards a contradiction that for some time $t_1 \geq t_0$ we have $|\text{Act}_{t_1+1}| < |\text{Act}_{t_1}|$. Then there exists a node i such that

$$s_i(t_1) = 0 \quad \text{and} \quad s_{(i+1)\%n}(t_1 + 1) \neq 0. \tag{3}$$

The latter implies that $s_{(i+1)\%n}(t_1) = p$ for some $p < p_{(i+1)\%n}$, which in turn implies $s_{(i+1)\%n}(t_1 - p) = 0$.

Since $p < p_{(i+1)\%n} \leq p^*$ and $t_1 \geq n + p^* - 1$, we have $t_1 - p - n \geq 0$. Thus

$$s_{(i+1)\%n}(t_1 - p - n) = 0. \tag{4}$$

But the first half of Equation 3 also implies that

$$s_i(t_1 - n) = 0 = s_{(i+1)\%n}(t_1 + 1 - n). \tag{5}$$

On the other hand, Equation 4 implies that $s_{(i+1)\%n}(t_1 - n) = p < p_{(i+1)\%n}$, which contradicts Equation 5. \square

Now let us derive the theorem. Let $D = D_c(n)$, and let $\vec{s}(0) \in St_N$.

(i) Let t_0 be as in Lemma 3. It follows from Lemma 4 that $t_0 \leq n + p^* - 1$, and hence Lemma 3(iv) implies point (i).

(ii) This follows from (i) since $p^* < n$ implies $n + 2p^* - 3 \leq 3n - 5$.

(iii) Suppose $p^* \geq n$. Then $\vec{s}(0)$ is in the basin of attraction of $\vec{s}_{\vec{p}}$. Wlog, we may assume that $p_1 = p^*$. If $s_1(t) > 0$ for all $t \in \{0, \dots, n-1\}$, then $\text{Act}_{n-1} = \emptyset$ so that $\vec{s}(n + p^* - 2) = \vec{s}_{\vec{p}}$.

Suppose $s_1(t) = 0$ for some $t \in \{0, \dots, n-1\}$. Let t_0 be the largest such time t . Then $s_1(t_0) = 0$ and $s_1(t_0 + t) = t < p_1 = p^*$ for $0 \leq t \leq n-1$. Therefore node 1 cannot fire at time $t_0 + n$, and $\text{Act}_{t_0+n} = \emptyset$. It follows that $s_1(t_0 + p^*) = p_1 = p^*$.

Now assume that for some node i with $i > 1$ we have $s_i(t) = 0$ for some time $t \geq n$. Then $t \leq t_0 + n - 1$, and we also have $s_i(t - n) = 0$. Thus $p_i \leq n - 1$ and node i reaches the end of its refractory period in at most $n - 1$ steps after its last firing. It follows that

$$\vec{s}(t_0 + \max\{p^*, 2(n-1)\}) = \vec{s}_{\vec{p}}.$$

Since $t_0 \leq n-1$, the length of the transient is at most $n-1 + \max\{p^*, 2(n-1)\}$. \square

Example 3.6.17 of [1] shows that the bound $3(n - 1)$ can be obtained for this case, so that the additional assumption $p^* < n$ is needed in point (ii) of Theorem 3. Example 5 below shows that the upper bound of Theorem 3(i) is optimal for $p^* = 2$, while Example 6 shows that this bound is optimal for all $p^* > 2$.

Example 5. Let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network with $D = D_c(n)$, where $n \geq 5$ such that $\vec{p} = [1, 2, 1, \dots, 1]$. Let $\vec{s}(0)$ be the initial state $[0, 2, 0, 1, \dots, 1]$, that is given by $s_1(0) = 0 = s_3(0)$, $s_2(0) = 2$, and $s_j(0) = 1$ otherwise. Then all nodes except 2 fire as soon as they receive firing input, and node 2 fires at times 1 and $n-1$. Thus after n steps we will have $\vec{s}(n) = [0, 1, 0, 1, \dots, 1]$, and it follows that $\vec{s}(n+1) = [1, 2, 1, 0, 1, \dots, 1]$. Thus $|\text{Act}_0| = \dots = |\text{Act}_n| = 2$ and $|\text{Act}_{n+1}| = 1$, and the length of this transient is at least $n+1$. In fact, it is easy to see that $\vec{s}(n+1)$ is already in an attractor; therefore the length of the transient is actually equal to $n+1$.

Example 6. Let $p^* > 2$ and let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network with $D = D_c(n)$, where $n \geq 2p^* + 1$ such that $\vec{p} = [1, \dots, 1, p^* - 1, p^*, 1, \dots, 1]$, where $p_{p^*-1} = p^* - 1$, $p_{p^*} = p^*$ and $p_i = 1$ otherwise. Let $\vec{s}(0)$ be the initial state $[0, 1, \dots, 1, p^* - 1, p^*, 0, 1, \dots, 1]$ that is given by $s_1(0) = 0 = s_{p^*+1}(0)$, $s_{p^*-1}(0) = p^* - 1$, $s_{p^*}(0) = p^*$, and $s_j(0) = 1$ otherwise. Then all nodes except p^* fire as soon as they receive firing input. In particular,

$$\begin{aligned} \vec{s}(n) &= [0, 1, \dots, 1, 2, \quad 1, \quad 0, \dots, \quad 1, 1, 1, \dots, 1], \\ \vec{s}(n+p^*-2) &= [1, 1, \dots, 1, 0, \quad p^*-1, \quad 1, \dots, \quad 1, 0, 1, \dots, 1] \\ \vec{s}(n+p^*-1) &= [1, 1, \dots, 1, 1, \quad p^*, \quad 1, \dots, \quad 1, 1, 0, \dots, 1]. \end{aligned}$$

It will take $p^* - 2$ additional steps for s_{p^*-1} to reach the end of its refractory period and thus for the trajectory to enter its attractor. Thus the length of this transient is $n + 2p^* - 3$.

4. Attractors in arbitrary digraphs. In this section we will derive some results on the lengths and structure of attractors in more general classes of networks.

Let us review some terminology and facts that will be used in this section.

Let A be an attractor in a network $N = \langle D, \vec{p}, \vec{th} \rangle$. A node i is *active* in A if it fires at least once (and hence infinitely often), or, equivalently, if $T_i > 1$. Note that the length $|A|$ of A is equal to $\text{lcm}\{T_i : i \in [n]\}$, where lcm denotes the least common multiple. If $\vec{s}(0) \in A$, then we may trace the trajectory of $\vec{s}(0)$ both forward and backward and consider unique states $\vec{s}(-t)$ with $t \in \mathbb{N}$ such that $\vec{s}(-t) = \vec{s}(k|A| - t)$ for all k with $k|A| - t \geq 0$.

Let D be a digraph. A *directed path* from node i to node j is a sequence $(i = i_1, i_2, \dots, i_k = j)$ of nodes such that $\langle i_\ell, i_{\ell+1} \rangle \in A_D$ for all $\ell \in [k-1]$, and the nodes i_1, i_2, \dots, i_k are pairwise distinct, with the possible exception of the nodes i_1, i_k , which may be equal to each other. An *undirected path* from node i to node j is defined similarly, except that we only require that for each $\ell \in [k-1]$ at least one of the arcs $\langle i_\ell, i_{\ell+1} \rangle, \langle i_{\ell+1}, i_\ell \rangle$ is in A_D . If there exists an undirected path in D from each node to every other node, then we say that D is *connected*; if there exists a directed path in D from each node to every other node, then we say that D is *strongly connected*.

A directed path (i_1, i_2, \dots, i_k) with $i_1 = i_k$ is called a *directed cycle*. While a directed cycle is formally a sequence, in order to simplify or notation we will often simply treat a directed cycle as the set of its nodes $\{i_1, i_2, \dots, i_{k-1}\}$. If the order of the nodes does matter, as in Definition 9(b), we will single out the arcs $\langle i_\ell, i_{\ell+1} \rangle$ by referring to them as the arcs *of the directed cycle*. A *Hamiltonian cycle* in D is a directed cycle that contains all nodes; a *Hamiltonian digraph* is one that contains a Hamiltonian cycle. For a given Hamiltonian cycle we will refer to all arcs that are not of this cycle as *shortcuts*. Thus the digraphs $D_c(n)$ that were studied in Section 3

are Hamiltonian cycles with no shortcuts. We let $D_c(n, n_1)$ denote the Hamiltonian digraph on $[n]$ that is obtained by adding exactly one shortcut $\langle n_1, 1 \rangle$ to $D_c(n)$.

Now let us begin our work with a motivating example.

Example 7. Let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network with D being a union of pairwise disjoint directed cycles C_1, \dots, C_m such that $p_i < |C_r|$ for all $r \in [m]$ and $i \in C_r$. Then there exists an attractor in N of length $\text{lcm}\{|C_1|, \dots, |C_m|\}$ such that for all $r \in [m]$ each node $i \in C_r$ has period $T_i = |C_r|$.

Since there are no arcs in D other than the ones in the cycles C_r , the dynamics on these individual directed cycles do not interfere with each other. Thus the condition $p_i < |C_r|$ implies the existence of fully active periodic attractors in these networks, and Proposition 1 implies that each such attractor has the desired properties.

Example 7 implies that the length of attractors in networks with n nodes can be as large as Landau's function $g(n)$, which is the maximum value of $\text{lcm}\{n_1, \dots, n_m\}$ where $n_1 + \dots + n_m \leq n$. The function $g(n)$ grows approximately like $e^{\sqrt{n \ln n + o(1)}}$ [17]. It is also immediately clear that $g(n)$ is the optimal upper bound for the class D of digraphs that are unions of pairwise disjoint directed cycles. We are interested in two related types of problems: What is the optimal upper bound for the lengths of attractors for other classes of networks? If Landau's function is not the optimal upper bound for a given class, which mechanisms may create longer attractors or prevent the existence of attractors of length $\geq g(n)$ for networks in this class?

Example 8. Consider the digraph D on $[10]$ that is a disjoint union of three directed cycles $C_1 = [3]$, $C_2 = \{4, 5, 6\}$, $C_3 = \{7, 8, 9\}$ of length 3 and a node 10 which is the target of three arcs $\langle 1, 10 \rangle, \langle 4, 10 \rangle, \langle 7, 10 \rangle$ which originate in C_1, C_2 and C_3 respectively. Suppose $p_i < 3$ for $i < 10$ and $p_{10} = 1$.

Then the network $N = \langle D, \vec{p}, \vec{1} \rangle$ has an attractor of length 6 for which $T_{10} = 2$ and $T_i = 3$ for all other nodes.

The mechanism for obtaining long attractors in Examples 7 and 8 is similar. The following definition aims at pinpointing the nature of this mechanism.

Definition 9. Let $N = \langle D, \vec{p}, \vec{1} \rangle$ be a neuronal network and let A be a periodic attractor in N . A set $\mathcal{C} = \{C_1, \dots, C_m\}$ of pairwise disjoint directed cycles in D is called a core for A if

- (a) every node in any C_r is active in A ,
- (b) if $\langle i, j \rangle$ is an arc of C_r for some $r \in [m]$, then along the attractor A we have $s_j(t+1) = 0$ whenever $s_i(t) = 0$,
- (c) for every node i^* that is active in A there exists a directed path in D from some node $i \in C_1 \cup \dots \cup C_m$ to i^* .

A core \mathcal{C} for A is complete if it is a maximal family of pairwise disjoint directed cycles in D .

Note that in view of Proposition 1 conditions (a) and (b) imply that for each C_r in a core there exists a number $T^r > 1$ that divides $|C_r|$ such that each node $i \in C_r$ has period $T_i = T^r$ in A .

The family $\mathcal{C} = \{C_1, \dots, C_m\}$ of Example 7 is a complete core for every fully active attractor A in the network.

Similarly, the family $\mathcal{C} = \{C_1, C_2, C_3\}$ of Example 8 is a complete core for every fully active attractor A in the network.

If A is a periodic but not fully active attractor in one of the networks of Examples 7, 8, then it still has a core, but not a complete one.

Theorem 4. *Suppose A is a periodic attractor in a network $N = \langle D, \vec{p}, \vec{th} \rangle$, and suppose A has a complete core $C = \{C_1, \dots, C_m\}$. If $p_i = 1$ for all $i \notin C_1 \cup \dots \cup C_m$, then $|A|$ divides $2 \operatorname{lcm}\{|C_1|, \dots, |C_m|\}$. Moreover, if there is no node $i \notin C_1 \cup \dots \cup C_m$ with $T_i = 2$, then $|A|$ divides $\operatorname{lcm}\{|C_1|, \dots, |C_m|\}$.*

Proof. Let N, A, C be as in the assumptions. Let $C = C_1 \cup \dots \cup C_m$. Define $T = \operatorname{lcm}\{|C_1|, \dots, |C_m|\}$ if there is no node of period 2 outside of C and $T = 2 \operatorname{lcm}\{|C_1|, \dots, |C_m|\}$ otherwise.

Assume $\vec{s}(0) \in A$ and consider a node $i \in [n]$. We will show that T_i is a divisor of T .

If i never fires in A , then $T_i = 1$, which is clearly a divisor of T . If i does fire in A , then by Definition 9(c) there must exist a directed path $P = (i^* = i_0, \dots, i_k = i)$ from some node $i^* \in C$ to i . Wlog we may assume that i^* is the last node of C in this path. Let r_i be the maximum length k of such a path. Since the nodes of any directed path must be pairwise distinct, r_i is well defined and does not exceed $n - |C|$. Now let $r = \max\{r_i\}_{i \in [n] \setminus C}$ and consider for $0 \leq q \leq r$ the set

$$L_q = \{i \in [n] : r_i \leq q\}.$$

Note that $L_0 = C$ and $L_0 \subseteq L_1 \subseteq \dots \subseteq L_r$.

Proposition 10. *If $\langle j, i \rangle \in A_D$ and $r_i > 0$, then $j \in L_{r_i-1}$.*

Proof. If $j \in C$, then $r_j = 0$ and the proposition is obvious. If $j \notin C$, then suppose towards a contradiction that $\ell = r_j \geq r_i$. Then there is a directed path $P^* = (i^* = j_0, \dots, j_\ell = j)$ from some $i^* \in C$ to j with $j_m \notin C$ for all $0 < m \leq \ell$. If $i = j_m$ for some $0 < m < \ell$, then $(i = j_m, j_{m+1}, \dots, j_\ell = j, i)$ forms a directed cycle in D that is disjoint from C and hence from all directed cycles in C , which contradicts the assumptions of the theorem. Thus $P^+ = (i^* = j_0, \dots, j_\ell = j, i)$ is a directed path from i^* to i of length $r_i + 1$, which contradicts the definition of r_i . \square

Since $|A| = \operatorname{lcm}\{T_i : i \in [n]\}$, it suffices to show by induction over q that if $i \in L_q$, then T_i divides T .

For $q = 0$ we have $L_0 = C$ and T_i divides T by the choice of C . Suppose that T_j divides T for all $j \in L_q$ and let i be a node with $r_i = q + 1$. Consider the set

$$J = \{j \in [n] : \langle j, i \rangle \in A_D\}.$$

By Proposition 10 and the inductive assumption, T_j divides T for all $j \in J$.

If $T_i = 2$, then T_i trivially divides T because $T = 2 \operatorname{lcm}\{|C_1|, \dots, |C_m|\}$; so let us focus on the case when $T_i > 2$. In this case there must exist a time t with $s_i(t) = s_i(t + 1) = 1$. Then

$$\forall j \in J \forall k \in \mathbb{N} |\{j \in J : s_j(t + kT) = 0\}| < th_i. \tag{6}$$

The values of $s_i(\tau)$ on any time interval of the form $[t + 2 + kT, \dots, t + 1 + (k + 1)T]$ are uniquely determined by $s_i(t + 1 + kT)$ and the sequences $s_j(\tau - 1)$ for $j \in J$ and τ in this interval. The latter sequences do not depend on k , and $s_i(t + 1 + kT) = 1$ for all k by Equation 6. Therefore T_i must divide T . \square

The following example shows that if one replaces the assumption $p_i = 1$ of Theorem 4 by the more general assumption that all refractory periods outside of

the core are equal to a fixed p , one cannot conclude that unless there is a node i outside the core with period $T_i \leq p + 1$, the length of the attractor must divide the least common multiple of the lengths of the directed cycles in the core. Moreover, the example shows that the length of attractors with complete cores may exceed $g(n)$. Thus larger refractory periods allow for richer possibilities of dynamics. It remains an open problem to characterize these possibilities in the sense of Theorem 4.

Example 11. Consider the digraph D on $[13]$ that is a disjoint union of two directed cycles $C_1 = [5]$ and $C_2 = \{6, \dots, 12\}$ of lengths 5 and 7 respectively, and a node 13 which is the target of two arcs $\langle 1, 13 \rangle, \langle 6, 13 \rangle$ which originate in C_1 and C_2 respectively.

Then the network $N = \langle D, \vec{p}, \vec{1} \rangle$ with $p_{13} = 7$ and $p_i = 1$ for $i < 13$ has an attractor of length $70 > g(13) = 60$ for which $T_i = 5$ for all $i \in C_1$ and $T_i = 7$ for all $i \in C_2$, while $T_{13} = 70$.

Example 8 shows that the assumption about the absence of nodes with period 2 is needed in Theorem 4 for obtaining the sharper estimate. The digraph D in Example 8 is connected but not strongly connected. For networks with strongly connected D and $\vec{p} = \vec{t\bar{h}} = \vec{1}$ the bound of Theorem 4 can be improved.

Proposition 12. Let A be an attractor in $N = \langle D, \vec{1}, \vec{1} \rangle$. If $\langle j, i \rangle \in A_D$ and $T_j = 2$, then $T_i = 2$. Thus if D is strongly connected and there exists a node i with $T_i = 2$, then $|A| = 2$.

Proof. Assume $T_j = 2$. If there exists t such that $s_j(t) = 0 = s_i(t + 1)$, then $s_j(t + 2\tau) = 0 = s_i(t + 1 + 2\tau)$ for all $\tau \in \mathbb{N}$, and $T_i = 2$. If not, then $s_j(t) = s_i(t)$ for all times t and we also have $T_i = 2$. The last sentence follows by induction from the fact that in strongly connected digraphs there exists a directed path from any node to every other node. □

Corollary 13. Suppose A is a periodic attractor in a network $N = \langle D, \vec{1}, \vec{1} \rangle$ with strongly connected D . If A has a complete core, then $|A| \leq g(n)$.

It is quite difficult to construct networks as in Corollary 13 with attractors whose lengths exceed the number n of nodes. Extensive numerical explorations of randomly chosen networks in this class did not produce any example [1], but such examples do exist. Recall that $Act_t = \{i \in [n] : s_i(t) = 0\}$ for each $t \geq 0$. If $\vec{p} = \vec{t\bar{h}} = \vec{1}$, then $Act_t = Act_\tau$ implies $\vec{s}(t) = \vec{s}(\tau)$. This allows us to represent the states in the attractor of the following example in terms of their active sets.

Example 14. Let $A_D = D_c(26, 10) \cup \{\langle 25, 11 \rangle\}$ and $\vec{p} = \vec{t\bar{h}} = \vec{1}$. Then D is a Hamiltonian cycle with two shortcuts. Let $\vec{s}(0)$ be the initial state such that $s_i(0) = 0$ for $i \in \{2, 5, 8, 10, 13, 15, 18, 21, 23, 25\}$ and $s_i(0) = 1$ otherwise. Then we have

Act_0	2	5	8	10		13	15	18	21	23	25	
Act_1	1	3	6	9	11		14	16	19	22	24	26
Act_2		2	4	7	10	12		15	17	20	23	25
\vdots						\vdots						
Act_{28}	3	6	8	10	11	13	16	19	21	23		26
Act_{29}	1	4	7	9		12	14	17	20	22	24	
Act_{30}		2	5	8	10		13	15	18	21	23	25

Since $Act_0 = Act_{30}$ and $Act_0 \neq Act_t$ for $0 < t < 30$, we have $\vec{s}(0) = \vec{s}(30)$ and $\vec{s}(0) \neq \vec{s}(t)$ for $0 < t < 30$. Thus, the length of the attractor is $30 > 26 = n$. The set $\{C_1, C_2\}$ forms a complete core for the attractor.

Conjecture 1. Let $N = \langle D, \vec{1}, \vec{1} \rangle$ be a network such that D is a strongly connected digraph on n . If $n < 26$, then N does not have attractors of length $> n$.

In other words, we believe that Example 14 is the smallest one of its type. We were able to verify the conjecture for quite a few $n < 26$, but not yet for all of them. Our partial results imply that $g(n)$ is not the optimal upper bound for attractor length in networks with strongly connected D and $\vec{p} = \vec{th} = \vec{1}$. We conjecture that the upper bound is less than $g(n)$ for this class and we leave it as an open problem to find an optimal upper bound.

The existence of a core is not a universal mechanism responsible for all periodic attractors in our networks.

Example 15. Let $A_D = D_c(8, 3)$, $\vec{th} = \vec{1}$, and let $p_i = 1$ if $i \in [8] \setminus \{4\}$ and $p_4 = 2$. Since $p_4 = 2$, node 4 can fire at most every third time step. Let $\vec{s}(0)$ be the initial state $[0, 1, 1, 0, 1, 1, 1, 1]$. Then we have

cell number	1	2	3	4	5	6	7	8
$\vec{s}(0)$	0	1	1	0	1	1	1	1
$\vec{s}(1)$	1	0	1	1	0	1	1	1
$\vec{s}(2)$	1	1	0	2	1	0	1	1
$\vec{s}(3)$	0	1	1	0	1	1	0	1
\vdots				\vdots				
$\vec{s}(10)$	1	1	0	2	1	1	1	0
$\vec{s}(11)$	0	1	1	0	1	1	1	1

Since $\vec{s}(0) = \vec{s}(11)$ and $\vec{s}(0) \neq \vec{s}(t)$ for $0 < t < 11$, the length of the attractor is $11 > 8 = n$, which is also the period of every node. Thus the attractor in this example does not have a core.

Hamiltonian cycles with one shortcut and arbitrary \vec{p} still have a complete core and satisfy the conclusion of Theorem 4 when $\vec{th} \neq \vec{1}$.

Lemma 16. Suppose $\vec{th} \neq \vec{1}$ and let $D = D_c(n, n_1)$. Then $[n_1]$ is a complete core for every periodic attractor A in any network $N = \langle D, \vec{p}, \vec{th} \rangle$ and $|A|$ is a divisor of n_1 .

Proof. Let node i be such that $th_i > 1$.

Note that the maximum possible inputs of each node except node 1 is 1. So if $i \in [n] \setminus \{1\}$, then node i will never fire along any attractor. But if node i never fires along any attractor, neither will nodes $i + 1, i + 2, \dots, n$.

Thus if $i \in \{2, \dots, n_1\}$, then the only attractor is the steady state attractor $\{\vec{s}_{\vec{p}}\}$.

Similarly, if $i \in [n] \setminus [n_1]$, then the whole dynamics is determined by the short cycle $[n_1]$. The result follows from Proposition 1 in this case.

Finally, if $i = 1$ and there exists a periodic attractor, we must have $th_1 = 2$ and node 1 will fire at time $t + 1$ if and only if both nodes n and n_1 fire at time t . Thus we get the same dynamics on any attractor if we change th_1 from 2 to 1 and remove the arc $\langle n, 1 \rangle$ from the digraph D . Again, the whole dynamics is determined by the short cycle $[n_1]$, and the result follows from Proposition 1. \square

However, the following example shows that periodic attractors may not have a core even if $\vec{p} = \vec{1}$ and D is strongly connected.

Example 17. Let $V_D = [9]$ and let

$$A_D = \{ \langle 2, 3 \rangle, \langle 3, 4 \rangle, \langle 4, 2 \rangle, \langle 5, 6 \rangle, \langle 6, 7 \rangle, \langle 7, 8 \rangle, \langle 8, 9 \rangle, \langle 9, 5 \rangle, \langle 2, 1 \rangle, \langle 5, 1 \rangle, \langle 1, 2 \rangle, \langle 1, 8 \rangle \},$$

Let $\vec{th} = [2, 1, \dots, 1], \vec{p} = \vec{1}$ and let $\vec{s}(0)$ be the initial state $[0, 1, 0, 1, 1, 0, 1, 1, 1]$.

cell number	1	2	3	4	5	6	7	8	9
$\vec{s}(0)$	0	1	0	1	1	0	1	1	1
$\vec{s}(1)$	1	0	1	0	1	1	0	0	1
$\vec{s}(2)$	1	1	0	1	1	1	1	1	0
$\vec{s}(3)$	1	1	1	0	0	1	1	1	1
\vdots					\vdots				
$\vec{s}(13)$	1	0	1	1	0	1	1	1	1
$\vec{s}(14)$	0	1	0	1	1	0	1	1	1

Then $\vec{s}(0) = \vec{s}(14)$ and $T_i = 14 > 9$ for every $i \in [9]$.

If $\vec{p} = \vec{th} = \vec{1}$, then every periodic attractor must have a core though.

Theorem 5. Let $N = \langle D, \vec{1}, \vec{1} \rangle$. Then any periodic attractor A has a core.

Proof. In this proof it will be convenient to consider, for $\vec{s}(0)$ in an attractor, states $\vec{s}(t)$ for all t in the set of integers \mathbb{Z} , where for $t \in \mathbb{N}$, the state $\vec{s}(-t)$ is the unique state in the attractor that maps to $\vec{s}(0)$ after t updating steps. Let $j \in [n]$, let $t \in \mathbb{Z}$ be such that $s_j(t) = 0$. Let $f_0(j, t) = t$. For each $k > 0$, define recursively

$$f_{k+1}(j, t) = \min\{\tau > f_k(j, t) : s_j(\tau) = 0\}$$

and

$$d_k(j, t) = f_{k+1}(j, t) - f_k(j, t).$$

Thus $f_k(j, t)$ is the time of the k -th firing of node j after time t , and $d_k(j, t)$ is the distance between the k -th and $k + 1$ -th firing times of this node after time t . Note that $d_k(j, t) \leq |A|$. While some nodes may never fire in A , whenever we use the notation $f_k(j, t)$ or $d_k(j, t)$ we will implicitly assume that $s_j(t) = 0$ and hence that node j fires infinitely often in A .

Let $K = |A|$. For $i, j \in [n]$ and $t, \tau \in \mathbb{Z}$ with $s_i(t) = s_j(\tau) = 0$ define $(i, t) \preceq (j, \tau)$ if the sequence $(d_1(i, t), \dots, d_K(i, t))$ precedes $(d_1(j, \tau), \dots, d_K(j, \tau))$ in the lexicographic pre-order, that is, if either

$$\forall k \in [K] \ d_k(i, t) = d_k(j, \tau) \tag{7}$$

or

$$\exists k \in [K] \ d_k(i, t) < d_k(j, \tau) \ \& \ \forall \ell \in [k - 1] \ d_\ell(i, t) = d_\ell(j, \tau). \tag{8}$$

Then \preceq defines a linear pre-order on all pairs (i, t) as above. We write $(i, t) \approx (j, \tau)$ if both $(i, t) \preceq (j, \tau)$ and $(j, \tau) \preceq (i, t)$.

Proposition 18. *Suppose $\langle j, i \rangle \in A_D$ and assume $s_i(t) = s_j(t - 1) = 0$. Then*

- (i) $d_1(i, t) \leq d_1(j, t - 1)$.
- (ii) *More generally, if $f_k(i, t) = f_k(j, t - 1) + 1$, then $d_{k+1}(i, t) \leq d_{k+1}(j, t - 1)$.*
- (iii) $(i, t) \preceq (j, t - 1)$.

Proof. If (i) fails, then $s_i(t - 1 + d_1(j, t - 1)) = 1 = s_i(t + d_1(j, t - 1))$ because $2 \leq d_1(j, t - 1) < d_1(i, t)$. But $s_j(t - 1 + d_1(j, t - 1)) = 0$, which gives a contradiction. The proof of (ii) is analogous, and (iii) follows from (ii) by induction. \square

Lemma 19. *Let i be an active node in A . Then there exists a directed cycle C in D so that the dynamics of A on C satisfies conditions (a) and (b) of Definition 9 and there exists a directed path in D from some node $i^* \in C$ to i .*

Proof. Let i be as in the assumption and let t be such that $s_i(t) = 0$. Since every firing of a node at some time τ must be induced by a firing of an adjacent node at time $\tau - 1$, there must exist at least one chain $I = (i(t), i(t - 1), \dots)$ of nodes with $\langle i(t - \ell - 1), i(t - \ell) \rangle \in A_D$ and $s_{i(t-\ell)}(t - \ell) = 0$ for all $\ell \in \mathbb{N}$ and $i(t) = i$.

Fix such I . By Proposition 18(iii) we have $(i(t - \ell), t - \ell) \preceq (i(t - \ell - 1), t - \ell - 1)$ for all $\ell \in \mathbb{N}$. Since there are only finitely many possible sequences $(d_1(i, t), \dots, d_K(i, t))$ there exists ℓ^+ such that

$$(i(t - \ell), t - \ell) \approx (i(t - \ell^+), t - \ell^+) \quad \text{for all } \ell \geq \ell^+. \tag{9}$$

Moreover, there exists i^* such that $i(t - \ell^{**}) = i(t - \ell^*) = i^*$ for some $\ell^{**} > \ell^* > \ell^+$ and $i^* \neq i(t - \ell)$ for all $\ell^* < \ell < \ell^{**}$. Then

$$C = \{i^* = i(t - \ell^{**}), i(t - \ell^{**} + 1), \dots, i(t - \ell^* - 1)\}$$

is a directed cycle in D that contains node i^* . Let $\tau = t - \ell^{**}$. Then $s_{i^*}(\tau) = 0 = s_{i^*}(\tau + |C|)$ and by our choices we also have $d_k(i^*, \tau) = d_k(i^*, \tau + |C|)$ for all $k \in [K]$. It follows that

$$\forall \hat{\tau} \in \mathbb{N} \quad s_{i^*}(\hat{\tau}) = s_{i^*}(\hat{\tau} + |C|), \tag{10}$$

and we conclude that T_{i^*} divides $|C|$.

By Equation 9, $(i(t - \ell^{**} + j), t - \ell^{**} + j) \approx (i(t - \ell^+), t - \ell^+) \approx (i(t - \ell^{**}), t - \ell^{**})$ for all $j \in [|C|]$. Since $K = |A|$, the latter implies that we have $d_k(i(t - \ell^{**} + j), t - \ell^{**} + j) = d_k(i(t - \ell^{**}), t - \ell^{**})$ not only $k \in [K]$ but for all $k \in \mathbb{N}$ and $j \in [|C|]$, and the analogue of Equation 10 holds for all nodes in C . This implies that the dynamics of A on C satisfies conditions (a) and (b) of Definition 9. The existence of the required directed path from i^* to i immediately follows from the choice of i^* . \square

Now choose for every active node i a directed cycle C_i as in Lemma 19. The family \mathcal{C}_0 of these C_i satisfies conditions (a), (b), (c) of Definition 9, but the C_i s will not in general be pairwise disjoint. Let \mathcal{C} be a maximal pairwise disjoint subset of \mathcal{C}_0 . Then \mathcal{C} still satisfies conditions (a) and (b), and each $C_i \in \mathcal{C}_0$ intersects some cycle in \mathcal{C} . This implies that for each node i^* in any C_i there exists a directed path from some i^{**} in the union of \mathcal{C} to i^* , which can be used to construct a directed path from i^{**} to i . Thus \mathcal{C} satisfies condition (c) as well. \square

Corollary 20. *Suppose A is an attractor in $N = \langle D, \vec{1}, \vec{1} \rangle$ such that D is a strongly connected digraph on n that does not contain two disjoint directed cycles. Then $|A|$ divides the length of some directed cycle in D . In particular, $|A| \leq n$.*

Proof. If $|A| = 1$ there is nothing to prove. If A is periodic, then by Theorem 5 A has a core. By the assumption on D , this core must consist of exactly one cycle C and must be complete. Now the result follows from Proposition 1, Theorem 4, and Proposition 12. \square

In particular, Corollary 20 implies that the length of every attractor in networks $N = \langle D_c(n, n_1), \vec{1}, \vec{1} \rangle$ must divide either n_1 or n . In contrast to Lemma 16, this is surprisingly difficult to prove directly (see [1]), but it follows trivially from Theorems 4 and Theorem 5. This underscores the usefulness of studying structural properties of attractors, such as the existence of a (complete) core. While our counterexamples show that there are other mechanisms that can create long attractors, we believe it may be feasible to classify all such mechanisms and the structure of the resulting attractors for interesting types of networks.

5. Discussion. In Sections 3 and 4 we explored provable restrictions on the number of attractors and the lengths of transients and attractors in certain types of networks. In Section 3 we completely characterized these dynamical properties for cyclic digraphs. As our explorations in Section 4 show, this is an important base case because the structure of attractors in more general networks crucially depends on their behavior on directed cycles in the network connectivity digraph D . This type of questions is a largely unexplored area of mathematics with many challenging open problems, some of which were posed in Section 4.

While the results in Section 3 and 4 were presented in purely mathematical terms, we believe that they have significant potential of furthering our understanding of actual neuronal networks. Most obviously, if and when it becomes experimentally feasible to map the connectivity of significant portions of actual neuronal networks and record the firing patterns of selected groups of cells, it will be important to understand how the observed patterns on these groups relate to the overall dynamics of the network. Our results in Section 4 (e.g., Theorem 5) underscore the importance of directed cycles in the network for this type of inferences and Theorem 4 gives some insight into the relation to the overall dynamics of attractors. Clearly, our results are only a beginning; we firmly believe that more results of this type will be needed to make meaningful inferences of this kind from partial recordings. But actual applications of such result may lie somewhat in the future.

Of more immediate interest is how our results relate to the question whether certain olfactory networks that may roughly conform to our model code odors by attractors or by transients. If perceptions are coded by attractors, then there need to exist at the minimum sufficiently many distinct such attractors. By Corollary 2 this condition is satisfied even for the very basic case of $D = D_c(n)$. Similar results can also be shown for other connectivities; see e.g. [1] for the case of the complete digraph on n nodes. Thus networks on two opposite ends of the spectrum of possible connectivities (maximally sparse vs. maximally dense) share the property of having exponentially many attractors, and we conjecture that this is a generic property of our networks. However, the existence of sufficiently many attractors is only a necessary prerequisite; neural coding in terms of attractors may also require that these attractors have certain structural properties. Theorem 5 indicates that if $\vec{p} = \vec{t}h = \vec{1}$, then for each periodic attractor there exists a set of directed cycles in the network on which the dynamics is independent from the remainder of the network and such that each firing of any node along the attractor must originate, in the sense of Definition 9(c), from one of these cycles. Similarly, Proposition 12 shows

that for strongly connected digraphs these networks cannot have moderately long attractors with a node of period 2. This clearly limits the range of possibilities for neural codes in terms of attractors. Our results indicate that the neural code would then need to either rely on relatively short attractors with a rather special structure, or would require firing thresholds or refractory periods that are larger than 1. Let us mention that relatively short attractors appear biologically plausible. The time constraints for animals to discriminate different inputs imply that the length of the trajectory (both transient and attractor) is short so that it will not exceed the number of neurons in the olfactory system.

However, if perceptions are coded by transients, then the network must have transients that are not too short. Our previously published results [13] indicate that generic initial states in relatively densely connected networks are too short for this purpose. Theorem 3 shows that the length of the transients can (slightly) exceed the size of the network even for cyclic connectivities, as long as not all neurons have the same refractory period (Theorem 2). Numerical explorations indicate that for sparsely connected digraphs the maximum length of the transients grows faster than linear in the number of nodes. For example, Table 3.2 at page 63 of [1] gives the maximum length $Tr(n)$ of transients for Hamiltonian cycles with exactly one shortcut for $n \leq 20$. In particular, $Tr(5) = 7$, $Tr(10) = 35$, $Tr(15) = 81$, and $Tr(20) = 165$. Finding precise scaling laws for the maximum or the expected lengths of transients for interesting types of sparse connectivities other than $D_c(n)$ may be another fruitful avenue for further research. These are maximal possible lengths of transients though; it remains to find a class of networks for which typical transients are sufficiently short to allow for the time constraints for odor discrimination faced by an animal, but not too short.

In terms of fast odor recognition, neuronal representation of different odorants must sufficiently decohere during the transient phase [9, 10, 19]. This means, roughly speaking, that the corresponding transients must contain states of sufficiently large Hamming distance. Similarly, in terms of odor identity and memory, there must be sufficiently many distinct attractors with sufficient decoherence. Exploration of the phenomenon of decoherence for the networks studied here might be another promising avenue for future research.

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