Transient termination of synaptically sustained spiking by stochastic inputs
in a pair of coupled Type 1 neurons

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We examine the effects of stochastic input currents on the firing behavior of two excitable neurons coupled with fast excitatory synapses. In such cells (models), typified by the quadratic integrate and fire model, mutual synaptic coupling can cause sustained firing or oscillatory behavior which is necessarily antiphase. Additive Gaussian white noise can transiently terminate the oscillations, hence destroying the stable limit cycle. Further application of the noise may return the system to spiking activity. In a particular noise range, the transition times between the oscillating and the resting state are strongly asymmetric. We numerically investigate an approximate basin of attraction, A, of the periodic orbit and use Markov process theory to explain the firing behavior in terms of the probability of escape of trajectories from A.

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Recent experiments [13] have shown that the spiking patterns of regular spiking and fast spiking neurons in the rat somatosensory cortex exhibit Type 1 and Type 2 behavior, respectively. Such differences were originally found by Hodgkin [9] in his investigations of the responses of squid axon preparations to applied currents. In some cases, the frequency of firing rose smoothly from zero as the current increased whereas in others, a train of spikes with a non-zero minimal frequency suddenly occurred at a particular input current. Cells that responded in the first manner were called Class 1 (which we call Type 1) whereas cells with discontinuous frequency-current curves were called Class 2 (Type 2). Mathematical explanations for the two types are found in the local normal form of a saddle node bifurcation) of a relatively simple neural model that exhibits Type 1 firing behavior. This is the quadratic integrate and fire (QIF) model [11] for which

\[ \dot{x} = (x - x_R)^2 + \beta, \]

where \( x \) is interpreted as the membrane potential of the neuron, \( x_R \) is its resting value and \( \beta \) is the mean input. Once the value \( x_C \) of \( x \) is so large that the r.h.s. of (1) is positive, it will become infinite in a finite time (of the order of 1/\( x_C \)) and then has to be reset to \(-\infty\). The upward excursion and resetting constitute a “spike” in this model. Problems with infinite values can be avoided by applying the transformation \( x - x_R = \tan \theta \), where \( \theta \) takes values in \([0, 2\pi]\), i.e., on the unit circle \( S^1 \) when we identify 0 and \( 2\pi \). This yields the \( \theta \)-neuron model [3, 8]

\[ \dot{\theta} = 1 - \cos \theta + (1 + \cos \theta)\beta, \]

where \( \theta = \pi \) corresponds to a spike of the neuron. Both of these equivalent formulations have been used previously for simulation and analysis of neural dynamics [3, 11].

We consider the case of two coupled identical QIF neurons \( i = 1, 2 \) with noise terms as follows [8]

\[ dX_1 = [(X_1 - x_R)^2 + \beta + g_s X_3]dt + \sigma dW_1 \] (3)
\[ dX_2 = [(X_2 - x_R)^2 + \beta + g_s X_4]dt + \sigma dW_2 \] (4)
\[ dX_3 = \left[ -\frac{X_3}{\tau} + F(X_2) \right]dt \] (5)
\[ dX_4 = \left[ -\frac{X_4}{\tau} + F(X_1) \right]dt \] (6)
where $X_1, X_2$ are random processes corresponding to the membrane potentials of the neurons while $X_3$ ($X_4$) is the synaptic input from neuron 2(1) to neuron 1(2). In these equations, $g_s$ is the coupling strength between the neurons and $W_1$ and $W_2$ are independent standard Wiener processes which enter with amplitude $\sigma$. The noise terms represent fluctuations in nonspecific inputs to each neuron as well as possibly intrinsic membrane and channel noise. The function $F$ is given by $F(x) = 1 + \tanh(x - x_{th})$, where $x_{th}$ characterizes the threshold effect of synaptic activation [18], so the variables $X_3, X_4$ take values in the interval $[0, 2]$. The corresponding $\theta$-neuron equations then are

$$d\Theta_i = (1 - \cos \Theta_i - (\sigma^2/2) \sin \Theta_i (1 + \cos \Theta_i) [\beta + g_s (X_{i+2})])dt + \sigma (1 + \cos \Theta_i) dW_i \quad (i = 1, 2),$$

where $\Theta_i = \pi$ corresponds to a spike of neuron $i$. Note that at this spike point, the effect of the noise term vanishes. As verified by Gutkin (unpublished), this, together with the strictly positive contribution of the term $1 - \cos \Theta_i$, ensures that the spike point $\Theta_i = \pi$ can only be passed in the direction of increasing values of $\Theta_i$. Therefore, this model is equivalent to the quadratic integrate and fire model with resetting at $\infty$.

For the purpose of this report we choose a negative value for $\beta$ so that each neuron in isolation will not fire by itself when its potential is near the resting value $x_R$, but only when perturbed beyond a threshold $x_T$. For the model described by (3)-(6), without noise, inducing firing in one neuron by perturbing it beyond threshold leads to sustained firing in both neurons when the coupling strength is above the bifurcation value $g_s = g^*_s$. At that value, two heteroclinic orbits between the unstable rest points where one of the neurons is at $x_R$, the other at $x_T$, turn into a periodic orbit of antiphase oscillations. We then have two stable attractors, the stable rest point where both neurons take the value $x_R$, and the antiphase oscillator. We note that the dynamics are equivalent for both versions of the model circuit: the QIF and the $\theta$-neuron.

Results and theory.— In the numerical work, the following constants are employed as the standard set throughout. $x_R = 0, x_{th} = 10, \beta = -1, g_s = 100$ and $\tau = 0.25$. In our simulations, we reset the state variables $X_1, X_2$ to the value $-x_C$ when they reach or exceed the value $x_C = 20$. The initial values of the neural potentials are $X_1(0) = 1.1, X_2(0) = 0$ and the initial values of the synaptic variables are $X_3(0) = X_4(0) = 0$. Results such as those in Figure 1 are obtained. The spike trains of the two coupled neurons and their synaptic inputs are shown on the left for no noise. The firing settles down to be quite regular and the periodic orbit is in part shown in the $(x_1, x_2)$-plane as the red curve in Figure 2.

The effects of weak noise on the spike trains are shown in the right column of Figure 1. In the top portion an example of the trajectory for $\sigma = 0.1$ is shown. Here three spikes arise in neuron 1 and two in neuron 2, but the time between spikes increases and eventually the orbit collapses away from the periodic orbit. In the example (lower part) for $\sigma = 0.2$ there are no spikes in either neuron. Extensive simulations showed that orbits tended to collapse away from the periodic orbit in the vicinity of the points $P_1$ and $P_2$, as shown in four trials in Figure 2. Here, the red curve depicts the stable periodic orbit in the absence of noise and the blue curves are trajectories with noise, $\sigma = 0.1$. These random paths always start precisely at the same point in $R^4$ on the periodic orbit - marked as “initial point”. The number of orbits completed is a random variable which we may quantify using $T_L$, which is the time of occurrence of the last spike in neuron 1. Inspection of histograms of $T_L$-values, based on 500 trials, for $\sigma = 0.1$ and 0.45, shows that the spiking stops after approximately an integer multiple of the first spike time. Furthermore, as $\sigma$ increases, the number of occasions on which no spike was generated increases. This is further illustrated in Figure 3 where the mean of $T_L$ is plotted against $\sigma$. Hence it is clear that noise tends to curtail firing. The theoretical basis of these plots is outlined in the next section.

Exit-time and orbit stability.— If a basin of attraction for the periodic orbit can be found, then the probability that the process with noise escapes from this basin gives

![FIG. 1: On the left are shown the solutions of (5)-(6) for two coupled QIF model neurons with the standard parameters and without noise. $X_1$ and $X_2$ are the potential variables of neurons 1 and 2 and $X_3$ and $X_4$ are the inputs to neurons 1 and 2, respectively. On the right are shown examples of trajectories of the potential variables when there is noise, $\sigma = 0.1$, in the top two parts and $\sigma = 0.2$ in the lower two parts. Note the absence of spikes in the trial for the larger noise case.](image-url)
the probability, in the present context, that spiking will cease. Since the system (3)-(6) is Markovian, we may apply standard first-exit time theory [17]. Let $A$ be a set in $(S^1)^2 \times [0,2]$ and let $y_1, y_2$ be the values assumed by $\Theta_1$ and $\Theta_2$ and let $y_3, y_4$ be the values assumed by the synaptic input variables $X_3$ and $X_4$. The probability $p(y_1, y_2, y_3, y_4)$ that the process ever escapes from $A$ is given by

$$\mathcal{L}_p \equiv \frac{\sigma_2^2}{2} (1 + \cos y_1)^2 \frac{\partial^2 p}{\partial y_1^2} + \frac{\sigma_2^2}{2} (1 + \cos y_2)^2 \frac{\partial^2 p}{\partial y_2^2} \quad (8)$$

$$+ \left[ 1 - \cos y_1 - (\sigma^2/2) \sin y_1 (1 + \cos y_1)(\beta + g_s y_3) \right] \frac{\partial p}{\partial y_1}$$

$$+ \left[ 1 - \cos y_2 - (\sigma^2/2) \sin y_2 (1 + \cos y_2)(\beta + g_s y_4) \right] \frac{\partial p}{\partial y_2}$$

$$+ \left( F(x_R + \tan \frac{y_2}{2}) - \frac{y_3}{\tau} \right) \frac{\partial p}{\partial y_3}$$

$$+ \left( F(x_R + \tan \frac{y_1}{2}) - \frac{y_4}{\tau} \right) \frac{\partial p}{\partial y_4} = 0,$$

where $(y_1, y_2, y_3, y_4) \in A$, and with boundary condition that $p = 1$ on the boundary of $A$ (since the process is continuous). If one also adds an arbitrarily small amount of noise for $X_3$ and $X_4$ (or considers those solutions of (8) that arise from the limit of vanishing noise for $X_3, X_4$), and uses the positivity of the drift term $1 - \cos \theta$ at $\theta = \pi$ where the diffusion coefficient $\frac{\sigma_2^2}{2} (1 + \cos \theta)^2$ vanishes, the solution of the linear elliptic partial differential equation (8) is unique and $\equiv 1$ so that the process will eventually escape from $A$ with probability 1. Hence, the expected time $f(y)$ of exit of the process from $A$ satisfies

$$\mathcal{L} f = -1, \quad y \in A$$

with boundary condition $f = 0$ on the boundary of $A$. This mean value corresponds closely with the expected value of $T_L$ depicted in Figure 3. In fact, for small noise, the logarithm of the expected exit time from $A$, that is, the time at which firing stops, behaves like the inverse of the square of the noise amplitude [4]. When the process escapes from $A$, it has to move into the basin of attraction of the stable rest point. With a small probability, noise can eventually also drive the process out of that latter basin, so that some intermittent spiking behavior may result. Near the bifurcation value $g_s = g_s^*$, however, the situation is not symmetric between the two attractors. The width of the basin of attraction of the stable rest point is always positively bounded from below; while just beyond the bifurcation value, the antiphase oscillator basin of attraction is very narrow because it emerges from two heteroclinic orbits linking the fixed points – the rest-points and the thresholds, and so, noise can relatively easily drive the dynamics out of it. Numerically we identified that the region of easiest escape from that basin is near the points $P_1$ and $P_2$ in Figure 2 for the given values of the parameters. This in fact, would be where the basin is the narrowest. In another approach we have investigated the system of differential equations for the moments [14] of the system (3)-(6) as given in the appendix. Numerical solutions showed that the variance

![Figure 2: Four examples which illustrate the noise-induced collapse away (blue paths) from the basin of attraction of periodic orbit, denoted by the red curve, in two coupled QIF neurons. The parameters are the standard set, with $\sigma = 0.1$, and the initial point is the same in all cases, being on the periodic orbit as indicated top left. The departure points are located either near $P_1$ or $P_2$. In the top left example there is a spike in neuron 2, then a spike in neuron 1 (both clipped) followed by escape from the basin of attraction before a second spike can occur in neuron 2.](image)

![Figure 3: The mean of the time $T_L$ to the last spike in neuron 1 versus the noise amplitude. This quantity measures the exit time from the basin of attraction of the periodic orbit. The 4-dimensional process $(X_1, X_2, X_3, X_4)$ is initially on the periodic orbit. Error bars denote 95% confidence intervals (500 trials).](image)
of $X_1$ and $X_2$ suddenly became extremely large in the vicinity of the exit-points $P_1$ and $P_2$ of Figure 2.

Discussion.— We have studied the effect of noise in systems of two coupled neurons of Type 1. Since the quadratic integrate and fire neurons represent the canonical model for type I excitability, our results are generic for that whole class of models. We found that while coupling can support asynchronous oscillatory activity in excitable neurons, noise can transiently terminate that sustained spiking (near to the bifurcation point where the asynchronous periodic orbit emerges). This circuit is a stochastic analogue of the deterministic case previously studied by Gutkin et al. (2001) who showed that transient synchronization can terminate sustained activity. This two-neuron circuit is a minimal circuit model of self-sustained neural activity. Such activity in the prefrontal cortex has been proposed as a neural correlate of working memory [3]. In numerical simulations we have previously noted [8] that the transitions between the two states can be quite asymmetric, given that the circuit is close to the bifurcation (i.e. the synaptic coupling is near the onset of sustained activity). Obviously for sufficiently weak noise the transition times are long: times for both turning off the sustained activity and turning it on to infinity as the strength of the noise goes to zero. Strong noise will produce intermittent excursions between the two states, possibly with comparable transition times. However, for a range of noise parameters, depending on the parameters of the circuitry (such as the value of the $\beta$ and the synaptic time constants), the time to turn off the activity is short while the time to turn it back on (by the noise) is long. In fact previous simulations (see [8]) have led us to believe that there is an optimal value of the noise to turn off the sustained activity without turning it on for any length of simulation so that the two transition times appear to be on separate time scales, and the noise effectively appears to turn off the sustained firing. We developed a geometrical interpretation, showing that the relative size and the geometry of the basin of attraction for the anti-phase oscillation is the key to this effect. Simulations hint at a different scaling for the mean life time of the sustained firing state and the silent state as a function of the noise strength. Hence we would speculate that the tuning for the noise dependent destruction of the limit cycle stability is evocative of stochastic resonance phenomena and may be loosely interpreted as a delay of bifurcation by noise. Such delays have been previously noted for excitatory single neurons [16] and more recently for spatially extended systems [10].

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Appendix— For the system of 4 stochastic differential equations (3)-(6) we may deduce, for small noise, the following differential equations for the first and second order moments, being the four means, denoted by $m_i, i = 1, \ldots, 4$ and the 10 covariances $C_{ij} = \text{Cov}[X_i, X_j]$, which includes the 4 variances, $V_i, i = 1, \ldots, 4$.

\[
\begin{align*}
\frac{dm_1}{dt} &= m_1^2 + b + g m_3 + V_1, \\
\frac{dm_2}{dt} &= m_2^2 + b + g m_4 + V_2, \\
\frac{dm_3}{dt} &= -\frac{m_3}{\tau} + 1 + \tanh(m_1 - x_{th}) \cdot \frac{\sinh(m_2 - x_{th})}{\cosh^2(m_2 - x_{th})} V_2, \\
\frac{dm_4}{dt} &= -\frac{m_4}{\tau} + 1 + \tanh(m_1 - x_{th}) \cdot \frac{\sinh(m_1 - x_{th})}{\cosh^2(m_1 - x_{th})} V_1, \\
\frac{dV_1}{dt} &= 4m_1 V_1 + 2g C_{13} + \sigma^2, \\
\frac{dV_2}{dt} &= 4m_2 V_2 + 2g C_{24} + \sigma^2, \\
\frac{dV_3}{dt} &= 2C_{23} \frac{2V_3}{\tau}, \\
\frac{dV_4}{dt} &= 2C_{14} \frac{2V_4}{\tau}, \\
\frac{dC_{12}}{dt} &= 2(m_1 + m_2) C_{12} + g(C_{14} + C_{23}), \\
\frac{dC_{13}}{dt} &= (2m_1 - \frac{1}{\tau}) C_{13} + g V_3 - \frac{C_{12}}{\cosh^2(m_2 - x_{th})}, \\
\frac{dC_{14}}{dt} &= (2m_1 - \frac{1}{\tau}) C_{14} + g C_{34} + \frac{C_{12}}{\cosh^2(m_1 - x_{th})}, \\
\frac{dC_{23}}{dt} &= (2m_2 - \frac{1}{\tau}) C_{23} + g C_{34} + \frac{V_2}{\cosh^2(m_2 - x_{th})}, \\
\frac{dC_{24}}{dt} &= (2m_2 - \frac{1}{\tau}) C_{24} + g C_{34} + \frac{C_{21}}{\cosh^2(m_1 - x_{th})}.
\end{align*}
\]
\[
\frac{dC_{34}}{dt} = \frac{C_{24}}{\cosh^2(m_2 - x_{th})} + \frac{C_{41}}{\cosh^2(m_1 - x_{th})} - \frac{2C_{34}}{\tau}
\]