



The Transient Precision of Integrate and Fire Neurons: Effect of Background Activity and Noise

M.C.W. VAN ROSSUM

Department of Biology, Brandeis University, 415 South Street, Waltham, MA 02454-9110

vrossum@brandeis.edu

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Abstract. We study the response of an integrate and fire neuron to a randomly timed step stimulus. We calculate the latency to the first spike after stimulus onset and its jitter. Background activity, seen in most neurons, reduces latency but causes substantial jitter in the response, indicating a tradeoff between timing precision and latency. The effect of intrinsic noise and synaptic noise on this tradeoff is studied. For synaptic noise we find that, unexpectedly, jitter does not increase for larger synaptic amplitudes, instead, jitter is practically independent of synaptic amplitude. Constant intrinsic noise interacts counterintuitively with latency and jitter, and depending on the stimulus strength, noise shifts the tradeoff in either direction.

Keywords: integrate and fire neurons, temporal coding, noise, precision

1. Introduction

Most natural stimuli our sensory system encounters have a transient character and occur unexpectedly. The nervous system should preferably react rapidly, reliably, and temporally precise to these stimuli. In other words, when a stimulus is repeatedly presented to a neuron, its spikes should have a short latency and little jitter from trial to trial. As these issues pose fundamental performance limitations to the nervous system, the reliability and precision of neurons has been studied extensively, both experimentally and theoretically. The results are complex. In some cases, like in the visual cortex, responses seem mostly noisy and unreliable (reviewed in Shadlen and Newsome, 1998). But strongly driven neurons show precise and reliable responses (Bryant and Segundo, 1976; Mainen and Sejnowski, 1995), as do neurons early in the visual system (Rieke, Warland, de Ruyter van Steveninck, and Bialek, 1996; Berry and Meister, 1998). Quantifying the precision has been further complicated because the

response variability depends on the stimulus (Mainen and Sejnowski, 1995; Bair and Koch, 1996; Nowak, Sanchez-Vives, and McCormick, 1997; Reich, Victor, Knight, Ozaki, and Kaplan, 1997). Simply, with strong stimuli the voltage crosses the threshold rapidly, and the variations in the spike timing are smaller than with weak stimuli for which the membrane voltage spends more time near the threshold (Cecchi, Sigman, Alonso, Martinez, Chialvo, and Magnasco, 2000).

Here we concentrate on the jitter in the spike timing. There are at least three contributions to this jitter. First, intrinsic noise in the neuron causes the membrane potential to follow a random walk, leading to variations in the spike time (Gerstein and Mandelbrot, 1964; Tuckwell, 1998). Second, synaptic input is noisy since it consists of discrete, stochastic vesicle release events. A small number of large events will lead to more jitter than many small events (Stein, 1967). Third, given that most neurons have a background firing rate of 2 to 5 Hz, the neuron will be in a different state every time the stimulus arrives; the neuron can be close or

far from threshold, leading to additional variations in the time to spike (Abeles, 1991). We assume that this background firing is caused by some unspecified input to the cell—for instance, provided by an asynchronous low activity state of the network (Abbott and van Vreeswijk, 1993).

In this study we combine these three contributions and show their effect on the latency and the jitter of the first spike after stimulus onset. In particular, we study the response of an integrate and fire (I&F) neuron to a step stimulus. The I&F neurons give a reasonable description of the transient response of real neurons and have been shown to reproduce the apparent counterintuitive dependence of the precision on the nature of the stimulus (Mainen and Sejnowski, 1995; Reich et al., 1997). As pointed out by many authors, it is therefore important to analyze the precision in the I&F neuron systematically. As the model allows for analytical expressions, the presented results are useful as reference for experimental and simulation studies. After some definitions, we first study the latency and jitter analytically for some simplified models. Next, we present simulation results for leaky, noisy I&F neurons.

2. Transient Precision

Consider the experiment depicted in Fig. 1: A neuron is spiking at a low background rate. At a random time a current step is injected to the neuron, strongly increasing the firing rate. When we repeat the same experiment the neuron spikes at a different time, that is, there is jitter in the spike times. The reason is that for every trial the neuron has a different membrane potential when the stimulus arrives. In addition there might be intrinsic or synaptic noise which will also contribute to the jitter. It is essential to distinguish between these contributions throughout this article.

We characterize the transient response by the latency and the jitter. The latency is as defined the mean time to first spike after stimulus onset, denoted $\langle t_1 \rangle$. We define the relative jitter as its coefficient of variation, $\text{CoV}(t_1) \equiv \text{std.dev.}(t_1)/\text{mean}(t_1)$. If there is not too much jitter, this corresponds to measuring the location of the peak and the relative width of the first peak in the poststimulus time histogram (PSTH). (If there is an extreme amount of jitter, the PSTH does not oscillate but rises steadily to its final value). Commonly, the jitter has been defined as the standard deviation of the spike time. We, however, prefer the CoV above the standard deviation, as the CoV will turn to be roughly

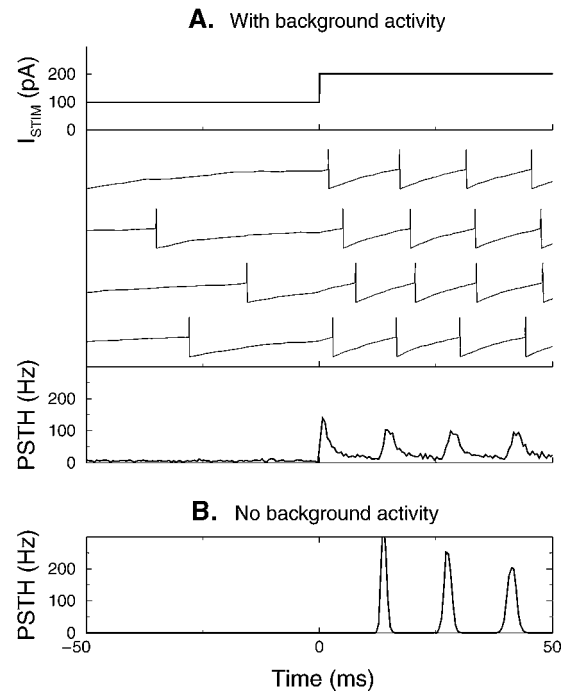


Figure 1. Measuring the transient precision of neurons. **A:** *Top graph:* At a random time the stimulus current increases from a background level to stimulus level. *Middle graph:* Four representative traces of the membrane potential after alignment to the stimulus onset time. The spike times differ from trial to trial because (1) intrinsic noise is present and (2) the random timing of the stimulus, causing the neuron to be in a different state every time the stimulus arrives. *Lower graph:* PSTH (averaged over 1,000 trials). The transient response is characterized by the mean time to first spike and its standard deviation. This corresponds approximately to the location and width of the first peak in the PSTH. **B:** Here the background current is absent, as a result there is no background activity. (The intrinsic noise is still present but is too small to cause spikes). The PSTH shows a longer latency and less broadening. The spreading in the PSTH is solely caused by the intrinsic noise.

constant across a wide range of conditions. For clarity we term the CoV *relative jitter*.

Finally, the setup is completely equivalent to studying the population response of a group of identical, noninteracting neurons (Knight, 2000; Nykamp and Trachina, 2000). By that method exact results for the PSTH can be calculated in some cases (Gerstner, 1999; Herrmann and Gerstner, 2000).

3. Analytical Results

We analyze the transient response for the experiment of Fig. 1 for various I&F neuron models (Tuckwell, 1988). We start with the simplest case: a nonleaky, noiseless integrate and fire neuron. To calculate the latency and

jitter we need to know the membrane potential at stimulus onset. This is done as follows. We suppose that an (arbitrarily) small background current is present. This current will cause the membrane potential to rise constantly to the threshold potential at which point it fires and is reset to the resting potential. For convenience we set $V_{\text{rest}} = V_{\text{reset}} = 0$ mV. As a function of time the membrane potential follows a sawtooth pattern, and as a consequence all membrane voltages between resting and threshold voltage occur equally likely. The chance to find the neuron with a membrane potential V_0 is therefore

$$P_V(V_0) = \frac{1}{V_T} \quad (0 < V_0 < V_T), \quad (1)$$

where V_T is the threshold potential.

At $t=0$ the stimulus arrives and the current switches from background level to I_S , where I_S is the stimulus current. From then on the membrane potential evolves as $V(t) = V_0 + tI_S/C$, where V_0 is the membrane potential at stimulus onset, and C is the membrane capacitance. The first spike following the stimulus occurs when the threshold is crossed, $t_1 = C(V_T - V_0)/I_S$. Averaging over many trials yields the distribution of time to first spike from the distribution of membrane potentials

$$P_t(t_1) = \int dV_0 P_V(V_0) P_t(t_1; V_0), \quad (2)$$

where $P_t(t_1; V_0)$ is the distribution of the time to the first spike, given the potential V_0 at stimulus onset. In general $P_t(t_1; V_0)$ will be some distribution, here it is a δ -function: $\delta(t_1 - (V_T - V_0)C/I_S)$. We have

$$\langle t_1 \rangle = \frac{1}{2} \frac{CV_T}{I_S}, \quad (3)$$

and

$$\text{CoV}(t_1) = \frac{1}{\sqrt{3}}. \quad (4)$$

That is, the relative jitter is independent of the stimulus current.

If no background current were present, the neuron is at rest at stimulus onset, and the latency is $\langle t_1 \rangle = CV_T/I_S$. The background firing halves the latency because the background firing elevates the average membrane potential to $\frac{1}{2}V_T$, independent of the background firing frequency. However, in the absence of background spiking, there would be no jitter. Thus there is a tradeoff between a fast response versus a jittered response.

3.1. Leaky Neuron

To be more realistic we include a leak conductance in the analysis. Again we first determine the distribution of membrane potentials at stimulus onset. Given that the background current is large enough to cause spikes, the distribution of membrane potentials is again calculated from the voltage trace of the cell

$$P_V(V_0) = \frac{1}{\log(V_B) - \log(V_B - V_T)} \cdot \frac{1}{V_B - V_0} \quad (0 < V_0 < V_T), \quad (5)$$

where $V_B = I_B R_m$ is the potential the neuron would reach if there were no threshold; the suprathreshold condition implies that $V_B > V_T$. Given a membrane potential V_0 at stimulus onset, the neuron will fire its first spike after stimulus onset at

$$t_1(V_0) = \tau \log \left(\frac{V_0 - I_S R_m}{V_T - I_S R_m} \right). \quad (6)$$

The latency follows from Eq. 2 as $\langle t_1 \rangle = \int dV_0 P_V(V_0) t_1(V_0)$, and similarly for the jitter. These integrals are complex but easily done numerically. It is helpful to plot the relative jitter against the latency (Kisley and Gerstein, 1999). This is plotted in Fig. 2a. For short

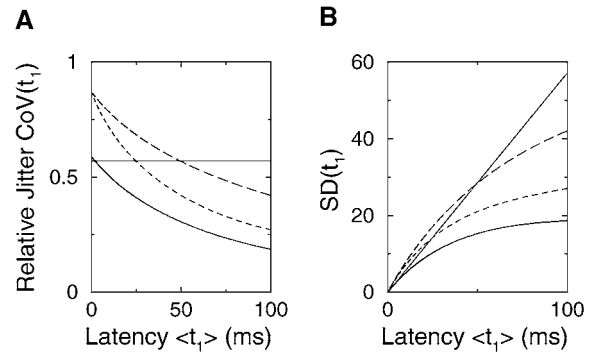


Figure 2. **A:** The relation between latency and relative jitter for a leaky, noiseless I&F neuron. The curves are constructed by plotting latency and jitter for a range of stimulus currents (a parametric plot with the stimulus current as parameter). The background current causes periodic firing of the neuron before stimulus onset. There is no intrinsic noise; the jitter is entirely due to the random stimulus timing. Solid curve: strong background current: $V_B = 50$ mV, cell's time constant $\tau = 20$ ms. Dotted curve: weak background current: $V_B = 11$ mV, $\tau = 20$ ms. Dashed curve: $V_B = 11$ mV, $\tau = 40$ ms. Horizontal line: neuron without leak, shown for comparison. Other parameters: $V_{\text{rest}} = 0$ mV, $V_T = 10$ mV. **B:** For comparison the absolute jitter—that is, the standard deviation of the time of the first spike—is plotted versus the latency.

latencies the relative jitter is worse than for the neuron without leak. But the leaky I&F neuron is also called a “forgetful” integrate and fire neuron and indeed, for longer latencies the relative jitter decreases: the neuron forgets what its state was at stimulus onset. For comparison we have also plotted the absolute jitter, Fig. 2b.

3.2. Noisy, Nonleaky Neuron

Next, consider the case that an intrinsic noise current is present in the neuron. We assume that the noise is independent of the stimulus. Such a current can be due to channel noise, but also synaptic noise can be roughly independent of the stimulus strength—namely, if the synaptic input consists of a balance between inhibition and excitation. If in that case the stimulus increases the excitatory rate and decreases the inhibitory rate, the noise is roughly independent of the stimulus current.

We describe the noise with a filtered Gaussian current noise with zero mean and correlation $\langle I(t)I(t + \delta t) \rangle = \sigma^2 \exp(-|\delta t|/\tau_\sigma)$, where σ^2 is the variance of the noise and τ_σ is the temporal correlation, which is much shorter than other time scales such as membrane time constant and latency. Although it is also possible to use white noise, filtered noise is a more biological description.¹ In this derivation leak conductance is absent.

Again we need the distribution of membrane potentials at the moment of stimulus onset. In this noisy case the distribution of membrane potentials is described by a Fokker-Planck equation (van Kampen, 1992). The distribution is derived by considering small steps in the membrane potential due to the either the background current or the noise. The equilibrium distribution obeys

$$0 = \frac{\sigma^2 \tau_\sigma}{C^2} \frac{d^2 P_V(V)}{dV^2} - \frac{I_B}{C} \frac{dP_V(V)}{dV}, \quad (7)$$

where I_B is again the background current. The spiking is described by a drain term at $V = V_T$, and a source term at $V = 0$, the new value of the potential after the neuron is reset; at these voltage values the distribution has cusps. The distribution is found by requiring continuity and $\int P(v)dV = 1$. It reads

$$\begin{aligned} P_V(V_0) &= \frac{1}{V_T} (1 - e^{-V_T/k}) e^{V_0/k}, & (V_0 < 0) \\ &= \frac{1}{V_T} (1 - e^{(V_0 - V_T)/k}), & (0 < V_0 < V_T) \\ &= 0, & (V_0 > V_T), \end{aligned} \quad (8)$$

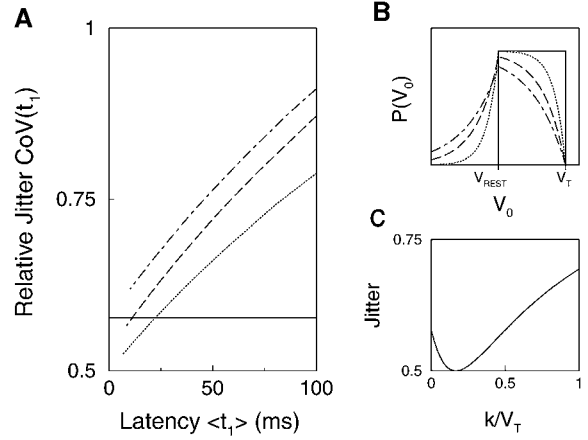


Figure 3. **A:** The relation between latency and relative jitter for a nonleaky neuron with intrinsic noise, Eqs. (10) and (11). Noise parameter k/V_T : 0 (solid line), $\frac{1}{6}$ (dotted line), $\frac{2}{6}$ (dashed line) and $\frac{3}{6}$ (dot-dashed line). **B:** the corresponding distributions of membrane potentials at stimulus onset (same notation). **C:** The relative jitter at zero latency as function of the noise parameter k , it is minimal if some noise is present.

where the parameter $k = \tau_\sigma \sigma^2 / (I_B C)$ describes the effect of noise and background current on the distribution. The distribution is plotted in Fig. 3b, for various values of k . As before, due to this distribution the spike times are jittered.

Another contribution to the jitter comes from the intrinsic noise, which after stimulus onset will distort the voltage trace to threshold. This well-known problem has been solved with a diffusion approach; the time to the first spike is distributed as (Gerstein and Mandelbrot, 1964; Tuckwell, 1998)

$$P_t(t; V_0) = \frac{C(V_T - V_0)}{2\sqrt{\pi \tau_\sigma \sigma^2 t^3}} e^{-(CV_T - CV_0 - tI_S)^2 / 4\tau_\sigma \sigma^2 t}. \quad (9)$$

Combining both distributions using Eq. (2), the latency and relative jitter are

$$\langle t_1 \rangle = \left(\frac{1}{2} V_T + k \right) \frac{C}{I_S}, \quad (10)$$

$$\text{CoV}^2(t_1) = \frac{\frac{1}{12} V_T^2 + k^2}{\left(\frac{1}{2} V_T + k \right)^2} + \frac{2\tau_\sigma \sigma^2}{\left(\frac{1}{2} V_T + k \right)^2 C^2} \langle t_1 \rangle. \quad (11)$$

This relation is plotted in Fig. 3a.

Eq. (10) shows that noise (k) increases the mean latency, because it lowers the average membrane

potential, see Fig. 3b. The reason for this is twofold: (1) the noise smears out the membrane potential distribution, allowing potentials below the reset potential, and (2) the noise reduces the probability of finding neurons very close to threshold.

In the equation for the jitter, Eq. (11), we can distinguish two terms: the first term is due the randomness of the membrane potential at stimulus onset. This term is dominant for strong stimuli, $\langle t_1 \rangle \ll 1$. Interestingly, this term is not minimal at zero noise ($k = 0$), but it is minimal if $k = \frac{1}{6} V_T$, see Fig. 3c. This means that *the noise can reduce the jitter in the spike*. The reason is that the membrane potential has a narrower distribution if some noise is present than in the absence of noise. More precisely, for short latencies the relative jitter equals the CoV of the membrane potential with respect to the threshold,

$$\text{CoV}(t_1) \stackrel{t_1 \rightarrow 0}{=} \frac{\text{std.dev.}(V_0)}{V_T - \langle V_0 \rangle}. \quad (12)$$

as was already noted by Abeles (1991). This holds in general: in the presence of background activity the jitter for short latencies is determined by the membrane potential distribution.

The second term in Eq. (11) is proportional to the mean latency and is dominant for long latencies; it is the standard Wiener process behavior (Tuckwell, 1998). For a Poisson process, $\text{CoV}(t_1)$ would be constant. Here, however, due to the accumulation of noise the relative jitter increases to supra-Poisson values if the latency is long. This behavior is also dominant for

long, constant stimulation where it can be rewritten as a relation between mean and standard deviation of the interspike interval $\langle \delta t_{isi} \rangle \propto \langle t_{isi} \rangle^{3/2}$. This has been observed for retinal ganglion cells in physiological data (Troy and Robson, 1992).

4. Simulation Results

We have seen that leak currents decrease the jitter for increasing latencies, whereas intrinsic noise increases the jitter for increasing latencies. The question arises how the above behavior generalizes for the more realistic case that both noise and leak currents are present. There is no easy answer: once both leak and noise currents are present both the expressions for the membrane potential distribution (Brunel, 2000), and the time to spike become complicated (Ricciardi and Sacerdote, 1979; Tuckwell, 1988). Therefore, we rely on simulations for this case. To this end we implemented an integrate and fire model: resting and reset potential 0 mV, threshold 10 mV, time constant 20 ms, capacitance 200 pF. The noise was a filtered Gaussian noise current with zero mean and a temporal correlation of 0.5 ms.

First, consider the case without background activity. If there is no background current, background activity is virtually absent (except for the highest noise level; see below). The jitter is negligible unless the noise is substantial, Fig. 4a. And, as expected, the relative jitter increases with increasing noise and increasing latency.

Next, a background current is applied. It's amplitude was slightly above 100 pA such that in the absence of

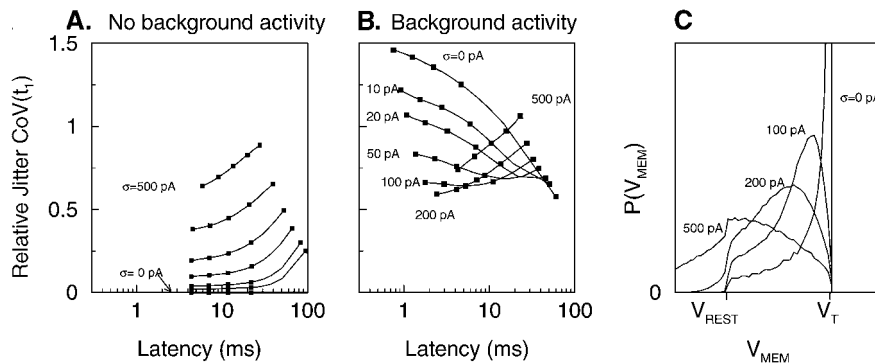


Figure 4. Effect of background activity and noise on transient response. **A:** Latency and relative jitter for a leaky I&F neuron with constant intrinsic noise; standard deviation of the noise: 0, 10, 20, 50, 100, 200, and 500 pA. The squares indicate the simulation current. No background current is present. **B:** The same as A, but now a background current is present (slightly above 100pA), causing background firing before stimulus onset. The jitter strongly increases. Furthermore, in the right region (long latency) increasing noise increases the jitter but speeds up the spike (the data points shift leftward). On the other hand, for short latencies the noise delays the spike and reduces the jitter. **C:** The distribution of membrane potentials at stimulus onset for the simulation in panel B. Noise standard deviations 0, 100, 200, and 500 pA.

noise the background firing rate is 5 Hz. The background activity drastically changes the relation between latency and jitter, Fig. 4b. One can distinguish two regions in the graph. In the right region (long latency) the noise reduces the latency. This is seen by comparing data points with the same stimulus current but different noise levels. In this region the potential wanders near the threshold, and the noise helps to kick it over the threshold, thus reducing the latency. The price is that the relative jitter increases. In the left region (short latencies) the dominant effect of the noise is that it lowers the average membrane potential, delaying the spike. Comparing the jitter at equal latency, the noise reduces the jitter. The reason is that the fluctuations of the membrane potential w.r.t. the threshold are smaller when noise is present. The transition between the two regimes occurs if the time to first spike is comparable to the time constant of the cell. One thus sees a tradeoff between faster, less precise spiking, and sluggish but precise spiking. Note that this result also holds when the standard deviation instead of the CoV is plotted versus the latency.

A possible complication is that the background activity changes with the added noise. The firing changes from almost periodic to irregular, and the background rate increases as the noise is added (to about 30 Hz for the largest noise amplitude). To examine if this confounds the observed effect, we ran simulations in which the background firing rate was kept constant by adjusting the background current as noise was added. At the highest noise level there is 10 Hz background activity even without any background current. In that case the background firing is purely noise induced and the neuron acts in a perfectly balanced mode (e.g., Shadlen and Newsome, 1998). Yet the relation between latency and jitter is not affected. This can be observed directly by comparing the curves for the highest noise level of Fig. 4a (no background current, 10 Hz background activity) and Fig. 4b (with background current, 30 Hz background activity). These curves are almost identical. This indicates that the results do not critically depend on the details of the background activity.

4.1. Synaptic Noise

In the above the amplitude of the noise was constant, independent of the stimulus. Now consider a neuron driven by purely excitatory synaptic input. The noise is due to the discrete character of the synaptic events. In this case the noise is proportional to the synaptic input

rate; the noise after stimulus onset is larger than during the background stimulation.

To model synaptic noise we use a current-based model of a synapse driven by a Poisson train. The synaptic current has an exponential time course with a time constant of 2 ms. The time to the first spike is measured for a range of synaptic amplitudes. We varied the EPSC amplitude 64-fold from small (12.5 pA), requiring 80 simultaneous events to threshold, to almost suprathreshold where two simultaneous events already cause a spike. To keep the net input current constant, the synaptic rate was set inversely proportional to the amplitude.

One might expect that larger unitary EPSCs would give more jitter. Indeed, if background activity is absent so that the membrane potential equals the resting potential, the jitter decreases with decreasing EPSC size, as was already analyzed by Stein (1967). This is plotted in Fig. 5a. In the presence of background activity, this is no longer true, see Fig. 5b. Remarkably, both for long and short latencies the relative jitter is almost independent of the EPSC amplitude, contrary to the intuition that larger EPSCs would bring more jitter. The reason is again the interaction between the membrane potential distribution and the noise; the fluctuations of the membrane potential w.r.t. to the threshold are less for the large EPSC amplitudes, Fig. 5c. The simulations show that the increase of noise and the effect of the membrane potential largely cancel. The mean latency behaves the same as in the case of constant background noise: for strong stimuli larger EPSCs increase the latency, whereas for weak stimuli large EPSCs decrease the latency.

As above, the background rate rises as noise increases (5 Hz for the smallest amplitude, 25 Hz for the largest EPSC size). In additional simulations we compensated for this by reducing the synaptic rate for the larger EPSCs, keeping background firing at about 5 Hz. Like above the relation between jitter and latency does not change.

5. Discussion

Although the importance of timing of single spikes in higher cortical areas is still a subject of debate (Bair and Koch, 1996; Reich et al., 1997; Shadlen and Newsome, 1998), for sensory systems there is little doubt that transients are important and are faithfully transduced (Rieke et al., 1996; Meister and Berry, 1999; Victor, 1999). In this study we have focused on the first

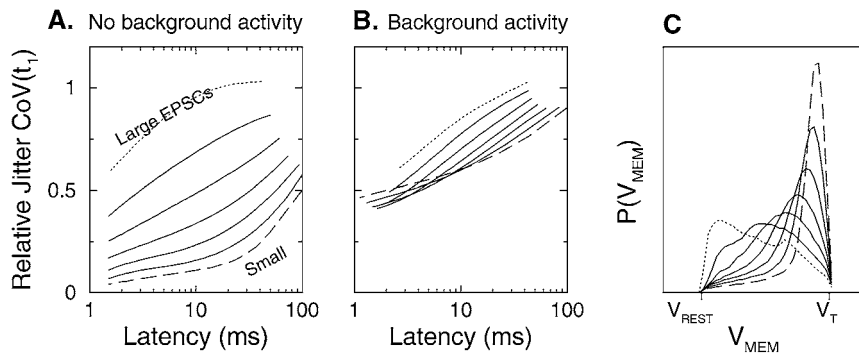


Figure 5. Effect of excitatory synaptic noise on the latency and relative jitter. The cell was synaptically stimulated with Poisson trains. **A:** At a random time the input rate was increased from zero to a high level. The EPSC amplitudes were 12.5 (dashed line), 25, 50, 100, 200, 400, and 800 pA (dotted line). In the absence of background activity the jitter strongly depends on synaptic amplitude. **B:** Now the input rate is increased from a background level to the stimulus level. With this background activity the jitter hardly changes despite the wide range of EPSC amplitudes. **C:** The membrane potential distribution at the time of the stimulus for the simulation in panel B.

spike after stimulus onset. We note that the second spike will always show more jitter if more noise is present, as the first spike resets the membrane potential. However, because synaptic depression and spike-frequency adaptation suppress subsequent spikes, we believe that the first spike is the most important for transient response (Marsalek, Koch, and Maunsell, 1997).

Comparing the results with and without background activity, the background activity substantially reduces the latency because it raises the average membrane potential. We have defined the relative jitter as the CoV of the time of the first spike. The jitter, strongly dependent on the noise in the absence of background activity, becomes approximately constant (0.4, . . . , 1.5) for both noise models and for a wide range of latencies and noise amplitudes. In other words, in the presence of background activity, the standard deviation of the time to first spike roughly equals a constant times the latency.

The effect of noise is subtle. Not only does it change when the cell crosses threshold after stimulus onset, but it also influences the distribution of membrane potentials. Mathematically, it changes both P_V and P_I in Eq. (2). Therefore, depending on the strength of the stimulus, constant intrinsic noise can have two effects: (1) for strong stimuli the jitter is dominated by the distribution of membrane potentials at stimulus onset; noise shifts this distribution such that it delays the spike, but reduces the relative jitter; (2) but for weak stimuli, the leaky neuron “forgets” the membrane potential at stimulus onset, and the jitter is dominated by the noise accumulating after stimulus onset. Here the

noise has a perhaps more anticipated effect: if noise is increased, the latency is reduced as the noise kicks the neuron over threshold, but the jitter increases. For synaptic noise the results show that the relative jitter is almost independent of the EPSC amplitude. This is counterintuitive as one might have thought that larger EPSCs would lead to more jitter, as is the case in the absence of background activity (Stein, 1967). In other words, in the presence of background activity, smaller EPSCs do not make responses in the nervous system less jittery.

As a realistic description of noise in neurons is difficult, we have used two noise models, which we think are extreme cases. The first case is constant background noise. This is a simplified model of channel noise. Constant background noise is also appropriate if the excitatory and inhibitory inputs to a cell are balanced: if the stimulus causes an increase in the excitatory rate combined with a decrease of the inhibitory rate, the synaptic noise will remain roughly constant. If, instead, the input to the cell is dominated by excitatory inputs, our second noise model is more relevant. The physiological situation that combines channel noise and noise from inhibitory and excitatory synapses should interpolate between these two extremes.

This also brings us to the question how sensitive our results are to the choice of model and its parameters. Undoubtedly, different neuron models such as Hodgkin-Huxley models or multicompartment models will give quantitatively different results, for instance, because in real neurons there is not always a fixed threshold voltage (Azouz and Gray, 2000). These

simplifications will be partly reflected in the distribution of membrane potentials, and thus the jitter. Yet, given the strong and robust effects, we think that our result have a general validity.

In other studies the reliability of spiking has been defined as the chance that a certain stimulus evokes a spike (Mainen and Sejnowski, 1995; Cecchi et al., 2000). In our setup a spike will always occur. For step stimuli with *finite* duration the reliability to evoke at least one spike is $\int_0^t P_t(t_1) dt_1$. For strong stimuli and reliabilities close to one, the tail of the membrane potential distribution dominates this reliability. Both for Gaussian and exponential membrane potential distributions, the reliability is close to one for small latencies and after a plateau, drops off sharply with increasing latency, as was observed in experiments (Mainen and Sejnowski, 1995).

Experimental tests of the presented results are possible. Although there have been various experimental studies on the latency and jitter in the nervous system, little systematic insight has been obtained. The present study indicates that results will greatly depend on the anesthesia as that strongly effects the background activity and the membrane potential distribution (e.g., Paré, Shink, Gaudreau, Destexhe, and Lang, 1998). Furthermore, the precision is best measured by the CoV. However, this requires precise measurement of the onset time of the stimulus, which is complicated, especially if the neuron is part of a network.

The question arises what the results imply for information processing. In general, our results show a tradeoff between a fast, jittery response and a response with long latency and less jitter. Currently, there is no theory that weighs these tradeoffs, but the fact that *in vivo* so many neurons show spontaneous activity, suggests that possibly the nervous system operates in a regime of fast, but jittery, responses. In addition, background activity improves the sensitivity of the neurons to small inputs (Hô and Destexhe, 2000) and improves the response time of attractor networks (Tsodyks and Sejnowski, 1995). The introduced jitter is not necessarily a problem: higher-order neurons can average the responses from many parallel pathways; such averaging reduces the jitter (Marsalek et al., 1997; Burkitt and Clark, 1999; Diesmann, Gewaltig, and Aertsen, 1999). Next, the stray spikes reduce the dynamic range of the neuron, but the background rate can be set fairly low, limiting the decrease in dynamic range. Finally, the stray spikes induced by the background activity might pose another problem as they could lead to false

positives. But inspection of Fig. 1 suggests that a simple threshold would get rid of these stray spikes.

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Note

1. But as a consequence of using filtered noise, $2\tau_\sigma\sigma^2$ replaces σ^2 in some known equations that were derived for white noise.

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