Transient termination of spiking by noise in coupled neurons

B. S. Gutkin¹, J. Jost² and H. C. Tuckwell²

¹ Group for Neural Theory, Département des Études Cognitives, Ecole Normale Supérieure, Collège de France
5, rue d’Ulm, 75005 Paris, France
² Max Planck Institute for Mathematics in the Sciences - Inselstr. 22, 04103 Leipzig, Germany

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Abstract – 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 by moving the dynamics away from the stable limit cycle. Further application of the noise may return the system to spiking activity. When the noise is sufficiently weak, the durations of the times spent in the oscillating and the resting states are strongly asymmetric. Hence weak noise tends to stop the spiking activity. When the noise is stronger, the periods of cessation of activity tend to be smaller. 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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Introduction. – Recent experiments [1] 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 [2] 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 former 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 bifurcation which accompanies the transition from rest state to the periodic firing mode. For Type 1 behavior, a resting potential vanishes via a saddle node bifurcation whereas for Type 2 the instability of the rest point is due to an Andronov-Hopf bifurcation; see for example [3].

The quadratic integrate and fire model and the $\theta$-neuron. – Computational models which include details of the complex anatomy and physiology of cortical neurons are too complicated to analyze mathematically. However, we can take advantage of the generic nature (as 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 [15] 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...
which is taken to be negative below. (Note that we use the convention that upper (lower) case variables are (non-)
random.) Once the value $x$ is so large that the r.h.s. of (1)
is positive, it will become infinite in a finite time, 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
$x - x_R = \tan^2 \theta$, 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 [6,16]

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

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 [6,15].

We consider the case of two coupled identical QIF
neurons $i = 1, 2$ with noise terms as follows [14]:

$$dX_1 = [\{X_1 - x_R\}^2 + \beta + g_s X_2]dt + \sigma dW_1,$$

$$dX_2 = [\{X_2 - x_R\}^2 + \beta + g_s X_1]dt + \sigma dW_2,$$

$$dX_3 = \left[ -\frac{X_1}{\tau} + F(X_3) \right] dt,$$

$$dX_4 = \left[ -\frac{X_2}{\tau} + F(X_4) \right] dt,$$

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 non-specific inputs to each neuron
as well as possibly intrinsic membrane and channel noise.
The function $F$ is given by $F(x) = 1 + \tan \hbar (x - x_{th})$,
where $x_{th}$ characterizes the threshold effect of synaptic
activation [17], so the variables $X_3, X_4$ take values in the
interval $[0, 2\pi]$. Note that here synaptic potentials arrive in
neuron 1(2) when the neuron 2(1) fires a spike whose
amplitude is large enough to activate the synapse.

If we use Itô calculus [18] the corresponding $\theta$-neuron
equations then are, with $i = 1, 2$,

$$d\Theta_i = (1 - \cos \Theta_i - (\sigma^2/2) \sin \Theta_i(1 + \cos \Theta_i)) \times [3 + g_s X_{i+2}]dt + \sigma (1 + \cos \Theta_i)dW_i,$$

$$dX_{i+2} = \left\{ -\left[ X_{i+2}^2/\tau + F(x_R + \tan (\Theta_{i+2}/2)) \right] \right\} dt,$$

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 $\infty$. (Note that the extra
contribution to the drift term comes from the Itô calculus.
However, the choice of calculus has no bearing on the
results obtained.)

For the purpose of this report we choose a nega-
tive value for $\beta$ so that each neuron in isolation will
not fire by itself when its potential is near the resting value
$x_{R,i}$, but only when perturbed beyond the thresh-
old $x_T = x_G + \sqrt{-\beta}$. As found in [19] for the model given
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 $x_{-i}$, the other at $x_{+i}$, with $x_{+i}$ determined
by $x_{+i} = \pm \sqrt{-\beta - g_s^* (1 + \tan (x_T - x_{th}))} + x_{R,i}$, turn into
a periodic orbit of antiphase oscillations. We then have
two stable attractors, the stable rest point where both
neurons take the value $x_0$ determined by the equation
$x_0 = \sqrt{-\beta - g_s^* (1 + \tan (x_T - x_{th}))} + x_{R,i}$, and the antiphase
oscillator. This behavior is generic insofar as it depends
on generic bifurcations. The only nongeneric aspect is the
symmetry between the two neurons caused by the fact that
they are both modelled with the same parameter values.
If the two neurons were equipped with different para-
meter values, the two heteroclinic orbits between the
above saddles would arise at different parameter values,
and the basin of attraction of the antiphase orbit would
consequently become asymmetric. 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: $x_{R,i} = 0, x_{th} = 10, \beta = -1, g_s = 100$ and $\tau = 0.25$.
In our simulations, we reset the state variables
$X_1, X_2$ to the value $-\infty$ when they reach or exceed the
value $x_C = 20$. The initial values of the neural potentials
are $X_i(0) = 11, X_{2i}(0) = 0$ and the initial values of the
synaptic variables are $X_3(0) = X_4(0) = 0$. Results such as
those in fig. 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 regular
and the periodic orbit is in part shown in the $(x_1, x_2)$-plane
as the red (on-line) curve in fig. 2.

The effects of weak noise on the spike trains are shown
in the right column of fig. 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 right part) for $\sigma = 0.3$ 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 fig. 2.
Here, the red (on-line) curve depicts the stable periodic
orbit in the absence of noise and the blue (on-line) curves
are trajectories with noise, $\sigma = 0.1$. These random paths

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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 fig. 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 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 [20]. Let $\mathcal{A}$ be a set in $(S^1)^2 \times [0, 2]^2$ 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 $\mathcal{A}$ is given by

$$\mathcal{L}p = \frac{\sigma^2}{2} (1 + \cos y_1)^2 \frac{\partial^2 p}{\partial y_1^2} + \frac{\sigma^2}{2} (1 + \cos y_2)^2 \frac{\partial^2 p}{\partial y_2^2}$$
$$+ [1 - \cos y_1 - (\sigma^2/2) \sin y_1(1 + \cos y_1)(\beta + g_s y_3)] \frac{\partial p}{\partial y_1}$$
$$+ [1 - \cos y_2 - (\sigma^2/2) \sin y_2(1 + \cos y_2)(\beta + g_s y_4)] \frac{\partial p}{\partial y_2}$$
$$+ \left( F \left( x_R + \tan \frac{y_2}{2} \right) - \frac{y_1}{\tau} \right) \frac{\partial p}{\partial y_3} + \left( F \left( x_R + \tan \frac{y_1}{2} \right) - \frac{y_4}{\tau} \right) \frac{\partial p}{\partial y_4} = 0,$$

where $(y_1, y_2, y_3, y_4) \in \mathcal{A}$, and with the boundary condition that $p = 1$ on the boundary of $\mathcal{A}$ (since the process

Fig. 1: (Colour on-line) Sample paths for the voltage variable $X_1$ of neuron 1 obtained from solutions of eqs. (3)–(6) for two coupled QIF model neurons with the standard parameters. In the noise-free case shown in the top left figure, a steady sequence of spikes occurs, with an antiphase sequence in neuron 2. As the noise increases the spiking ceases at earlier times (see fig. 3). Note that these are chosen as representative paths as in the cases with noise there may be zero, one or many spikes.

Fig. 2: (Colour on-line) 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 in the top figure. The departure points are located either near $P_1$ or $P_2$. In the top 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.
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 \( \sigma^2/2(1+\cos \theta)^2 \) 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. Furthermore, if the expectation of the exit time of the process from \( A \) is denoted by \( f(y_1, y_2, y_3, y_4) \) then by a theorem in Markov processes [20] we have

\[
\mathcal{L}f(y) = -p(y) = -1,
\]

with boundary conditions that \( f = 0 \) on the boundary of \( A \). We have not attempted to solve this partial differential equation directly, but its solutions correspond closely with the expected value of \( T_L \), the time of the last spike in neuron 1, depicted in fig. 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 [21]. 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 \( g_4 = g_4^* \), 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 fig. 2 for the given values of the parameters. This in fact, would be where the basin is the narrowest. It is apparent by examination of the escaping paths and by numerically examining the effects of perturbations away from the periodic orbit that the basin of attraction is narrower to the right of \( P_1 \) and to the left of \( P_2 \).

Moment analysis. – Without solving the partial differential equation (8), we may obtain insight into the cessation of spiking activity by using another approach in which the first and second order moments of the variables \( X_1(t), X_2(t), X_3(t) \) and \( X_4(t) \) are computed. For the system of 4 stochastic differential equations (3)–(6) we may deduce [22], for small noise, a system of 14 coupled ordinary (deterministic) differential equations (ODE) for the first- and second-order moments, being the four means, denoted by \( m_i(t), i = 1, \ldots, 4 \) and the 10 covariances \( C_{ij}(t) = \text{Cov}(X_i(t), X_j(t)) \), which includes the 4 variances, \( V_i(t), i = 1, \ldots, 4 \). These equations are given in the appendix. The solutions of these ODEs approximate the moments of the process well when \( X_1(t)\ldots X_4(t) \) are approximately normally distributed, as we verified by simulations.

This system of differential equations is easily solved using Runge-Kutta methods. Numerical solutions showed that the variance of \( X_1 \) \((X_2) \) suddenly became large in the vicinity of the exit point \( P_2 \) \((P_1) \) of fig. 2. Here, \( P_2 \) is near the unstable rest point where \( x_1 \) takes the value \( x_+ \) and \( x_2 \) the value \( x_- \). It can be seen from the moment equations that \( \frac{dm_1}{dt} \) here is proportional to \( V_1 \) with a positive factor \( m_1 \) that varies only slowly because \( \frac{dm_1}{dt} \) is close to 0 whereas \( \frac{dm_2}{dt} \) has the negative coefficient \( m_2 \) for \( V_2 \).

Discussion. – We have studied the effect of noise in systems of two coupled neurons of Type 1. The model we have employed is embryonic in the sense that it contains some of the elements of physiological neural networks. The results we have obtained will be a guide to the examination of more complex models to see whether the same phenomena are robust under more general input conditions. Nevertheless, since the quadratic integrate and fire neurons represent the canonical model for Type-1 excitability, our results are generic for that whole class of models. We have 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 [23]. In numerical simulations we have previously noted [14] that the transitions between the two states can be quite
The circuitry (such as the value of the parameter) produces intermittent excursions between the two states, the strength of the noise goes to zero. Strong noise will produce sustained activity and turning it on go to infinity as the noise strength. Hence we would speculate that the size and geometry of the basin of attraction for the noise-dependent escape from the basin of attraction (asymmetric, given that the circuit is close to the bifurcation). Obviously, for sufficiently weak noise the transition times are long: times for both turning off the sustained activity and turning it on to infinity is short while the time to turn it back on (by the noise) is long. In fact previous simulations (see [14]) 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 lifetime 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 escape from the basin of attraction of the limit cycle 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 excitable single neurons [24] and more recently for spatially extended systems [25].

Simulations of larger networks with detailed conductance-based models of cortical pyramidal neurons coupled with AMPA synapses show a qualitatively similar behavior: weak noise stops the sustained activity. A detailed report on these networks is in preparation. We have also investigated the effects of noise in coupled Type-2 model neurons; these results will also be reported elsewhere.

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Appendix: Moment equations. – The following system of coupled ordinary differential equations is found [22] for the first- and second-order moments of the stochastic system (3)-(6):

\[
\frac{dV_1}{dt} = 4m_1V_1 + 2g_xC_{13} + \sigma^2, \quad \frac{dV_2}{dt} = 4m_2V_2 + 2g_xC_{24} + \sigma^2,
\]

\[
\frac{dV_3}{dt} = \frac{2C_{23}}{\cosh^2(m_2 - x_{th})} - \frac{2V_3}{\tau},
\]

\[
\frac{dV_4}{dt} = \frac{2C_{14}}{\cosh^2(m_1 - x_{th})} - \frac{2V_4}{\tau},
\]

\[
\frac{dC_{12}}{dt} = 2(m_1 + m_2)C_{12} + g_x(C_{14} + C_{32}),
\]

\[
\frac{dC_{13}}{dt} = \left(2m_1 - \frac{1}{\tau}\right)C_{13} + g_xV_3 + \frac{C_{12}}{\cosh^2(m_2 - x_{th})},
\]

\[
\frac{dC_{14}}{dt} = \left(2m_1 - \frac{1}{\tau}\right)C_{14} + g_xV_3 + \frac{V_1}{\cosh^2(m_1 - x_{th})},
\]

\[
\frac{dC_{23}}{dt} = \left(2m_2 - \frac{1}{\tau}\right)C_{23} + g_xV_3 + \frac{V_2}{\cosh^2(m_2 - x_{th})},
\]

\[
\frac{dC_{24}}{dt} = \left(2m_2 - \frac{1}{\tau}\right)C_{24} + g_xV_4 + \frac{C_{21}}{\cosh^2(m_1 - x_{th})},
\]

\[
\frac{dC_{34}}{dt} = \frac{C_{24}}{\cosh^2(m_2 - x_{th})} + \frac{C_{13}}{\cosh^2(m_1 - x_{th})} - \frac{2C_{34}}{\tau},
\]

For the validity of the underlying approximation for \(\sigma \to 0\), see [21], p. 56f.

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