

1 Synaptic Depression Model

We model the inputs into the cortex from the thalamus as a background plus a stimulus, $f(t) = f_0 + a(t)$ where f_0 is the background and $a(t)$ is the overlaid stimulus. Inputs will be filtered through a simple model for synaptic depression which we now describe. Let $s(t)$ denote the synaptic resources available. If $s(t) = 1$ then there is no SD. Abbott and other have modeled spike-by-spike SD as follows. Each time the presynaptic cell fires, s is decremented by an amount proportional to s : $s \rightarrow (1 - \gamma)s$ where γ is a number that is less than 1. In absence of any inputs, s returns to its baseline value of, say, 1 with a time constant τ_d . Formally, we can write the dynamics as:

$$\frac{ds}{dt} = (1 - s)/\tau_d - \gamma \sum_k \delta(t - t_k)s$$

where $\delta(t)$ is the impulse function and t_k are the times of the spikes. We do not want to explicitly model spikes, but rather, the firing rates of the inputs. Over many trials, the mean of the above sum becomes the instantaneous firing rate. Thus, our model for SD is just

$$\frac{ds}{dt} = (1 - s)/\tau_d - \gamma f(t)s \tag{1}$$

We point out that this is equivalent to the Tsodyks model:

$$\frac{ds}{dt} = (U - s)/\tau_d - U f(t)s.$$

To see this, let $s = U s'$, and see that s' obeys (1) with $\gamma = U$. The only difference is that there is a reduction in the total synaptic strength by an amount U .

The effect of SD is to attenuate the thalamic input into the cortex so that the net input is $s(t)f(t)$. We now describe the behavior of (1) when the input consists of a constant background plus a short transient, $f(t) = f_0 + a(t)$. Since equation (1) is linear, we can write a closed form solution to $s(t)$ given a function $a(t)$, but little is gained from this. Instead, we derive an approximation which works very well. We first note that if $a(t) = 0$, then the steady state degree of depression is:

$$s_0 = \frac{1}{1 + \tau_d \gamma f_0}$$

which is a decreasing function of the background. The net input is:

$$f_0 s_0 = \frac{f_0}{1 + \tau_d \gamma f_0}$$

an increasing, but concave down function of the background activity. Abbott and others have noted that SD provides a mechanism to take the derivative of inputs so that it is sensitive to temporal contrast. This is the essence of MCA's results. However, as we show below, it is not sufficiently sensitive to

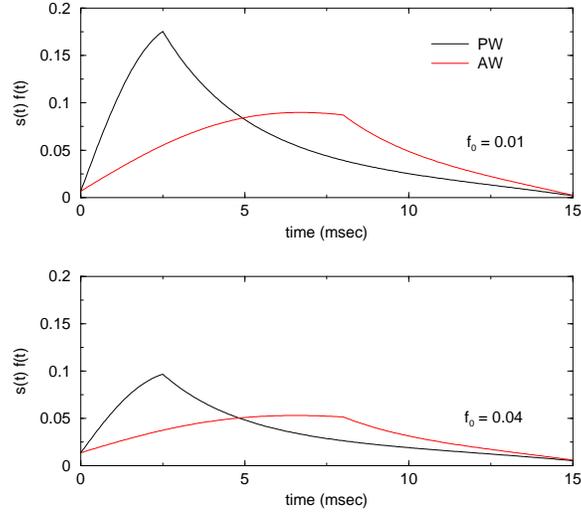


Figure 1: Net input to triangles at different background levels of excitation. Top panel shows PW and AW net responses when the background is 10 Hz and bottom show the response with a 40 Hz background.

temporal contrast to explain the huge differences between adjacent and principle whisker stimulation. In fact we will show that the differences between PW and AW stimulation are actually smaller with large background activity than with smaller, in contradiction of the experimental results.

We use as our stimulus short triangles of duration 15 msec and reaching a peak at various times. The peaks will be 2.5, 5, and 8 msec, while the amplitudes are 0.35, 0.3, and 0.25 spikes per msec. The extremes correspond to PW and AW inputs which tend to be larger and better synchronized. We use $\gamma = 0.75$ and $\tau = 65$ msec, similar the that use in other studies. Figure 1 shows the net input, $s(t)f(t)$ into the cortex given a triangle input and SD. Clearly, the AW response is always much smaller than the PW response and furthermore, both responses are diminished as the background level increases.

Suppose that there is no recurrent cortical connectivity; that is, we have a strictly feedforward response. Then the firing rate output of the cortex is just some nonlinear monotonic function of the input, $P(t) = G(s(t)f(t))$ where G is the nonlinear gain function. Suppose, for example, that it is a threshold linear function. Then, graphically, we can draw a horizontal line through the curves in Figure 1 and the area above the curve is the total cortical response in spike per stimulus. For example, suppose that we assume the baseline background is 0.015 (slightly higher than in the figure) and that the activated background is 0.04. Suppose we choose 0.05 as the threshold. Then we find the AW:PW ratio is about 1:2 in the baseline case and about 1:12 in the activate case. This would seem to be in good agreement with MCA's data. However, an important point in his data is the ratio of the PW before and after, which is about 1.36.

The change in the PW responses is rather small compared to the changes in the AW response. For the present example, the ratio is over 3. That is, the PW response is diminished way out of proportion to what it should be. One could argue that with a different kind of nonlinearity, it may be possible to achieve consistent results or that different values of parameters might be able to give better answers. But, one fact makes this very difficult to achieve and would thus require extremely fine tuning of the system. The fact is that the ratios of the peak inputs between AW:PW is always largest at the largest background activities. That is, SD has a proportionally greater effect on the PW response than it does on the AW response.

We now show why this is. We rewrite (1) as:

$$\frac{ds}{dt} = (1 - s)/\tau_d - \gamma f_0 s - \gamma a(t)s$$

Let $A(t)$ be the integral of $a(t)$. Since we are starting from the background level of activity, $s = s_0$ where s_0 is as above. Note that s_0 satisfies,

$$(1 - s_0)/\tau_d - \gamma f_0 s_0.$$

Thus, we will ignore these terms in the above equation so that

$$\frac{ds}{dt} \approx -\gamma a(t)s$$

which we solve yielding

$$s(t) \approx s_0 \exp(-\gamma A(t)).$$

The peak response always occurs during the upstroke of the triangle, so for $t < t_{peak}$, $A(t) = Kt^2/(2t_{peak})$. We thus obtain the net response to the upstroke of the triangle:

$$R(t) = (f_0 + Kt/t_{peak})s_0 e^{-\gamma Kt^2/(2t_{peak})}.$$

We first note that K/t_{peak} appears as a single ratio which we call μ . Using calculus, can find the peak response time, t_R :

$$t_R = \frac{-f_0 + \sqrt{f_0^2 + 4\mu/\gamma}}{2\mu} \sim \sqrt{\frac{t_{peak}}{A\gamma}} - \frac{f_0 t_{peak}}{2A} + \dots,$$

This is valid as long as $t_R < t_{peak}$, that is, roughly, $t_{peak} > 1/(A\gamma)$.

The expression for the peak amplitude is rather unwieldy so we just write the leading order behavior for A/t_{peak} large:

$$R_{peak} \sim s_0 e^{-1/2} \left(\sqrt{\frac{A}{t_{peak}\gamma}} + f_0 + \frac{f_0^2}{4} \sqrt{\frac{\gamma A}{t_{peak}}} + \dots \right).$$

As expected, the faster the triangle or the larger its amplitude, the quicker the peak response is reached and the larger the actual response. The peak varies as the square root of the magnitude, A/t_{peak} .

We can use this expression to see why it is difficult to reproduce MC's results without a cortical network. (Note that MC says in later papers that the field potential he records is due to TC synaptic activation and not intrinsic cortical synaptic activation ???) The main differences between PW and AW activation are that in the PW, the amplitude is larger and the time to peak is smaller than in the AW. Thus, as this simple analysis reveals, the key is the ratio, A/t_{peak} . The ratio of the peaks between AW and PW are approximately:

$$\frac{AW}{PW} = \frac{\sqrt{\gamma\mu_{AW} + f_0}}{\sqrt{\gamma\mu_{PW} + f_0}}$$

This ratio is maximal at the lowest value of f_0 , which implies that at higher values of background activity, the peak input ratio is less than at low values of activity. One way to rectify this and still maintain a purely feedforward theory is to put the response through a nonlinear gain function. Such a function must necessarily be concave up, since a concave down function will only exacerbate the ratio problem.

Let's look at the ratio of the peaks at two different levels of background activation, f_0 (Lo) and f_1 (Hi):

$$\frac{Lo}{Hi} = \left(\frac{1 + \gamma\tau f_1}{1 + \gamma\tau f_0} \right) \left(\frac{\sqrt{\gamma\mu} + f_0}{\sqrt{\gamma\mu} + f_1} \right)$$

This approximation shows that the Lo:Hi ratio will be larger for the larger value of μ , again contradicting the data. That is, for small values of μ corresponding to the adjacent whisker stimulus, this ratio will be smaller than for large values of μ corresponding to the principle whisker stimulus. As above, this could be rectified, perhaps, by putting it through a carefully chosen nonlinearity, however, this would require very careful tuning of the nonlinearity and all of the interactions would have to occur below the inflection point since small differences will have to be drastically amplified.

1.1 Periodic stimuli

One piece of information that comes out of MC's work is the role of background activity on the response to periodic stimuli. In particular, it is possible to calibrate the SD model based on the ratio of the first spike to the steady state at different frequencies. We begin with equation (1) where $f(t)$ is now a periodic function of time. As with the single stimulus, it is possible to write a closed form solution for the solution to (1), but the resulting cumbersome expression gives little insight. Suppose that we reduce the stimulus to an impulse in which the total number of spikes per stimulus cycle is given by A . (Think of A as the area under the PSTH above the background.) Then equation (1) can be formally written as:

$$\frac{ds}{dt} = \frac{1-s}{\tau} - \gamma(f_0 + A\delta_P(t))$$

where δ_P is the periodically applied unit impulse function. At the onset of the periodic stimulus, the magnitude of s is just the background value, $s_0 =$

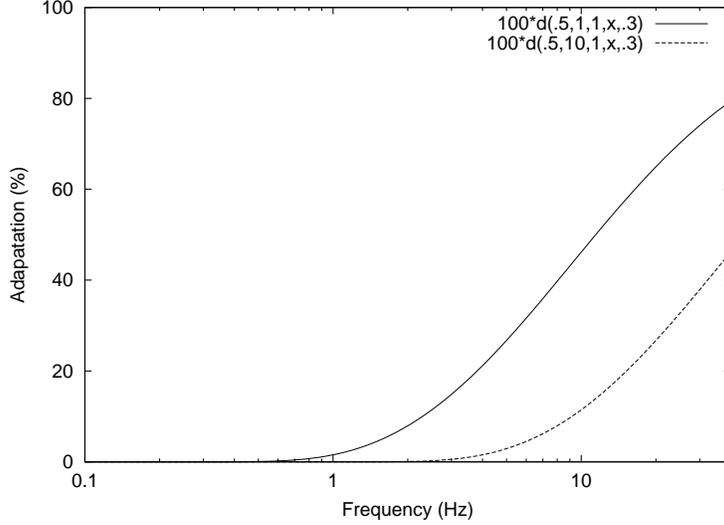


Figure 2: Degree of adaptation for simple SD model as a function of frequency for low and high (10 times higher) background activity. $\tau = 500$ msec. (Parameters in D are $A\gamma = 0.3$ and $f_0\gamma = 1, 10$.)

$1/(1 + f_0\gamma\tau)$. The amplitude at the onset of the n^{th} pulse stimulus given a period, P is easily computed to satisfy:

$$s_{n+1} = s_0 - (s_0 - (1 - \gamma A)s_n)E,$$

where

$$E = e^{-P(1/\tau + f_0\gamma)}.$$

Note that as P gets large, the synapse recovers completely to the background state. The term, $0 \geq (1 - \gamma A) \leq 1$ is fraction of synaptic resource remaining after a spike. The steady state is

$$s_\infty = s_0 \frac{1 - E}{1 - (1 - \gamma A)E}$$

and the ratio of the first to steady state stimulus is

$$\rho = \frac{1 - E}{1 - (1 - \gamma A)E},$$

MCM plots what he calls the degree of adaptation which is just $D = 1 - \rho$. The figure shows a plot of D for a fixed value of τ and at two different levels of activation. (We have made no attempt to rigorously fit this, but rather chose parameters so that it is roughly similar.)

2 Cortical networks & SD

We now turn to a more complex model for the role of SD in thalamo-cortical processing. We explicitly include cortical dynamics in the model