Quantifying neuronal network dynamics through coarse-grained event trees

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Animals process information about many stimulus features simultaneously, swiftly (in a few 100 ms), and robustly (even when individual neurons do not themselves respond reliably). When the brain carries, codes, and certainly when it decodes information, it must do so through some coarse-grained projection mechanism. How can a projection retain information about network dynamics that covers multiple features, swiftly and robustly? Here, by a coarse-grained projection to event trees and to the event chains that comprise these trees, we propose a method of characterizing dynamic information of neuronal networks by using a statistical collection of spatial–temporal sequences of relevant physiological observables (such as sequences of spiking multiple neurons). We demonstrate, through idealized point neuron simulations in small networks, that this event tree analysis can reveal, with high reliability, information about multiple stimulus features within short realistic observation times. Then, with a large-scale realistic computational model of V1, we show that coarse-grained event trees contain sufficient information, again over short observation times, for fine discrimination of orientation, with results consistent with recent experimental observation.

Encoding of sensory information by the brain is fundamental to its operation (1, 2); thus, understanding the mechanisms by which the brain accomplishes this encoding is fundamental to neuroscience. Animals appear to respond to noisy stimulus swiftly within a few 100 ms (3–7). Hence, an immediate important question is what statistical aspects of network dynamics in the brain underlie the robust and reliable extraction of the salient features of noisy input within a short observation window $T_{\text{obs}} = 0(100 \text{ ms})$ (7, 8). Although the full spatiotemporal history of the high-dimensional network dynamics might contain all of the salient information about the input, an effective and efficient method for extracting the relevant information ultimately entails a projection or “coarse-graining” of the full dynamics to lower dimensions. To be successful, this projection must retain and effectively capture the essential features of noisy input, in a robust and reliable manner, over short observation times $T_{\text{obs}}$. Quantifying neuronal network dynamics by information carried by the firing rates of individual neurons is certainly low-dimensional, but it may require excessively long integration windows when the firing rate is low (9, 10). Here, we propose a method for quantifying neuronal network dynamics by a projection to event trees, which are statistical collections of sequences of spatiotemporally correlated network activity over coarse-grained times. Through idealized networks and through a large-scale realistic model (11, 12) of mammalian primary visual cortex (V1), we show that this event tree-based projection can effectively and efficiently capture essential stimulus-specific, and transient, variations in the full dynamics of neuronal networks. Here, we demonstrate that the information carried by the event tree analysis is sufficient for swift discriminability (i.e., the ability to discriminate, over a short $T_{\text{obs}}$, fine input features, allowing for the reliable and robust discrimination of similar stimuli). We also provide evidence that suggests that, because of their dimensionality, event trees might be capable of encoding many distinct stimulus features simultaneously† (note that $n$ features constitute an $n$-dimensional space that characterizes the input). The idealized networks presented here establish proof of concept for the event tree analysis; the large-scale V1 example presented here indicates that event tree methods might be able to extract fine features coded in real cortices, and our computational methods for analyzing event trees may extend to useful algorithms for experimental data analysis.

Many hypotheses about coding processes in neuronal networks [such as in synfire chains (14)] postulate that the individual spikes or spike rates from specific neurons constitute signals or information packets that can be tracked as they propagate from one neuron to another (15–17). This notion of signal propagation is essentially a feedforward concept; hence, it is restricted to feedforward architecture, where the cascade of signals across neurons in the network can be treated as a causal flow of information through the network (10, 15–17). In contrast, in our event tree analysis, each individual firing event of a particular neuron is never treated as a signal as such. Instead, the entire event tree serves as the signal within the network. Event trees carry information that is a network-distributed (or space–time-distributed) signal, which is a function of both the dynamic regime of the network and its architecture. Here, we will show that this event tree signal can be quantified collectively and statistically without restriction to any particular type of network architecture. In addition, as will be shown below, information represented through the event tree of a network, such as reliability and precision, can differ greatly (and be improved) from those of individual neurons that constitute the components of that network.

Results

To describe and understand the event tree method, it is useful first to recall the information-theoretic framework (1, 2) of “type analysis” (18, 19), a standard projection down to state chains to analyze the dynamics of a system of $N$-coupled neurons that interact through spikes. Type analysis consists of (i) reducing the high-dimensional network dynamics to a raster (a sequence of neuronal firing events); (ii) coarse graining time into $\tau$-width bins and recording within each bin the binary “state vector” of spiking neurons within the network (within each time bin, each neuron can spike or not, and a system of $N$ neurons has $2^N$ possible states); and (iii) estimating the conditional probabilities of observing any particular state, given the history of inputs and $m$ previous system states. Type analysis suffers from the curse of dimensionality: it is difficult

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†We note that this feature has been discussed within spike metric coding (13).

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to obtain, over realistically short observation times, accurate statistical approximations to the probabilities of observing any particular sequence of states. For example, if the total observation time of the system $T_{\text{obs}} \sim m \tau$, then only $\sim 1$ sequence of $m$ states is observed (of a possible $2^m$ such sequences). Therefore, this curse limits the ability of type analysis to characterize a short observation of a system.

In contrast, our notion of an event tree invokes a different projection of the system dynamics, namely, down to a set of event chains, instead of state chains. To define event chains, we need the following notation: let $\sigma_j$ denote a firing event of the $j$th neuron at time $t$ (not discretized), and let $\sigma^m$ denote any firing event of the $j$th neuron that occurs during the time interval $I$. Now, given any time scale $\alpha$, an $m$-event chain, denoted by $\{\sigma^{0} \rightarrow \sigma^{1} \rightarrow \ldots \rightarrow \sigma^{m}\}$ (spanning the neurons $j_1, \ldots, j_m$, which need not be distinct), is defined to be any event $\sigma^m$ conditioned on (i.e., preceded by) the events $\sigma^{[m-1]} \rightarrow \sigma^{0}$, $\sigma^{[m-2]} \rightarrow \sigma^{1}$, etc. Unlike type analysis, in which both neuronal firing and nonfiring events affect the probability of observing each state chain (19), our event chain construction limits the relevant observables to firing events only, as motivated by the physiological fact that neurons only directly respond to spikes, with no response to the absence of spikes. Indeed, it seems impossible for the brain itself to respond uniquely to each chain of states consisting of both firing and nonfiring events (e.g., even for a small system of $N = 15$ neurons and a history dependence of $m = 4$ states, the number of possible state chains exceeds the number of cells in a single animal).

Given an observation window $T_{\text{obs}}$ of the system, one can record every $m$-event chain for all $m$ up to some $m_{\text{max}}$. Note that the number of observed one-event chains $|\sigma^{i_j}|$ corresponds to the total number of spikes of the $j$th neuron during $T_{\text{obs}}$; the number of observed two-event chains $|\sigma^{j_1} \rightarrow \sigma^{j_2}|$ corresponds to the total number of spikes on the $j_2$th neuron that occur within $\alpha$ ms after a spike of the $j_1$th neuron; and so forth. We will refer to the total collection of all possible $m_{\text{max}}$ event chains with their occurrence counts as the $m_{\text{max}}$-event tree over $T_{\text{obs}}$.

Fig. 1 provides a simple example of the event chains produced by a network of $N$ coupled integrate-and-fire (I&F) neurons (20). The system is driven by two slightly different stimuli $I_1$ and $I_2$. The natural interaction time scale in this system is the synaptic time scale $\alpha \sim 4$ ms, and we record all pairs of events in which the second firing event occurs no later than $\alpha$ ms after the first. Three such two-chains, $\{\sigma^1 \rightarrow \sigma^2\}$, $\{\sigma^3 \rightarrow \sigma^4\}$, and $\{\sigma^2 \rightarrow \sigma^3\}$, are highlighted (within Fig. 1G) by light, dark, and medium gray, respectively. Note that the events $\sigma^1$, $\sigma^2$, $\sigma^3$, $\sigma^4$ each occurs two times within both rasters in Fig. 1A and B. Fig. 1C and D shows representations of the two-event tree corresponding to A and B, respectively. Note that the event chain $\{\sigma^1 \rightarrow \sigma^4\}$ occurs twice within raster B but zero times in raster A, whereas the event chain $\{\sigma^1 \rightarrow \sigma^3\}$ occurs zero times within raster B but twice within raster A. Fig. 1E and F shows representations of the two-event trees associated with very long $T_{\text{obs}} = \infty$ observations of the dynamics under stimuli $I_1$ and $I_2$, respectively (where the occurrence counts have been normalized by $T_{\text{obs}} \gg 1$ and displayed as rates).

The event tree as described above is a natural intermediate projection of the system dynamics that is lower dimensional than the set of all state chains [dim = $N^{m_{\text{max}}}$ in contrast to dim = $(2^m)^{m_{\text{max}}}$], but higher dimensional than, say, the firing rate. Nevertheless, there is still a severe undersampling problem associated with analyzing the set of event trees produced by the network over multiple trials of a given $T_{\text{obs}}$. Namely, given multiple $T_{\text{obs}}$ trials, each trial will (in general) produce a different event tree, and it is very difficult to estimate accurately the full joint probability distribution (over multiple trials) of the $\sum_{m = 1}^{m_{\text{max}}} \text{various event chains comprising the event trees}$. However, we can circumvent this difficulty by considering the probability distribution (over multiple trials of $T_{\text{obs}}$ ms) of the observation count of each event chain individually and then considering the full collection of all of these observation–distributions of event chains (which we will also refer to as an event tree). It is this object that we will use below to assess the discriminability of network dynamics, i.e., how to classify the stimulus based on a $T_{\text{obs}}$ sample of the dynamics. In the remainder of the article, the discriminability function is constructed based on standard classification theory (2), by assuming the observation counts of event chains are independent [for details see Methods or Fig. S1 in the supporting information (SI Appendix)].

It is important to note that event chains are much more appropriate than state chains for this particular method of
estimating observation–distributions and assessing discriminiability. As we discussed above, there is a curse of dimensionality for state chain analysis: only $\sim 1$ sequence of $m$ states is observed over $T_{\text{obs}} \sim m^2$. In contrast, because many distinct event chains can occur simultaneously, there can be a very large number of distinct, stimulus-sensitive event chains (spanning different neurons in the network) even within short ($T_{\text{obs}} \sim 100$ ms) observations of networks with low firing rates. Because event chains are not mutually exclusive, multiple event chains can occur during each $T_{\text{obs}}$ and a collection of accurate $T_{\text{obs}}$ observation–distributions (one for each event chain) can be estimated with relatively few trials (in contrast to the $O(2^{N_{\text{max}}})$ trials required to build a collection of observation–distributions of state chains). As will be seen below, it is this statistical feature that enables our event tree projection to characterize robustly, over short $T_{\text{obs}}$, the transient response and relevant dynamic features of a network as a whole (reflecting the dynamic regime the network is in as well as the time-varying inputs). A neuronal network contains information for swift discriminability when that network can generate sufficiently rich, effectively multidimensional event chains that reflect the salient features of the input, as demonstrated in Figs. 1 and 2. Therefore, we call a network functionally powerful (over $T_{\text{obs}}$) if the event tree (comprising the $T_{\text{obs}}$ distribution of event chains) is a sensitive function of the input.\footnote{The $T_{\text{obs}}$ distribution of event chains is a statistical collection that includes the occurrence counts of every $\alpha$-admissible event chain, and is more sensitive to stimulus than the rank order of neuronal firing events (21).}

In Fig. 1, the discrepancies between Fig. 1 $C$ and $D$ are highly indicative of the true discrepancies in the conditional probabilities shown in Fig. 1 $E$ and $F$. The $T_{\text{obs}} = 128$ ms rasters in Fig. 1 $A$ and $B$ clearly show that firing rate, oscillation frequency, and type analysis (with $\tau \approx 4$ ms) cannot be used to classify correctly the input underlying these typical $T_{\text{obs}} = 128$ ms observations of the system. However, the two-event trees over these $T_{\text{obs}} = 128$ ms rasters can correctly classify the inputs (either $I_1$ or $I_2$). Furthermore, for this system, a general $128$ ms observation is correctly classified by its two-event tree $\sim 85\%$ of the time.

In Fig. 2 we illustrate the utility of event tree analysis for swift discriminability within three model networks (representative of three typical dynamic regimes). The networks are driven by independent Poisson stimuli $I_k$ that are fully described by input rate $v_k$ spikes per ms and input strength $f_k$, $k = 1, 2, 3$ with $(v_k, f_k) = (0.5, 0.005), (0.5, 0.005)$, and $(0.5, 0.00525)$. A–C (left) Typical 1024-ms rasters under stimulus $I_1, I_2$, or $I_3$. (Middle) Log-linear plots of the subthreshold voltage power spectra under stimulus $I_k$. These power spectra strongly overlap one another under different stimuli. With these very similar inputs, the spectral power of synchronous oscillations fails to discriminate the inputs within $T_{\text{obs}} \approx 512$ ms. For large changes in the stimulus, these networks can exhibit dynamic changes that are detectable through measurements of firing rate. However, for the cases shown in Fig. 2, with very similar inputs, the firing rate also fails to discriminate the inputs within $T_{\text{obs}} \approx 512$ ms.

Fig. 2A illustrates a phase oscillator regime, where each neuron participates in a cycle, slowly charging up its voltage under the drive. Every $\sim 70$ ms, one neuron fires, pushing many other neurons over threshold to fire, so that every neuron in the system either fires or is inhibited. Then the system starts the cycle again. In this regime, the synchronous network activity strongly reflects the architectural connections but not the input. Note that here the order of neuronal firing within each synchronous activity is independent of the order within the previous one because the variance in the input over the silent epoch is sufficient to destroy the correlation between any neurons resulting from the synchronous activity (data not shown). In this simple dynamic state, neither the firing rate, the power spectrum, nor event tree analysis can reliably discriminate between the two stimuli within $T_{\text{obs}} \approx 512$ ms. This simple state, with oscillations, is not rich enough dynamically to discriminate between these stimuli.

Fig. 2B illustrates a bursty oscillator regime, where the dynamics exhibits long silent periods punctuated by $\sim 10$- to 20-ms synchronous bursts, during which each neuron fires 9–10 times. The power spectrum and firing rates again cannot discriminate the stimuli, whereas deeper event trees ($m_{\text{max}} = 4, 5$) here can reliably differentiate $I_1$ and $I_3$ within $T_{\text{obs}} \approx 512$ ms. (As a test of statistical significance, the discriminability computed by using an alternative event tree with neuron labels shuffled across each event chain performs no better than mere firing rates.) We comment that we can also use different time scales $\alpha$ for measuring event trees. For example, in this bursty oscillator regime, we estimated that the variance in input over the silent periods of $T_e \sim 80$ ms cannot sufficiently destroy the correlation between neurons induced by the synchronous bursting. Thus, event trees constructed with $\alpha \sim T_e$ observed across silent periods by including multiple sustained bursts, can also be used to discriminate the inputs (data not shown).

Fig. 2C illustrates a sustained firing regime, where the power spectrum and one-event tree (i.e., firing rates) cannot discrim-
Fig. 3. Functional power of the network vs. reliability of individual neurons. Here, we illustrate that the functional power of a network is not simply an increasing function of the synaptic reliability of individual neurons within that network. More details about this model network may be found in Fig. S2 in the SI Appendix. The discriminability is plotted for a set of different $p_{\text{fail}}$ (the dots indicate data points, the dashed line is to guide the eye only).

To summarize, the dynamics shown in Fig. 2 B and C is sufficiently rich that the event trees observed over a short $T_{\text{obs}} \approx 256 \text{ ms}$ can be used to classify correctly the stimulus $\sim 75\%$ of the time. Incidentally, a label-shuffled event tree performs the discriminability task at nearly chance (i.e., firing rate) level. The fact that the five-event tree can be used to distinguish among these three stimuli implies that event tree analysis could be used to discriminate robustly between multiple stimuli (such as f and v).

In the present work we did not investigate the map from high-dimensional stimulus space to the space of observation-distributions of event chains (13). However, we have tested the ability of the sustained firing regime (see Fig. 2C) to distinguish between up to six different stimuli (which differ along different stimulus dimensions) simultaneously. We chose uniform independent Poisson stimulus $J_i$ such that: (i) $I_1$ had fixed strength f and rate $v_1$; (ii) $I_2$ had fixed strength f and rate $v_2$; (iii) $I_3$ had fixed strength f and rate $v_3$; (iv) $I_4$ had strength f and rate $v_4[\cos (2\omega t)],$ a rectified sinusoid oscillating at 64 Hz; (v) $I_5$ had strength f and rate $v_5[\cos (2\omega t)],$ a rectified sinusoid oscillating at 128 Hz; and (vi) $I_6$ had strength f and rate given by a square wave oscillating at 64 Hz and amplitude $v_6$. We fixed $f_2, v_3, v_4, v_5, v_6$ so that the firing rates observed under stimuli $I_1, \ldots, I_6$ were approximately the same. Specifically, within this six-stimulus discrimination task, the one-, two-, three-, four-, and five-event trees over $T_{\text{obs}} \approx 512 \text{ ms}$ could be used to classify correctly the stimuli $\sim 18\%, \sim 20\%, \sim 22\%, \sim 25\%, \text{ and } \sim 34\%$ of the time, respectively. Only the deeper event trees contained sufficient information over $T_{\text{obs}}$ to discriminate the stimuli at a rate significantly greater than the chance level of 17%. Again, for this discrimination task, label-shuffled event trees perform at nearly chance (i.e., firing rate) level.

We emphasize that the functional power of a network is not simply related to the individual properties of the neurons composing the network. For instance, the functional power of a network can increase as its components become less reliable, as is illustrated in Fig. 3 (and described in more detail in Fig. S2 in the SI Appendix). Fig. 3 shows an example of a model network whose discriminability increases as the probability of synaptic failure (20) increases, making the individual synaptic components of the network less reliable. Here, we model synaptic failure by randomly determining whether each neuron in the network is affected by any presynaptic firing event with $p_{\text{trans}} = (1 - p_{\text{fail}})$ as transmission probability. We estimate the functional power of this network as a function of $p_{\text{fail}}$. The system was driven by three similar inputs, $I_1, I_2, I_3$, and we record the $T_{\text{obs}} = 512 \text{ ms}$ three-event trees. We use the three-event trees to perform a three-way discrimination task (33% would be chance level). The discriminability is plotted against $p_{\text{fail}}$ in Fig. 3, which clearly demonstrates that the event trees associated with the network are more capable of fine discrimination, when $p_{\text{fail}} \sim 60\%$ than when $p_{\text{fail}} = 0\%$. If there is no synaptic failure in the network, then the strong recurrent connectivity within the network forces the system into one of two locked states. However, the incorporation of synaptic failure within the network allows for richer dynamics. A possible underlying mechanism for this enhanced reliability of the network is “intermittent desuppression” (12): synaptic failure may “dislodge” otherwise locked, input-insensitive, responses of the system. As a consequence, the dynamics escapes from either of these locked states and generates more diverse input-sensitive event trees over a short $T_{\text{obs}}$ thus leading to a system with a higher sensitivity to inputs and a higher functional power.

It is important to emphasize that the analysis of network dynamics using information represented in event trees and characterization of functional power can be extended to investigate much larger, more realistic neuronal systems, such as the mammalian V1. Neurons within V1 are sensitive to the orientation of edges in visual space (22). Recent experiments indicate that the correlations among spikes within some neuronal ensembles in V1 contain more information about the orientation of the visual signal than do mere firing rates (23, 24). We investigate this phenomenon within a large scale model of V1 (see refs. 11 and 12 for details of the network).

For these larger networks, it is useful to generalize the notion of events from the spikes of individual neurons to spatiotemporally coarse-grained regional activity, as illustrated in Fig. 4, in which a regional event tree is constructed by using regional events, defined to be any rapid sequence of neuronal spikes (viewed collectively as a single “recruitment event”) occurring within one of the N_r cortical regions of the model V1 cortex. More specifically, we define $N_r$ sets of neurons (i.e., “regions”) $\{J_i\}$, each composed of either the excitatory or inhibitory neurons within a localized spatial region of the V1 model network (see shaded regions in Fig. 4), and we say that a regional event $J_i$ takes place any time $N_{\text{local}}$ neurons within a given region fire within $T_{\text{local}} \text{ ms}$ of one another. We define the time of the regional event $T_{\text{local}}$ as the time of the final local firing event in this short series. This characterization of regional events within regions of excitatory neurons (using $N_{\text{local}} \sim 3$–5 and $T_{\text{local}} \sim 3$–6 ms) serves to quantify the excitatory recruitment events we have observed and heuristically described within the intermittently desuppressed cortical operating point of our cortical V1 model (11). The choice of $T_{\text{local}}$ corresponds to the local correlation time scale in the system, and the choice of $N_{\text{local}}$ corresponds to the typical number of neurons involved in recruitment. We have observed (12) that recruitment events in neighboring regions are correlated over time scales of 10–30 ms. These recruitment events are critical for the dynamics of our V1 model network, and the dynamic interplay between recruitment events occurring at different orientation domains can be captured by a regional event tree defined by using $\alpha \sim 15 \text{ ms}$.

In Fig. 4, we demonstrate that the coarse-grained event tree associated with the dynamics of our large-scale ($\sim 10^6$ neurons) computational, recurrent V1 model (11, 12) is indeed sufficiently rich to contain reliably information for small changes in the input.
The event tree analysis does not rely on specific architectural assumptions such as the feedforward assumption underlying many coding descriptions of synfire chains; in fact, event tree analysis is applicable to both feedforward and strongly recurrent networks. Discriminability relies, particularly for fine discrimination tasks, on the network operating with sufficiently rich dynamics. In this regard, we have demonstrated that networks locked in simple dynamics, no matter whether characterized by oscillation frequencies through power spectrum or event trees, cannot discriminate between fine stimulus characteristics. However, as has been demonstrated above, there exist networks that exhibit complex dynamics that contains sufficient information to discriminate stimuli swiftly and robustly, information that can be revealed through an event tree projection but not by merely analyzing power spectrum of oscillations. Moreover, we have shown that event trees of a network can reliably capture relevant information even when the individual neurons that comprise the network are not reliable. There are other useful high-dimensional projections of network dynamics, such as spike metric (13, 25) and ensemble encoding (26), which may also be capable of extracting information that can be used to discriminate stimuli robustly and swiftly. It would be an interesting theoretical endeavor to investigate these issues by using these alternative projections and to compare their performance with event tree analysis.

We expect that our computational methods for collecting, storing, and analyzing event trees can be used by experimentalists to study network mechanisms underlying biological functions by probing the relevance and stimulus specificity of diverse subsets of events within real networks through methods such as multielectrode grids.

The features described above make the event tree analysis intriguing. Here, we have addressed how information could be represented in a network dynamics through coarse-grained event trees. As an extended space–time projection, it will probably require an extended space–time mechanism for other neurons to read out the information contained in event trees. A theoretical possibility would be that read-out neurons employ the mechanism of temptron (27) to reveal the information that is represented through event trees.

Finally, we mention a possible analytical representation of the dynamics of event trees in the reduction of network dynamics to a much lower dimensional effective dynamics. For example, in the phase oscillator dynamics of Fig. 2A, the event tree observed during one synchronous activity is uncorrelated from that observed during the next synchronous activity. This independence allows us to reduce the original dynamics to a Markov process of successive event trees (data not shown). However, for more complicated dynamics, reduction cannot be achieved by this simple Markov decomposition. Instead, a hierarchy of event chains, namely, chains of chains, needs to be constructed for investigating correlated dynamics over multiple time scales.

**Methods**

Standard computational model networks of conductance-based I&F point neurons (20), driven by independent Poisson input, are used to test event tree analysis. For details, see SI Appendix. For application to V1, we use the large-scale, realistic computational model of conductance based point neurons described in refs. 12 and 28.

**Discussion**

We have proposed a method of quantifying neuronal network dynamics by using information present in event trees, which involves a coarse-grained statistical collection of spatiotemporal sequences of physiological observables. We have demonstrated that these spatiotemporal event sequences (event chains) can potentially provide a natural representation of information in neuronal network dynamics. In particular, event tree analysis of our large-scale model of the primary visual cortex (V1) is shown to provide fine discriminability within the model and hence possibly within V1. Importantly, the event tree analysis is shown to be able to extract, with high reliability, the information contained in event trees that simultaneously encodes various stimuli within realistic short observation times.
network’s $m_{\text{max}}$-event tree (over multiple independent observations with fixed $T_{\text{obs}}$ under each stimulus $i_1, i_2$). With this collection of data, we obtain, for each stimulus, the empirical distributions of each $m$-event chain’s occurrence count for all $m \leq m_{\text{max}}$. Thus, for each stimulus $i$ and for each event chain $(e^1 \rightarrow e^2 \rightarrow \ldots \rightarrow e^m)$ we obtain a set of separate probabilities $P(e^1 \rightarrow e^2 \rightarrow \ldots \rightarrow e^m)$ for each chain to occur $k$ times within a given $T_{\text{obs}}$, for each integer $k \geq 0$ and each stimulus $i = 1, 2$. We then apply standard methods from classification theory and use this set of observation count distributions, along with an assumption of independence for observation counts of different event chains, to perform signal discrimination from a single $T_{\text{obs}}$ observation. For completeness, we describe our procedure below.

Typically, some event chains are not indicators of the stimulus (i.e., the $T_{\text{obs}}$ distribution of occurrence count is very similar for distinct stimuli). However, other event chains are good indicators and can be used to discriminate between stimuli. For example, as depicted in Fig. S1E in the SI Appendix the $T_{\text{obs}}$ = 512 ms distribution of occurrence counts of the four-event chain $e^4 \rightarrow e^2 \rightarrow e^2 \rightarrow e^2$ is quite different under stimulus $i_1$ than under stimulus $i_2$. Given (estimates of) these two distributions $P_1(i)$ and $P_2(i)$, one obtains from a single $T_{\text{obs}}$ measurement the occurrence count $p$ of the $e^4 \rightarrow e^2 \rightarrow e^2 \rightarrow e^2$ event chain. We choose $i_1$ if $P_1(p) > P_2(p)$, otherwise we choose $i_2$. Then, we use the two distributions to estimate the probability that this choice is correct, resulting in a hit rate $H = \frac{1}{2} \sum_{p=1}^{\infty} \frac{P_1(p)}{P_1(p) + P_2(p)}$ and a false alarm rate $F = 1 - H$, and the information ratio $I = H - F = A / B$.

The procedure described above classifies the stimulus underlying a single $T_{\text{obs}}$ observation by considering only a single-event chain (i.e., a single element of the event tree). We can easily extend this procedure to incorporate every event chain within the event tree constructed from one $T_{\text{obs}}$ observation. For example, given a $T_{\text{obs}}$ observation and its associated event tree, we can use the procedure outlined above to estimate, for each chain separately, which stimulus induced the tree. Thus, each event chain “votes” for either stimulus $i_1$ or $i_2$, weighting each vote with the log of the information ratio $(I_{i_1} - I_{i_2})$. We then sum up the weighted votes across the entire event tree to determine the candidate stimulus underlying the sample $T_{\text{obs}}$ observation. We define the discriminability of the $m_{\text{max}}$-event tree (for this two-way discriminability task) to be the percentage of sample observations that were correctly classified under our voting procedure. To perform three-way discriminability tasks, we go through an analogous procedure, performing all three pairwise discriminability tasks for each sample observation and ultimately selecting the candidate stimulus corresponding to the majority. Note that the discriminability is a function of $\alpha$, $T_{\text{obs}}$, and $m_{\text{max}}$. For most of the systems we have observed, the discriminability increases as $m_{\text{max}}$ and $T_{\text{obs}}$ increase.

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**Supplementary Figure S1** (Best viewed electronically): **The methods and the utility of our event-tree analysis** within model networks of conductance-based I&F neurons, driven by independent Poisson input. For reference, we briefly describe the standard conductance-based integrate-and-fire (I&F) point neuron (Koch, 1999). Given a network of \(N\) I&F neurons with label \(i\), each with voltage \(V_i\), conductances \(G^\text{input}_i, G^\text{ex}_i, G^\text{in}_i\), and type \(\tau_i = \{\text{ex, in}\}\), its dynamics is governed by

\[
\frac{dV_i}{dt} = -G^L_i(V_i(t) - \epsilon^L) - G^\text{input}_i(t) (V_i(t) - \epsilon^\text{ex}) - G^\text{ex}_i(t) (V_i(t) - \epsilon^\text{ex}) - G^\text{in}_i(t) (V_i(t) - \epsilon^\text{in})
\]

where \(\theta(t)\) is the Heaviside function. The voltage \(V_i(t)\) evolves continuously until it reaches a threshold \(V_i(t) = \epsilon^T\). At this point in time the \(s^\text{th}\) neuron produces a spike (the \(k^\text{th}\) spike of neuron \(i\) is recorded as \(T_{i,k}\)), and the voltage \(V_i\) is reset to \(\epsilon^R\), and held there for an absolute refractory period of \(\tau_{\text{ref}}\) ms. Here, \(G^L\) is the leak conductance and \(\epsilon^L\) is leakage potential. The various synaptic conductances \(G^Q (Q = \text{ex, in})\) are characterized by their different decay time scales \(\sigma^Q\) and reversal potentials \(\epsilon^Q\). Each spike from the \(j^\text{th}\) neuron gives rise to an instantaneous increase in the \(Q\)-type conductance of neuron \(i\) of magnitude \(S^Q_{\tau_i,\tau_j} \Delta_{i,j}\). The coupling matrix \(\Delta_{i,j}\) (with entries either 0 or 1) indicates the network connectivity. The coupling strengths \(S^Q_{\tau_i,\tau_j}\) (indicating the amount of \(Q\)-type conductance added to \(\tau_i\)-type neurons by \(\tau_j\)-type firing events) only depend on the types of neurons \(i\) and \(j\), and not directly on their index. The system is also driven by feedforward input. The \(k^\text{th}\) input spike from the feedforward input to the \(i^\text{th}\) neuron is denoted by \(T_{i,k}^F\), and instantaneously increases that neuron’s \(G^\text{input}\) conductance by magnitude \(f F_{\tau_i}\). For the simulations presented in Fig. 2 in the main text, we use the following parameters (with conductance in units of [ms]):

- \(G^L = 0.00667\text{ms}^{-1}\)
- \(\epsilon^R = \epsilon^L = 60.95\text{mV}\)
- \(\epsilon^T = -48\text{mV}\)
- \(\epsilon^\text{ex} = 0\text{mV}\)
- \(\epsilon^\text{in} = -70\text{mV}\)
- \(\tau_{\text{ref}} = 2\text{ms}\)
- \(\sigma^\text{ex} = 2\text{ms}\)
- \(\sigma^\text{in} = 10\text{ms}\)

For the three regimes described in Fig. 2, the inputs to each neuron in the system are independent Poisson processes with rate \(\nu \sim 0.5\text{kHz}\) and strength \(f \sim 0.005\).

(i) For the **phase-oscillator regime** in Fig. 2A, the coupling strengths are given by

\[
S^\text{ex}_{\text{ex},\text{ex}} = 0.350, \quad S^\text{ex}_{\text{in},\text{ex}} = 0.165, \quad S^\text{in}_{\text{ex},\text{ex}} = 0.361, \quad S^\text{in}_{\text{in},\text{in}} = 0.0424,
\]

and the network connectivity illustrated in Panel A. Panel A indicates the coupling matrix \(\Delta_{i,j}\), with grey squares indicating entries of 1, and blank squares indicating entries of 0. The neurons labeled by blue numerals denote inhibitory neurons, and the red denote excitatory neurons.

(ii) For the **bursty-oscillator regime** in Fig. 2B, the coupling strengths are given by

\[
S^\text{ex}_{\text{ex},\text{ex}} = 0.350, \quad S^\text{ex}_{\text{in},\text{ex}} = 0.165, \quad S^\text{in}_{\text{ex},\text{ex}} = 0.148, \quad S^\text{in}_{\text{in},\text{in}} = 0.0424.
\]
The network connectivity is the same as in Panel A.

(iii) For the **sustained-firing regime** in Fig. 2C, the coupling strengths are given by

\[
S_{\text{ex,ex}}^{\text{ex}} = 0.118, \quad S_{\text{in,ex}}^{\text{ex}} = 0.165, \quad S_{\text{ex,in}}^{\text{in}} = 0.0856, \quad S_{\text{in,in}}^{\text{in}} = 0.0751,
\]

and the network connectivity is illustrated in Panel B.

We emphasize that there is a broad range of parameter values of coupling strengths and connectivity matrices that produce similar dynamics with the same qualitative coding properties. Specifically, the general phenomena of (a) robust event-tree discriminability and (b) the ability of event-tree analysis to distinguish between multiple stimuli (which may differ along distinct stimulus dimensions) persist for a large class of parameter values, and for a wide variety of dynamical regimes similar to the bursty-oscillator and sustained-firing regime.

Event trees are extended space-time entities. In Panel C, we display a representation of the 3-event-tree collected over \( T_{\text{obs}} = \infty \) (with \( \alpha = 2\text{ms} \)) of the sustained-firing regime (Fig. 2C) under stimulus \( I_1 \) (with input rate \( \nu_1 = 0.5\text{kHz} \) and strength \( f_1 = 0.005 \)). The colors, in general, correspond to occurrence rate, plotted logarithmically from 1 occurrence per second to 256 occurrences per second. Event-chains with an occurrence rate less than 1 occurrence per second have intentionally not been plotted. The representation of an event tree begins by fixing the number \( N \) of neurons (or the number \( N \) of coarse-grained sets of neurons), the maximum length \( m_{\text{max}} \) of the event chains in the tree, the time \( T_{\text{obs}} \) of observation, and the coarse-grained time interval \( \alpha \). The tree is then represented by a collection of rings (circles). On each ring, the discrete set of angles \( \theta_j = 2\pi (j - 0.5) / N, j = 1, \ldots, N \) labels the \( N \) neurons (or coarse-grained sets of neurons).

The collection of rings which represents the 3-event tree in panel C is organized as follows. In panel C, the three black circles indicate the organization of event-chains by the depth of events in the chain. The central black circle contains 1-event-chains, the interior annulus contains 2-event-chains, and the outer annulus contains 3-event-chains. The location of each \( m \)-event-chain is specified by \( m \) angles, which correspond to the indices of the \( m \) neuronal events defining that event-chain. For example, consider the 3-event-chain \( \sigma^8 \rightarrow \sigma^6 \rightarrow \sigma^2 \) indicated by the three grey pie-slices. The smallest darkest pie slice contains a single circle. This single circle lies within a hierarchical structure — a ring of rings of rings. The location of this single circle can be defined in terms of the following three angles: the angle of the major ring in which it lies (the largest light grey pie slice corresponds to the orientation angle \( 2\pi (j - 0.5) / 8 \) with \( j = 8 \), since the first event is \( \sigma^8 \)), followed by the angle of the medium ring in which it lies (the medium grey pie slice corresponds to the orientation angle \( 2\pi (j - 0.5) / 8 \) with \( j = 6 \), since the second event is \( \sigma^6 \)), followed again by the angle of the smallest ring in which it lies (the smallest darkest grey pie slice corresponds to the orientation angle \( 2\pi (j - 0.5) / 8 \) with \( j = 2 \), as the third event is \( \sigma^2 \)). Thus, the color of this single circle corresponds to the occurrence rate of the 3-event-chain \( \sigma^8 \rightarrow \sigma^6 \rightarrow \sigma^2 \). All of the 3-event-chains are organized this way within the outer annulus. All the 2-event-chains can be organized in a similar hierarchical structure — namely, a ring of rings. This smaller ring of rings has been scaled, and placed in the middle annulus. Finally, the single ring corresponding to the set of 1-event-chains is also appropriately scaled and placed in the
our de

coarse-graining. For example, in this case of

would contain both the

shorter observation windows

for clarity of visualization.

Supplementary Fig. S3. For short observation windows, different presentations of the same stimulus will produce different $m_{\text{max}}$-event-trees. As event-trees may differ only slightly for different but similar stimuli, the probability distribution of event chains over many independent trials can be used to disentangle the dynamical differences caused by distinct stimuli from the fluctuations caused by short $T_{\text{obs}}$ observation windows. These distributions can be a sensitive function of the stimulus and thus can provide a statistically accurate measurement that can distinguish between distinct stimuli.

In summary, Panel C depicts a 3-event-tree collected over a very long observation window $(T_{\text{obs}} = \infty)$. Similar diagrams can be used to depict event-trees of different lengths $m$ and shorter observation windows $T_{\text{obs}}$. This event-tree representation provides a succinct means of organizing the data associated with an entire collection of event-chains up to a specified length, and can also serve to pinpoint relevant features within a network’s dynamics. For another example, see Supplementary Fig. S3. For short observation windows, different presentations of the same stimulus will produce different $m_{\text{max}}$-event-trees. As event-trees may differ only slightly for different but similar stimuli, the probability distribution of event chains over many independent trials can be used to disentangle the dynamical differences caused by distinct stimuli from the fluctuations caused by short $T_{\text{obs}}$ observation windows. These distributions can be a sensitive function of the stimulus and thus can provide a statistically accurate measurement that can distinguish between distinct stimuli.

Note that although the event $\sigma^7 \rightarrow \sigma^7$ does not occur very often (the location is blank), the event $\sigma^7 \rightarrow \sigma^\pi \rightarrow \sigma^j$ (for $j \neq 7$) occurs more often. This peculiar phenomenon stems from our definition of event-chains associated with the particular choice of $\alpha = 2\text{ms}$ for temporal coarse-graining. For example, in this case of $\alpha = 2\text{ms}$, the set of events $\{\sigma_1^1, \sigma_2^2, \sigma_3^1\}$ would contain both the 2-event-chain $\sigma^7 \rightarrow \sigma^1$ and the 3-event-chain $\sigma^1 \rightarrow \sigma^1$, but not the 2-event-chain $\sigma^7 \rightarrow \sigma^7$. There are many alternative definitions of event-chains which produce event-trees capable of robust discriminability, but we will not fully discuss those here. As an example, given a set of time scales $\alpha_1, \ldots, \alpha_{m-1}$, we can easily define an $m$-event-chain, denoted by $\{\sigma_1^1, \alpha_1^1 \rightarrow \sigma_2^2, \alpha_2^2 \rightarrow \ldots \rightarrow \alpha_{m-1}^m \rightarrow \sigma_{m}^m\}$, as the event $\sigma_{m}^m$, preceded by the events $\sigma_{m-1}^m, \ldots, \sigma_1^1$ (with $I_k = [t - \sum_{i=k}^{m-1} \alpha_i, t - \sum_{i=k}^{m-1} \alpha_i]$). Such an event-chain can capture correlations within and across multiple synchronous activities within a system. For clarity, we have chosen uniform $\alpha_k = \alpha$, but this is in no way essential to our general results. Our definition of event-chains is structured to allow for efficient data collection techniques which (a) treat every spike computationally equally, and (b) produce event-trees which are invariant to time-translation of the system dynamics. This can be contrasted with a definition of event-chains which employs a global time discretization, and therefore produces event-trees which depend on the particular choice of time bins. Our techniques will be discussed in future work.

In Panel D, we display a representation of the 4-event-tree collected over $T_{\text{obs}} = \infty$ (with $\alpha = 2\text{ms}$) of the sustained-firing regime under stimulus $I_1$ (where $I_1 = (\nu_1 = 0.5, f_1 = 0.005)$ and $I_2 = (\nu_2 = 0.525, f_2 = 0.005)$ are the same as those in Fig. 2). The diagram of panel C is nested in the center of this diagram.

Panels C and D display measurements of the $T_{\text{obs}} = \infty$ event-tree of the system under stimulus $I_1$. However, in general (see text), each different trial presentation of a particular stimulus over a shorter $T_{\text{obs}}$, say $T_{\text{obs}} = 512\text{ms}$, will produce a different $m_{\text{max}}$-event-tree. The
distribution of \( m_{\text{max}} \)-event-trees over \( T_{\text{obs}} = 512 \text{ms} \), measured by collecting multiple trials, can be a sensitive function of the stimulus. Thus, in order to estimate the functional power of this network, we may attempt to estimate the difference between the \( T_{\text{obs}} \)-distribution of the \( m_{\text{max}} \)-event-trees produced by this system under stimulus \( I_1 \) and the \( T_{\text{obs}} \)-distribution produced under \( I_2 \), with \( T_{\text{obs}} = 512 \text{ms} \), and \( m_{\text{max}} = 4 \). If the difference between these two \( T_{\text{obs}} \)-distributions is significant, then the event-tree-projected network dynamics observed within a typical single trial of \( T_{\text{obs}} = 512 \text{ms} \) can be used to discriminate between the stimuli \( I_1 \) and \( I_2 \).

In practice, one usually cannot measure the full multi-dimensional \( T_{\text{obs}} \)-distribution of the 4-event-tree for a system, as such a joint probability distribution of occurrence counts of multiple different event-chains is defined on a space of dimension \( N + N^2 + N^3 + N^4 \sim N^5 \). For stationary inputs, as in our example here, such joint distributions are only measurable for \( T_{\text{obs}} \) either extremely small (i.e., only a few short event-chains occur once within each trial, and most event-chains do not occur at all, thus the \( T_{\text{obs}} \)-distribution reduces to the joint distribution of singleton events) or extremely large (i.e., the \( T_{\text{obs}} \) distribution is well represented by the \( T_{\text{obs}} = \infty \) event-tree, which captures the mean occurrence count, or observation rate of each event-chain). To circumvent this curse of dimension, instead of constructing the \( T_{\text{obs}} \)-distribution of the 4-event-tree for this system, we measure the \( T_{\text{obs}} \)-distribution of each 4-event-chain within the 4-event-tree separately. In other words, we first record many independent samples of this network’s \( m_{\text{max}} \)-event-tree (over multiple independent \( T_{\text{obs}} = 512 \text{ms} \) observations) under both stimulus \( I_1 \) and \( I_2 \). With this collection of data, we obtain the empirical observation distributions of each \( m \)-event-chain’s occurrence count (for \( m \leq m_{\text{max}} \)). Thus, for each event-chain \( \{ \sigma^{j_1} \rightarrow \sigma^{j_2} \rightarrow \cdots \rightarrow \sigma^{j_m} \} \), we obtain the collection of probabilities \( P(\{ \sigma^{j_1} \rightarrow \sigma^{j_2} \rightarrow \cdots \rightarrow \sigma^{j_m} \} \) occurs \( k \) times within a given \( T_{\text{obs}} = 512 \text{ms} \) | stimulus \( I_l \)) for each integer \( k \geq 0 \) and each stimulus \( l = 1, 2 \).

Some event-chains are not indicators of the stimulus (i.e., the \( T_{\text{obs}} = 512 \text{ms} \) distribution of occurrence count is very similar for \( I_1 \) and \( I_2 \)). However, there are other event-chains that can be used to discriminate between the stimuli. For example, the \( T_{\text{obs}} = 512 \text{ms} \) distribution of occurrence counts of the 4-event-chain \( \sigma^4 \rightarrow \sigma^1 \rightarrow \sigma^2 \rightarrow \sigma^8 \) is quite different under stimulus \( I_1 \) than under stimulus \( I_2 \). The corresponding observation distributions are plotted in Panel E, with the blue and red histograms, \( P_1 \), and \( P_2 \), corresponding to \( I_1 \) and \( I_2 \) respectively (the overlapping region is purple). Note that the mean occurrence count for this 4-event-chain actually decreases when the rate of the input increases. The occurrence count of this event-chain alone can be used to discriminate the inputs \( I_1 \) and \( I_2 \). For example, we may take many sample \( T_{\text{obs}} = 512 \text{ms} \) observations of the network’s dynamics under different randomly chosen stimuli (either \( I_1 \) or \( I_2 \), with equal probability). For each of these samples, we examine the occurrence count \( \rho \) of the \( \{ \sigma^4 \rightarrow \sigma^1 \rightarrow \sigma^2 \rightarrow \sigma^8 \} \) event-chain, and determine a possible candidate stimulus. We choose \( I_1 \) if \( P_1(\rho) > P_2(\rho) \), otherwise we choose \( I_2 \) (e.g., in this case in Panel E, we guess \( I_2 \) if \( \sigma^4 \rightarrow \sigma^1 \rightarrow \sigma^2 \rightarrow \sigma^8 \) occurs 9 or fewer times, otherwise we guess \( I_1 \)). Applying this procedure to many different independent sample trials results in a hit rate \( A = \frac{1}{2} \int_0^\infty \max(P_1, P_2) \, dn \), and false alarm rate \( B = 1 - A \), and the “information ratio” \( \frac{\text{max}^{I_1, I_2} T_{\sigma^1 \rightarrow \sigma^2 \rightarrow \sigma^4 \rightarrow \sigma^8}}{\text{max}^{I_1, I_2} T_{\sigma^4 \rightarrow \sigma^1 \rightarrow \sigma^2 \rightarrow \sigma^8}} = A/B = 1.7 \)
The procedure described above classifies the stimulus underlying a single sample $T_{obs}$-observation by considering only the occurrence count of a single event-chain (i.e., a single element of the event-tree) associated with that $T_{obs}$-observation. We can easily extend this procedure to incorporate every event-chain within the observed event-tree. For example, given a sample $T_{obs} = 512$ms observation, and its associated event-tree, we can independently use the occurrence count of each event-chain within that event-tree to identify a possible candidate stimulus (which will be different, in general, for each event-chain). Thus, in this procedure, each event-chain ‘votes’ for either stimulus $I_1$ or $I_2$ (i.e., a vote of ±1, respectively). We then sum up the votes across the entire event-tree to determine a single candidate stimulus underlying the sample $T_{obs}$-observation. It is natural to weight each vote with the factor $\log \left( \prod_{I_{1j} \rightarrow \cdots \rightarrow I_{1m} \rightarrow I_1, I_2} \sigma_{ij} \right)$, which is a function of the information ratio of the contributing event-chain. This weighting implies that $N$ votes of all 1’s with error rate $B$ have the same weight as a single vote with a far smaller error rate $\frac{B^N}{(1-B)^N + BN}$. We define the ‘discriminability’ of the $m_{max}$-event-tree (for this 2-way discriminability task) to be the percentage of sample observations which were correctly classified under our voting procedure. To perform 3-way discriminability tasks, we go through an analogous procedure, performing all three pairwise discriminability tasks for each sample observation, and ultimately selecting the candidate stimulus corresponding to the majority (with triple dead heats or other exceptional cases automatically counted as incorrect). Note that the discriminability is a function of $\alpha$, $T_{obs}$ and $m_{max}$. For most of the systems we have observed, the discriminability increases as $m_{max}$ and $T_{obs}$ increase.
A  

B  

Raster Plot: No Synaptic Failure  

Raster Plot: 60% Synaptic Failure  

D  

E  

3-way Discriminability  

Number of Observations within $T_{obs}=512\text{ms}$  

$pfail=0\%$  

$pfail=60\%$  

0 0.5 25  

Probability  

0 5 10 15  

0 1/10 1/20  

0 25 50 75  

% Failure  

75%
Supplementary Figure S2: Functional power vs. reliability of neurons. Here we illustrate that the functional power of a network is not simply an increasing function of the synaptic reliability of neurons within that network. For clarity, we focus on a specific I&F neuronal network with $N = 4$ neurons. We model synaptic failure by randomly determining if each neuron in the network is affected by any presynaptic firing event (If the probability of spike transmission is $(1 - p_{\text{fail}})$, we scale the synaptic strength by $1/(1 - p_{\text{fail}})$, in order to keep the mean network properties the same). (A): The network is composed of 2 excitatory neurons (red), and 2 inhibitory neurons (blue), with connectivity indicated by the arrows. We examine this network’s dynamics under drive with each neuron receiving independent Poisson input. If there is no synaptic failure in the network (i.e., the inter-neuronal connections are 100% reliable, and the synaptic failure probability $p_{\text{fail}} = 0$%), then the strong recurrent connectivity within the network forces the system into one of two states: Either neurons 1 and 3 repeatedly fire (suppressing neurons 2 and 4), or neurons 2 and 4 repeatedly fire (suppressing neurons 1 and 3). However, if the synapses within the network have a probability of failure, then it is possible for the system to escape from either of these locked states, and all four neurons may fire. (B): Upper Panel: A typical 1024ms raster plot indicating locked activity when $p_{\text{fail}} = 0$%. Lower Panel: A typical 1024ms raster plot illustrating the type of unlocked activity observed when $p_{\text{fail}} = 60$%. (C): Representations of the 3-event-trees associated with these two dynamics, with the upper and lower panels corresponding to the $p_{\text{fail}} = 0$% and $p_{\text{fail}} = 60$% dynamics, respectively (These event trees were collected over $T_{\text{obs}} = \infty$, with $\alpha = 32$ms). The colorscale stands for the occurrence rate of any particular event-chain, ranging logarithmically from 0.5Hz to 25Hz. The observation rate of the event $\sigma^{j_1} \rightarrow \cdots \rightarrow \sigma^{j_m}$ is plotted at complex vector location $\Sigma_{k=1}^{m} 3^{k-1} e^{2\pi i(j_k - 0.5)/4}$ with respect to the center of each panel. Events with an observation rate of less than 0.01Hz are not plotted, with their locations intentionally left blank. The concentric circles indicate the separation between 1-event-chains (central circle), 2-event-chains (interior annulus) and 3-event-chains (exterior annulus). Clearly, the event-tree structure is far richer in the case of failure, than in the case without failure. (D): As a test of the network’s functional power, we drive the $p_{\text{fail}} = 60$% system with two similar inputs $I_1$ and $I_2$, (where $I_1$ and $I_2$ are the same as those in Fig. 2) and record the $T_{\text{obs}} = 512$ms 3-event-trees. The red (blue) histogram illustrates the distribution of $T_{\text{obs}} = 512$ms occurrence counts, as observed under stimulus $I_1$ ($I_2$), for a typical 2-event-chain. These histograms indicate that the occurrence count of individual event-chains can be used to distinguish between these two stimuli, even within $T_{\text{obs}} = 512$ms (discrimination based solely on the single event-chain corresponding to the histograms shown is accurate 58% of the time). Moreover, the entire 3-event-tree (i.e, the collection of event-chains, along with their occurrence counts) can be used to discriminate these two stimuli (over $T_{\text{obs}} = 512$ms) with $\sim 70$% accuracy. (E): We estimate the functional power of this network as a function of $p_{\text{fail}}$. We drive the system with three similar inputs, $I_1$, $I_2$, $I_3$, (where $I_1$, $I_2$ and $I_3$ are the same as those in Fig. 2) and again record the $T_{\text{obs}} = 512$ms 3-event-trees. We use the 3-event-trees to perform a 3-way discrimination task (33% would be chance level). The discriminability is plotted for a set of different $p_{\text{fail}}$ (the dots indicate data points, the dashed line is to guide the eye only), which clearly demonstrates that the event-trees associated with the network’s dynamics are richer, and more capable of fine discrimination, when $p_{\text{fail}} \sim 60$%, than when $p_{\text{fail}} = 0$%. Fig. 4 in
the main text is reproduced as Panel $E$ here for completeness.
Supplementary Figure S3 (Best viewed electronically):  Illustration of the utility of the graphical representation of event-trees. We consider a specific sparsely coupled I&F neuronal network with $N = 12$ neurons operating in a sustained firing regime. We drive the network with two similar inputs, $I_1$ and $I_2$. Shown in the first row of the figure are (A) the 2-event-tree collected over $T_{obs} \gg 1$ for stimulus $I_1$, and (B) the 3-event-tree collected over $T_{obs} \gg 1$ for stimulus $I_1$. The occurrence counts are normalized by $T_{obs}$ and plotted as occurrence rates with colors corresponding to the colorbar on the right side of the figure (occurrence rates below 0.25 Hz are not plotted). The set of occurrence rates are organized as explained in Figure S1. Panels (C) and (D) display analogous event-trees collected for stimulus $I_2$. It can readily be seen by comparing the inner rings of panels A and C that the observed firing rates under $I_1$ are nearly indistinguishable from the firing rates observed under $I_2$. There are, however, apparent differences between the occurrence rates of 2-chains and 3-chains under $I_1$ and under $I_2$, which can be seen by comparing the outer rings of panels A and C (for 2-chains), or the outer rings of panels B and D (for 3-chains).