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Controlling self-sustained spiking activity by adding or removing one network link

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Abstract – Being able to control the neuronal spiking activity in specific brain regions is central to a treatment scheme in several brain disorders such as epileptic seizures, mental depression, and Parkinson's diseases. Here, we present an approach for controlling self-sustained oscillations by adding or removing one directed network link in coupled neuronal oscillators, in contrast to previous approaches of adding stimuli or noise. We find that such networks can exhibit a variety of activity patterns such as on-off switch, sustained spikes, and short-term spikes. We derive the condition for a specific link to be the controller of the on-off effect. A qualitative analysis is provided to facilitate the understanding of the mechanism for spiking activity by adding one link. Our findings represent the first report on generating spike activity with the addition of only one directed link to a network and provide a deeper understanding of the microscopic roots of self-sustained spiking.

Pattern formations in excitable neural systems have been studied for several decades, producing a wealth of physics on working memory of information encoding, storing and retrieval [1–3], heart pacemaker [4], sleep-related rhythms [5,6], and others. External stimuli and inherent noise in the brain are known to affect the neuronal activity patterns in the brain, not only in normal [4], but also in pathological brain activity such as seizures [7–10]. The treatment of some brain disorders essentially involves beginning or ending certain patterns of spiking activity from specific regions. In epileptic seizures, the treatment aims to stop the spread of brain activity by cutting brain connection fibers. In case of severe mental depression and Parkinson's disease, the neuronal activity in specific brain regions is initiated by external stimulation. Here, in this simulation study, we look into the possibility of a minimal network intervention approach to control the spiking activity in the brain.

Rhythmic spiking and bursting in the cerebral cortex are generated by the cortical circuits [5]. One hypothesis about the sleep-related rhythms is that they are only the brain's way of disconnecting the cortex from the sensory input. When you are awake, thalamus allows sensory information to pass through it and be relayed up to the cortex. While you are asleep, thalamic neurons enter a self-sustained spontaneous activity state that sensory information cannot be sent to the cortex [11–13]. An important question is, how do local cortical networks generate this recurrent activity and how do afferent inputs start and stop it? It was shown that local cortical circuits do indeed operate through local recurrent connections, and that the operation of such circuits can generate

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self-sustaining activity that can be turned on and off by synaptic inputs [6]. Experimental studies of cortical areas [14] showed that the degree of heterogeneity in the connections significantly impacts the input-output function, rhythmicity, and synchrony. Yet, qualitative effects induced by connection heterogeneities are still poorly understood theoretically.

Self-sustained oscillations is currently a topic of intense research in excitable systems on complex networks [4,15–20]. Roxin *et al.* made the pioneering study in small-world networks and found that the structure of small-world network will seriously influence the self-sustained persistent activity or the failure time [15]. Their results are based on statistical ensemble average and thus are in the stage of macroscopic mechanism. Qian *et al.* revealed that a loop in the complex networks may behave as a pacemaker to sustain the spiral waves [4]. However, all these works need stimuli or noise to initiate a spike. Whether such self-sustained behavior can be generated by a third way, *i.e.*, a change of network structure, remained an open problem. Especially, it will be a very interesting problem when the change is only a tiny part of the network or even only one network link, which has received considerable attention in the fields of self-organization in critical phenomena, epileptic seizure, and cascading failures etc. [21–23].

In this work, we investigate self-sustained spikes through slightly varying network structure and report the first topology variation-induced patterns in a network with a loop core. We present a simple neural network model to exhibit a variety of activity patterns such as on-off switch, sustained spikes, and short-term spikes. We surprisingly find that without external stimuli or noise, a spike can be generated by adding only one link, *i.e.*, the third way. The condition for a link to be the controller of on-off effect is also investigated. Moreover, a qualitative analysis is provided to explain the mechanism of generating spike by adding one link to the network. This work is distinguished from ref. [15] in three points: i) it does not need an initial stimulus or noise; ii) it focuses on the microscopic root of self-sustained spiking, *i.e.*, the existence of an effective loop; iii) it shows how to control the patterns.

We first consider a loop of excitable nodes with bidirectional coupling and size N. That is, the neuron i will be connected to both the neuron $i+1$ and the neuron $i-1$ and the periodic boundary condition will be used. We then choose one node from the loop and let it be a source node. Without loss of generality, we let node 1 be the source node. Starting from the source node 1, we add some unidirectional links to other nodes, see the solid lines in the schematic fig. 1 with their arrows denoting the coupling direction. After a finite time evolution, we may slightly change the network structure by adding some new links such as the dashed line in fig. 1.

We let each node in fig. 1 be an excitable FitzHugh-Nagumo (FHN) neuron [24–28] and let the coupling be a chemical coupling. The dynamics of neuron i can be

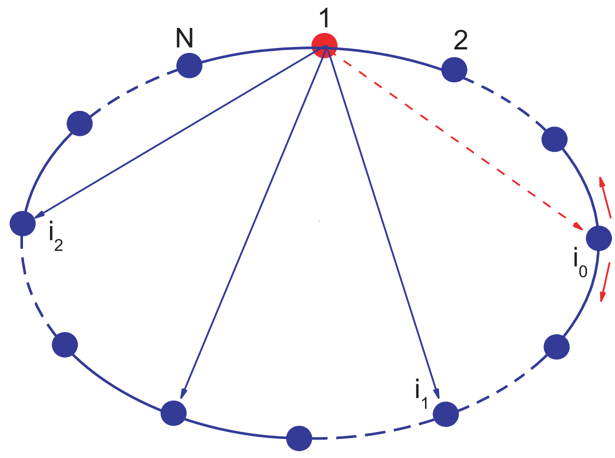

Fig. 1: (Color online) Schematic figure of the coupled neural network where node 1 represents the source node and the arrows denote the coupling directions. The solid lines such as $1 \to i_1$ and $1 \to i_2$ are part of the network and cannot be removed, while the dashed line $1 \to i_0$ is not on the network initially but will be added later. The two arrows at node i_0 represent its two coupling directions along the loop. The dashed parts on the circle imply that some nodes here are omitted.

described as

$$\begin{aligned} \varepsilon \dot{u}_i &= u_i - \frac{u_i^3}{3} - v_i + I_1\Delta(i) + I_{i-1} + I_{i+1}, \\ \dot{v}_i &= a u_i + b v_i + d, \end{aligned} \tag{1}$$

where $i = 1, 2, \dots, N$, $I_{N+1} = I_1, I_0 = I_N$, and u_i and v_i represent the fast and slow variables, respectively. ε is a small parameter which warrants a clear separation between the slow and fast time scales. We fix the parameters $\varepsilon = 0.01$, $a = 0.08$, $b = -0.064$, and $d = 0.056$ as in ref. [25] so that an isolated neuron will be in the excitable state. We notice that there is a spontaneous miniature synaptic potential in excitable neurons [29,30], which may contribute a small quantity f to the synaptic conductance g_{syn}. We also notice that a realistic synaptic conductance g_{syn} varies with time and has a finite duration in both its rising and decay phases [24,31]. Thus, we consider the synaptic coupling current as $I_i = g_{syn}(u_{syn} - u_i)$ with

$$g_{syn} = f + g_{max}[e^{-(t-t_j^{sp}-\tau)/\tau_d} - e^{-(t-t_j^{sp}-\tau)/\tau_r}], \tag{2}$$

where g_{max} describes the maximal synaptic conductance between neurons, u_{syn} denotes the synaptic reversal potential, τ is the time delay between adjacent neurons, t_j^{sp} represents the presynaptic spiking, τ_d and τ_r stand for the decay and rise time of the function and determine the duration of the response. We define $\Delta(i) = 1$ if there is a link from the source node 1 to node i, otherwise $\Delta(i) = 0$. In this paper, we take the parameters as $g_{max} = 0.2\,\mathrm{mS/cm^2}$, $u_{syn} = 0$, $\tau = 0.5\,\mathrm{ms}$, $\tau_d = 10\,\mathrm{ms}$ and $\tau_r = 1\,\mathrm{ms}$.

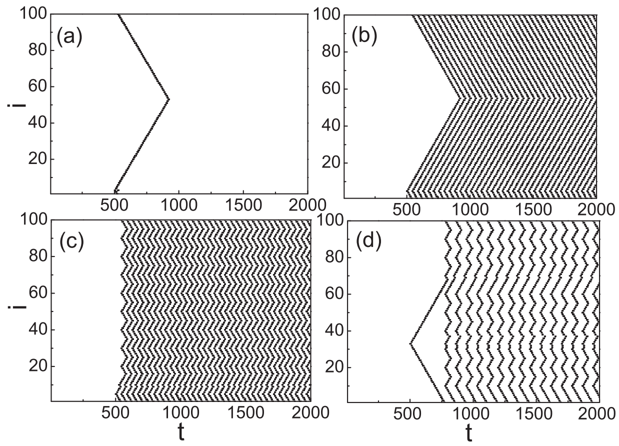

Fig. 2: Pattern formations on the network. (a) and (b): cases of adding a directional link on an isolated loop from the source node 1 to nodes 3 and 5 at the time $t = 500$, respectively. (c) and (d): cases of adding a new link from the source node 1 to nodes 5 and 33 at the time $t = 500$, respectively, where the initial network has 9 directional links from the source node 1 to the nodes $10, 20, \ldots, 90$.

Let us numerically check how the topology of fig. 1 works for generating and sustaining spikes for fixed $N = 100$. We first consider the specific case of an isolated loop without any directional couplings from the source node 1 to node i. We let the system (1) evolve with random initial conditions. After a short time of evolution, the system will reach a steady state. Then, we add a directional link from the source node 1 to node 3 at the time $t = 500$. We surprisingly find that the new link will induce a spike and the spike can be propagated to other nodes but cannot be sustained. Figure 2(a) shows the result. This finding implies that a spike can be generated by slightly changing the network topology, in contrast to previous understanding that a spike can be induced by stimulus or noise. Encouraged by this finding, we have studied other cases of adding different links between any two nodes on the loop and found that the induced spikes can be even sustained in the network. Figure 2(b) shows the result when a directional link is added from the source node 1 to node 5 at the time $t = 500$. Finally, we consider a more general case where the network initially has 9 directional links from the source node 1 to the nodes $mod(i, 10)$, *i.e.*, $10, 20, \ldots, 90$, see the topology of fig. 1. We add a new directional link from the source node 1 to node 5 at the time $t = 500$, see the dashed link in fig. 1 with $i_0 = 5$. Figure 2(c) shows the result which is similar to fig. 2(b), indicating that it is a general phenomenon for a new adding link to generate and then sustain spikes.

To understand how the spikes are sustained, we check all the spikes at each time t. It is easy to see that both the first spike in fig. 2(a) and (b) are generated at the nodes 3 and 5 at the time $t = 500$, respectively, and these two nodes 3 and 5 are always the peaks of the curves. Another common point in fig. 2(a) and (b) is that there is a bottom node on all the curves. The difference is that the spikes in fig. 2(a) end at the bottom node 53, while the spikes in fig. 2(b) do not end at the bottom node 55 but periodically repeat the process. From these observations we conclude that 1) the generated spike by the new adding link will be gradually spread out to both the directions along the loop; 2) once a node is spiked, it will enter its refractory status for a short time, *i.e.*, not spiking again when it receives a transmitted stimulus immediately; 3) the existence of a unidirectionally coupled loop, *i.e.*, pacemaker loop, is the necessary condition to sustain spikes. These three conditions explain why fig. 2(a) does not have sustained spikes while fig. 2(b) does. Let us first analyze fig. 2(a) in detail. The link $1 \to 3$ leads to two unidirectionally coupled loops in the network. One is the big loop $1 \to 3 \to 4 \cdots \to N \to 1$ and the other is the small loop $1 \to 3 \to 2 \to 1$. For the big loop, the first spike generated at node 3 will be transmitted along its two directions, *i.e.*, $3 \to 4 \to 5 \cdots$ and $3 \to 2 \to 1 \to N \to N-1 \cdots$. When these two transmitting spikes meet at node 53, they have to stop there because both the neighboring nodes 52 and 54 have just spiked and thus are in the refractory status, resulting in the end of the transmitting process. For the small loop, there is only one transmitting direction $3 \to 2 \to 1 \to 3$. However, because the loop is too small, the node 3 will be still in the refractory status when the spike generated at node 3 is transmitted back to itself through the source node 1, also resulting in the end of the spreading process. Therefore, fig. 2(a) cannot have sustained spikes. After understanding fig. 2(a), it is now easy to understand fig. 2(b). For the same reason, the big loop in fig. 2(b) will not have the sustained spikes. However, the small loop $5 \to 4 \cdots \to 1 \to 5$ in fig. 2(b) is different. Node 5 will be out of the refractory status when the spike is transmitted back to itself through the source node 1, thus node 5 will stimulate a spike again by the source node 1 and then form the sustained spikes in the network, indicating that this small loop is the pacemaker loop to sustain spikes.

The three conditions can also be used to explain fig. 2(c) although its pattern is much complicated than fig. 2(a) and (b). The new adding link $1 \to 5$ at the time $t = 500$ in fig. 2(c) will induce a spike at node 5 and then the spike will be transmitted along two paths, *i.e.*, $5 \to 4 \to 3 \cdots$ and $5 \to 6 \to 7 \cdots$, see the two red arrows at node i_0 in fig. 1. When the spiking on the first path is transmitted to the source node 1, it will be transmitted to 11 different paths (*i.e.*, $1 \to 5, 1 \to 10, 1 \to 20, \cdots, 1 \to 90$, and $1 \to N$) at the same time. Then, except the node N, each spiking at the 10 nodes $5, 10, 20, \ldots, 90$ will be continuously transmitted by two paths, *i.e.*, $i \to i+1$ and $i \to i-1$. The spiking at node N will be only transmitted to node $N-1$ but not back to node 1 as it is in the status of refractory. An interesting phenomenon occurs: the spikes from two neighboring paths will meet and then end the spreading process as both of their next locations are in the refractory status. For example, the spiking from the path $N \to N-1\cdots$ will meet with that from $90 \to 91\cdots$ at node 95 and then end the spreading process there. This is the reason why we have observed the peaks at nodes $N, 90, \ldots, 5$ and the bottoms at nodes $95, 85, \ldots$ in fig. 2(c). After all the ending processes, only the spiking on the path $5 \to 4 \to 3\cdots$ remains, which consists of the pacemaker loop and then repeats the cycle through the source node 1.

Figure 2(c) tells us that the rightmost link $1 \to i_0$ in fig. 1 is the key to sustain spikes in the network. An interesting question would be what will happen if the link $1 \to i_0$ is not the rightmost link. To answer this question, we let i_1 and i_2 be the rightmost and leftmost links of the initial network, see fig. 1. In concrete, we here have $i_1 = 10$ and $i_2 = 90$. Then, instead of adding a link $1 \to 5$ at $t = 500$, we add a link $1 \to 33$ at $t = 500$ which is between i_1 and i_2. Figure 2(d) shows the result. Obviously, the pattern in fig. 2(d) is quit different from that in fig. 2(c), especially the recurrent periods. This phenomenon can be also explained by the above three conditions. We notice that in the second cycle of transmissions, the two transmitting directions $1 \to 33 \to 32\cdots$ and $1 \to 33 \to 34\cdots$ will be ended by the neighboring transmitting directions $1 \to 30 \to 31\cdots$ and $1 \to 40 \to 39\cdots$, respectively. Thus, the link $1 \to 33$ will not be the key to sustain spikes again. In contrast, the link $1 \to 10$ now becomes the closest one to the source node 1 and thus is the key to sustain spikes, indicating that the pacemaker loop consists of $10 \to 9\cdots \to 1 \to 10$. Considering that the period of the pattern is determined by the size of the pacemaker loop, we predict that the period will be proportional to 5 in fig. 2(c) and 10 in fig. 2(d), which gives the ratio 1/2. This prediction can be easily confirmed by counting the numbers of curves in fig. 2(c) and (d), respectively. For example, we focus in the range $1000 < t < 2000$ and find that the numbers are 24 and 12, respectively, which gives the frequency ratio 24/12 and thus the period ratio $12/24 = 1/2$. In sum, sustained spikes and their period are determined by the size of pacemaker loop.

The above discussions are based on the adding of a new link. An intuitive question will be how about the removing of a link. To study this problem, we make a slight change on the network of fig. 2(c): remove the link $1 \to 5$ at the time $t = 1000$, then add the link $1 \to 5$ again at the time $t = 1500$, then remove the link $1 \to 5$ again at the time $t = 2000$ and so on. We find that these operations result in an effect of on-off switch, implying that the pattern can be controlled by only one link! Figure 3(a) shows the result. The underlying mechanism is that there are two transmitting directions $5 \to 4\cdots$ and $5 \to 6\cdots$ before removing the link $1 \to 5$. After removing the link $1 \to 5$, these two transmissions will meet at node 10 and then cannot continue to transmit toward the direction $10 \to 9\cdots$ because node 9 is in the refractory status, resulting the end of sustained spikes. Our numerical simulations further reveal that the sustained spikes will be ended, provided that the two transmissions will meet between i_0 and i_1 in fig. 1. For example, when the link $1 \to 5$ is replaced by $1 \to 4$, the two transmissions will meet at node 9 and thus end the sustained spikes. Moreover, when the initial links from the source node 1 to the nodes $mod(i, 10)$ is replaced by $mod(i, 20)$, we will have more choice of $1 \to i_0$ such as those links from $1 \to 4$ to $1 \to 9$ satisfying the condition that its two transmissions will meet between i_0 and i_1, which results in ending the sustained spikes. Therefore, we conclude that the condition for the link $1 \to i_0$ to be a controller of on-off switch is that (1) the link $1 \to i_0$ in fig. 1 must be the one to make the pacemaker loop; and (2) the two transmissions $1 \to i_0 \to i_0 - 1\cdots$ and $1 \to i_0 \to i_0 + 1\cdots$ have to meet between i_0 and i_1. When these conditions are broken, we cannot observe the effect of on-off switch. For example, when we replace the link $1 \to 5$ in fig. 3(a) by $1 \to 33$, the recurrent operations of adding and removing the link $1 \to 33$ will not influence the sustained spikes. Figure 3(b) shows the result.

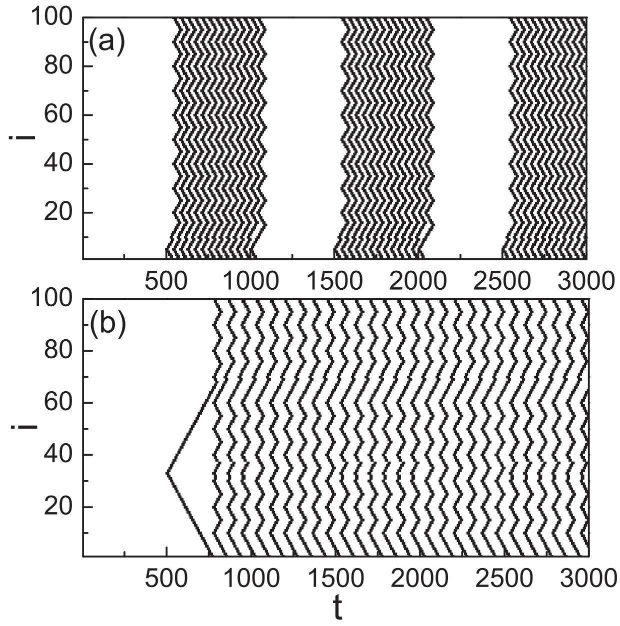

Fig. 3: Effect of on-off switch with the initial network of 9 directional links from the source node 1 to the nodes $10, 20, \ldots, 90$. A new link will be added at the time $t = 500$, removed at $t = 1000$, added again $t = 1500$, removed again at $t = 2000$ and so on. (a) and (b) represent the cases of adding the new link from the source node 1 to nodes 5 and 33, respectively.

An interesting question is how the time delay τ in eq. (2) influences the sustained spikes? To figure out the answer, we take the case of fig. 2(c) as an example. We find that there is a critical point $\tau_c \approx 0.73$. The pattern is the same as in fig. 2(c) when $\tau < \tau_c$. Figures 4(a) and (b) show the results for two typical $\tau = 0.4$ and 0.7, respectively. While for $\tau > \tau_c$, the pattern will become another denser one. Figures 4(c) and (d) show the results for two typical $\tau = 0.75$ and 1.0, respectively. Therefore, the sustained

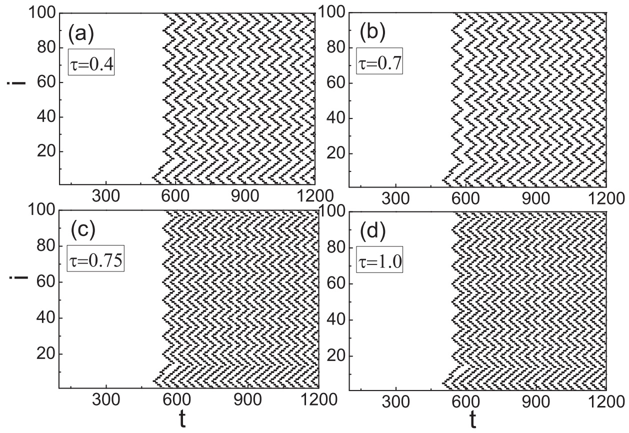

Fig. 4: The case of time delay with the same parameters as in fig. 2(c). Panels (a)–(d) represent the cases of $\tau = 0.4, 0.7, 0.75$ and 1.0, respectively.

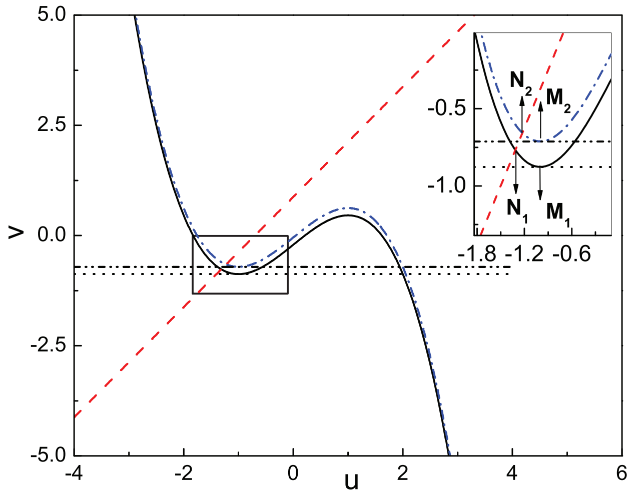

Fig. 5: (Color online) Qualitative analysis to the mechanism of induced spike by adding a new link.

spikes are robust to the delay, indicating that the delay is not an important parameter here.

We now turn to analyze the mechanism of inducing spike by adding a new link. Figure 5 shows the schematic figure where the solid and dashed lines represent the u-nullcline ($u - u^3/3 - v = 0$) and v-nullcline ($au + bv + d = 0$), respectively, and their intersection N_1 denotes the equilibrium point [5], see the inset. Before adding the new link, the system stays nearby the point N_1 which is on the stable branch of the u-nullcline. Let $\Delta I = u_{N_1} - u_{M_1}$ with M_1 denoting the bottom of u-nullcline. A spiking can be induced if an external stimulus is greater than ΔI [5]. In our case, when a new link is added, it will cause an input I_1 to the variable u (see eq. (1)) and then make the u-nullcline shift upward a distance $M_2 - M_1 > \Delta I$, see the dash-dotted line in fig. 5. The consequence is that the original N_1 is now locating below the new bottom M_2 and thus is in the region of self-excitatory of the new u-nullcline and the trajectory from N_1 to N_2 goes through the right branch of the new u-nullcline, thereby resulting in a spike.

To figure out the mechanism of sustained spikes, all the above discussions are based on the existence of source node 1. However, our extensive numerical simulations show that the patterns of sustained spikes can also be obtained by no source node. That is, the sustained spikes can also be observed by randomly adding links between any two nodes on the loop. Thus, the source node in the schematic fig. 1 is only for the convenience of illustrating the mechanism of sustained spikes but not the necessary condition to sustain the spiking. We also find that the effect of on-off switch can be implemented by adding and removing more links at the same time. Therefore, the configuration of fig. 1 and its variations will produce abundant patterns. This property is very good for short-term memory where a diversity of synchronized patterns is guaranteed for sufficient coding capability in brain oscillations [15,32]. The ability to generate different periods of self-sustaining provides a computationally powerful mechanism by which cortical networks may solve a large variety of tasks [6].

In conclusion, we have provided a simple neural network model to discuss the process of generating and sustaining of spikes. In contrast to the previous two ways of adding stimulus or noise to control spiking activity in excitable systems, we discover a new way of controlling spiking activity. We find that the existence of a small pacemaker loop in the network is the key to sustained spikes, *i.e.*, the other parts of the network are sustained by the small pacemaker loop. Moreover, we find the effect of on-off switch by periodically adding and removing a link. The condition for a link to be a controller is that it must be the one to make the pacemaker loop and its two transmissions have to meet between i_0 and i_1. These findings reveal the qualitative relationship between the long-time and short-time memory and the local structure of neuron networks and may help us understand the origin of the sustained activity in the brain underlying human cognition.

* * *

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