Appendix

Here, we examine the representation of transient elevations in spike rate (pulses) by ensembles of spiking neurons. We develop an exercise that complements the representation of brief sinusoidal modulations in spike rate considered in the main text. Like the exercise in the main text, we compare the ensemble representation of modulating and stationary signals over a time scale that the brain might use for computations.

The signals that are compared in this exercise consist of either a single pulse of variable duration, or a pair of pulses, each 2 ms wide, separated by a gap of variable duration ($\Delta t$). The average spike rate is 100 spikes/s during the pulse(s) and 0 spikes/s otherwise. These two signal types are illustrated at the top of Fig. S1.

The problem we need to consider is not whether the pulse (P) and pulse-gap-pulse (PgP) are discriminable—they are discriminable on the basis of total spikes—but whether the ensemble rate contains the right number of bumps. Specifically, for the ensemble representation to be useful it should be possible to detect two modes in the ensemble spike histogram representation of PgP and just one in the representation of P. Of course it is hard to detect 2 modes when $\Delta t$ is small and it is hard to detect only one mode when $\Delta t$ is large. In the present example, we consider a narrow range of $\Delta t$ from 3 to 50 ms. We make the assumption that neural circuits must be capable of using both P and PgP signals across this time span. In other words, we consider neural computations that would utilize signals that change faster than \(\sim 20\) Hz.

For each $\Delta t$, we generated ensemble representations of P and PgP using the method of random spike sequences (see Methods). The ensembles contained 500 neurons with a CCG shape represented by the green trace in Fig. 6c ($r = 0.2$, width = 9 ms). Fig.
**S1** shows the ensemble representation of P and PgP for gaps ranging from 10 to 50 ms. Four samples of the ensemble discharge are shown for each signal. We examined the ensemble rate functions for evidence of bimodality by applying Harnad’s dip test\(^1\). To apply the test, the ensemble rate function is interpreted as a frequency distribution of spike times. If the test is positive (\(p<0.05\)) the representation is classified as multimodal (red in **Fig. S1**). We repeated the test 100 times under each condition to estimate the probability that the ensemble representation would contain more than one mode (values in parentheses in **Fig. S1**). The dip test is ideally suited for this problem because it is based on the null hypothesis that the unimodal distribution is uniform, like P. It does not make any assumptions about the bin size in the frequency histograms because it works on the cumulative distribution of spike times, each of which is represented with a precision of 0.1 ms. Also, for present purposes it helps that the test is fairly conservative (e.g., it fails to detect bimodality in a samples of 1000 random numbers described by an equal mixture of two Gaussian distributions unless they are separated by at least 3\(\sigma\)).

The rate histograms in **Fig. S1** are colored red if they contain more than one mode (\(p<.05\)). Ideally, all signals on the left side should be red whereas those on the right should be black. When no smoothing of the rate function was performed (**Fig. S1a**), almost all representations of PgP with \(\Delta t>3\) ms gave ensemble responses which were appropriately classified as multimodal. However, the representation of the longer P also contains several erroneous peaks which arise because of the weak correlation between neurons in the ensemble. The P lasting 54 ms (i.e., \(\Delta t = 50\)) was misclassified in 78% of the samples, and >90% of pulses lasting 75-100 ms contained at least two distinct modes. This is not acceptable because any brain mechanism that would care about detecting 2
events over short epochs could not afford to be fooled by the existence of similar events in a 50 ms time span. The problem is easily remedied.

A simple means for attenuating the erroneous peaks in the ensemble response is to blur the rate signal. To achieve this in our simulations, we replace each spike that occurs at $t_i$ with one that occurs at $t_i + \xi$, where $\xi$ is a random number drawn from an exponential distribution with mean $\tau$. The process is equivalent to smoothing the rate function by a filter with time constant $\tau$. After smoothing with $\tau = 10$ ms, the longer pulse is almost always classified as unimodal (Fig. S1b). However, this smoothing leads to a higher probability that PgP will be misclassified as unimodal when $\Delta t$ is short. Accordingly, the neural ensemble can now represent signals lasting at least 50 ms but it can no longer represent changes occurring in less than 10 ms. Thus we have achieved accurate representation at long time scales at the cost of accurately representing brief changes. We obtained similar results using ensemble sizes of 100, 200 and 500 neurons and using a narrower CCG width. For the narrowest case (2 ms half width, identical to that used in Figs. 1-5 of the main text) the erroneous modes are narrower and more abundant for $\Delta t = 50$ ms. Nevertheless, smoothing with a time constant of 10 ms permits accurate representation of the longer pulses.

This illustration complements the exercise with brief sinusoidal modulations pursued in the main text. In both cases, fluctuations in ensemble spike rate resulting from the weak coupling between neurons masquerade as fast changes in spike rate. In the exercise using sinusoidal wavelets, we found that modulations occurring faster than $\sim 100$ Hz would not be distinguishable from the fluctuations accompanying a constant spike rate. In the present example, we smoothed away these noise fluctuations at the cost of
representing brief signals separated by 10 ms or less. We may conclude from this exercise that the brain would do best to ignore rate fluctuations on this time scale. Importantly, neither exercise implies any limitation on temporal comparisons or on the precision in estimating the time of a signal. For example, the center of a blurred pulse can be estimated with arbitrary precision. Both exercises expose a limit on the ability to encode fluctuations in variables that are represented by ensembles of neurons: any signal that would be lost upon averaging over an epoch of ~10 ms will fail to be represented or transmitted by the cortex.