Dynamically Adjustable Contrast Enhancement from Cortical Background Activity

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Abstract

An experimentally supported model of cortical background activity is used to investigate the role of such activity in neural gain control. The model demonstrates the feasibility of a scheme for contrast enhancement where by the overall intensity of an input pattern adjusts the dynamic range of a neuron such that it remains sensitive to contrast over a wide range of overall intensities.

1   Introduction

An important aspect of processing in many neuro-sensory systems is the ability to remain sensitive to contrast within a stimulus over a wide range of overall stimulus intensities. This is required, for example, in the identification of sounds that may be either loud or quiet, or in the identification of visual objects that may either bright or dim. One way to achieve this is through the dynamical control of neural gain. In this process the dynamical range of the neuron is adjusted to suit the overall intensity of the stimulus and thus allow the neuron to respond sensitively to contrast within the stimulus. Recently Chance *et al.* [4] have proposed that background activity in the cortex may act to regulate neural gain. A variety of modelling studies have supported this idea by showing that an increase in model background activity leads to a downwards adjustment in the gain [4, 3]. They show that the adjustment

is the result of the interaction of two key characteristics of cortical background activity that are experimentally well supported [7]: the many-fold increase in neural conductance *in vivo* compared to *in vitro* (where background activity is absent), and the irregularity of neural spiking. The adjustment is regulated by the change in membrane conductance that occurs with changes in the level of background activity (via the synaptic conductances), whereas the irregularity is necessary for the effect, but does not change with level of background activity.

One problem with some previous modelling studies of this mechanism is that they have relied on some *ad hoc* assumption in order to model the background activity, such as exact balance between excitation and inhibition [4, 3]. Meanwhile, other studies have successfully modelled background activity as a self-sustained reverberation of random neural activity [5, 6]. These latter models robustly reproduce values obtained experimentally for five quantities that characterize cortical background activity, namely the mean rate, ν, and coefficient of variation, CV, of neural spiking, the mean, μ, and variance, σ^2, of membrane potential fluctuations and the effective membrane time constant, τ. These studies have shown that assumptions such as exact balance between excitation and inhibition in background activity do not necessarily hold. Consequently the present study investigates whether a modulation of gain will occur with a model of background activity that is experimentally supported. It is shown that the model does produce a form of gain control such that the neurons remain sensitive to contrast within a stimulus over a wide range of overall stimulus intensities.

2 Model and Methods

The model is composed of neurons $j = 1, \ldots, N$, of which N_e are excitatory and N_i are inhibitory. The external input (denoted x) to the network represents the stimulus and is given by a pattern of mean firing rates, $\nu_{\mathrm{x},j}^k = \xi_j^k$, that parameterize independent Possion spike trains impacting on synapses $k = 1, \ldots, C_\mathrm{x}$ of neuron j. In general each different stimulus will have a different pattern of ξ_j^k, while the same stimulus at a different intensity will be represented by the same pattern multiplied by a constant. In addition to external excitatory connections, neurons are sparsely and randomly connected to each other, with each having C_e excitatory and C_i inhibitory recurrent synapses. This recurrent connectivity is responsible for the reverberating background activity.

The neurons are modelled as single-compartment, leaky integrate-and-fire neurons with synaptic conductances. The membrane potential $V(t)$ of a model neuron is the integrated activity of its excitatory and inhibitory synaptic inputs, and it decays in time with a characteristic time constant

$$dV = -\frac{(V - V_\mathrm{p})}{\tau_\mathrm{p}} dt - \sum_{b=\mathrm{x,e,i}} \gamma_b(V - V_b)\, dP_b(t). \tag{1}$$

The first term models the passive leak of the membrane, with resting potential V_p and passive membrane time constant τ_p. The remaining terms represent the synaptic contribution due to network activity from the excitatory $(dP_\mathrm{e}(t))$, inhibitory $(dP_\mathrm{i}(t))$ and excitatory external $(dP_\mathrm{x}(t))$ neurons. The recurrent inputs are determined by the firing times t_j^n of pre-synaptic neurons j, $dP_b(t) = \sum_j \sum_n \delta(t - t_j^n - D_j)$, where $b = \mathrm{e, i}$ and D_j is a transmission delay drawn from a distribution $P_D(D)$. V_e and V_i are the reversal potentials. The parameters γ_e, γ_i and γ_x represent the integrated conductances over the time course of the synaptic event divided by the neural capacitance (and are thus dimensionless). When the membrane potential reaches a threshold V_th, an output spike is generated and the membrane potential is reset to a value $V_\mathrm{r} < V_\mathrm{th}$ after an absolute refractory period τ_r.

Two critical parameters are the overall intensity of the input pattern $I = \langle \nu_{\mathrm{x},j}^k \rangle_{jk}$ (where $\langle . \rangle_{jk}$ denotes the average over all neurons j and all synapses k) and the ratio of recurrent inhibition to recurrent excitation, $r = |C_\mathrm{i}\langle \nu_{\mathrm{i},j} \rangle_j q_\mathrm{i}/C_\mathrm{e}\langle \nu_{\mathrm{e},j} \rangle_j q_\mathrm{e}|$ (where $\nu_{\mathrm{e},j}$ ($\nu_{\mathrm{i},j}$) is the firing rate of excitatory (resp. inhibitory) neuron j, and $q_\mathrm{e} = \gamma_\mathrm{e}(V_\mathrm{e} - \bar{V})$ (resp. q_i) is an estimate of the average charge entering a neuron as the result of a single synaptic event using an average membrane potential of $\bar{V} = (V_\mathrm{th} + V_\mathrm{r})/2$. With $\gamma_\mathrm{e} = \gamma_\mathrm{x} = 0.0032$, then $\gamma_\mathrm{i} = 0.064r$ using the simplifying assumption of equal levels of background activity for excitatory and inhibitory neurons, $\langle \nu_{\mathrm{e},j} \rangle_j = \langle \nu_{\mathrm{i},j} \rangle_j$. The remaining parameters are fixed: $C_\mathrm{e} = C_\mathrm{x} = 4000$, $C_\mathrm{i} = 1000$, $\tau_\mathrm{p} = 22$ ms, $\tau_\mathrm{r} = 2$ ms, D is chosen from the uniform distribution between 0 and 3 ms, $V_\mathrm{p} = -80$ mV, $V_\mathrm{r} = -70$ mV and $V_\mathrm{th} = -55$ mV, $V_\mathrm{e} = 0$ mV and $V_\mathrm{i} = -75$ mV in accord with experimental observations.

The gain,

$$g = \frac{d\nu}{d\nu_\mathrm{d}}, \tag{2}$$

defined as the marginal change in output firing rate, ν, with a marginal change in input driving rate, ν_d, is studied as a function of intensity, I. The output firing rate ν_j of neuron j may be calculated under the assumptions that each neuron receives

many small inputs per integration time ($\gamma_b \ll |(V_{\text{th}} - V_{\text{r}})/(\bar{V} - V_b)|$, $b = \text{e}, \text{i}, \text{x}$) and the network has sparse but numerous connectivity ($1 \ll [C_{\text{e}}, C_{\text{i}}] \ll N$). A Fokker-Planck formalism then leads to the Siegert formula which is a good approximation for the mean firing rates [1, 6].

$$\nu_j = \left(\tau_{\text{r}} + \tau_j \sqrt{\pi} \int_{y_{\text{r},j}}^{y_{\text{th},j}} e^{u^2}(1 + \text{erf}(u))du\right)^{-1} \tag{3}$$

where erf(.) is the error function, $y_{\text{th},j} = (V_{\text{th}} - \tilde{\mu}_j)/\sqrt{2}\tilde{\sigma}_j$, (similarly $y_{\text{r},j}$) and τ_j, $\tilde{\mu}_j$ and $\tilde{\sigma}_j^2$ [1] are approximated by [2]

$$\frac{1}{\tau_j(t)} = \frac{1}{\tau_p} + \sum_{b=\text{x},\text{e},\text{i}} C_b \gamma_b \bar{\nu}_{b,j}(t) \tag{4}$$

$$\tilde{\mu}_j(t) = \tau_j(t)\left(\frac{V_0}{\tau_p} + \sum_{b=\text{x},\text{e},\text{i}} C_b \gamma_b V_b \bar{\nu}_{b,j}(t)\right) \tag{5}$$

$$\tilde{\sigma}_j^2(t) = \frac{\tau_j(t)}{2} \sum_{b=\text{x},\text{e},\text{i}} C_b \gamma_b^2 (V_b - \tilde{\mu}_j(t))^2 \bar{\nu}_{b,j}(t), \tag{6}$$

with $\bar{\nu}_{\text{e},j}(t) = \bar{\nu}_{\text{i},j}(t) = \langle \int \nu_l(t - D)P_D(D)\,dD \rangle_l = \nu_0$ independent of j and $\bar{\nu}_{\text{x},j}(t) = \langle \nu_{\text{x},j}^k \rangle_k$ independent of time. By averaging over all neurons j, Eq.(3) becomes a self-consistent equation for the mean background activity ν_0 once it is substituted with Eqs.(4)-(6). Equations for the other four quantities characterizing background activity ($\text{CV}_0, \tau_0, \mu_0, \sigma_0$) can be found in [6]. The output firing rates of each neuron, j, may be calculated from Eq.(3). A linear stability analysis may be performed on the Fokker-Planck equation by expanding about the stationary state to ensure the stability of the stationary mean-field solution to Eq. (3)[6].

3 Results

In a previous study [6] it was shown that the model reproduces the characteristics of cortical background activity (ν_0, CV_0, μ_0, σ_0 and τ_0) provided I is greater than some small critical value I_c (below which the network becomes quiescent) and provided r is greater than 1 (below which recurrent excitation dominates inhibition leading to excitatory run away). These results are summarized in Fig.1 for the simplest case in which the external input $\nu_{\text{x},j}^k = \{1, 2, 4, 8\} \times \nu_{\text{th}}$ is the same for all neurons and synapses (ν_{th} is the level of constant external input required to just bring the neuron to threshold). Figs.1B-F show the predicted values of the five characteristics of background activity as a function of r for four different levels of

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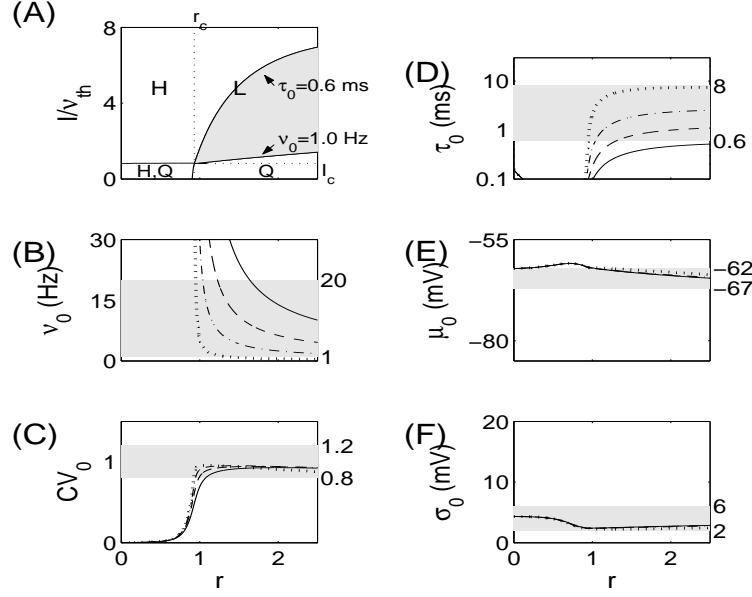[1] The tilde denotes the 'free' membrane potential that is unrestricted by the threshold.

Figure 1: Model predictions for the five quantities characterizing cortical background activity, ν_0 (B), CV_0 (C), τ_0 (D), μ_0 (E) and σ_0 (F), as a function of r for $I = \{1, 2, 4, 8\} \times \nu_{\mathrm{th}}$ (corresponding to dotted, dot-dashed, dashed and solid line resp.). Experimentally observed ranges are shown in gray shade. The region of the (r, I)-plane for which model predictions agree with experimental ranges for all five quantities is shown in gray shade in (A) along with the regions corresponding to low rate, irregular firing (L), high rate, regular firing (H) and the quiescent state (Q).

$I = \{1, 2, 4, 8\} \times \nu_{\mathrm{th}}$, together with the range of values observed experimentally [7] (gray-shade). The region of the (r, I)-plane for which all five characteristics are within experimentally observed ranges is shown in gray-shade in Fig.1A. It shows that there is a large region of parameter space (as described above) for which the model agrees with experimental data. An important aspect to note is that the level of background activity, ν_0, increases with the overall intensity, I, and that this is primarily mediated by a change in the effective membrane time constant τ_0, rather than the mean or the standard deviation of the membrane potential, μ_0 or σ_0.

The effect of model background activity on neural gain was studied using the four levels of background activity shown in Fig.1, corresponding to the input pattern intensities $I = \{1, 2, 4, 8\} \times \nu_{\mathrm{th}}$. To investigate the gain, a driving input was intro-
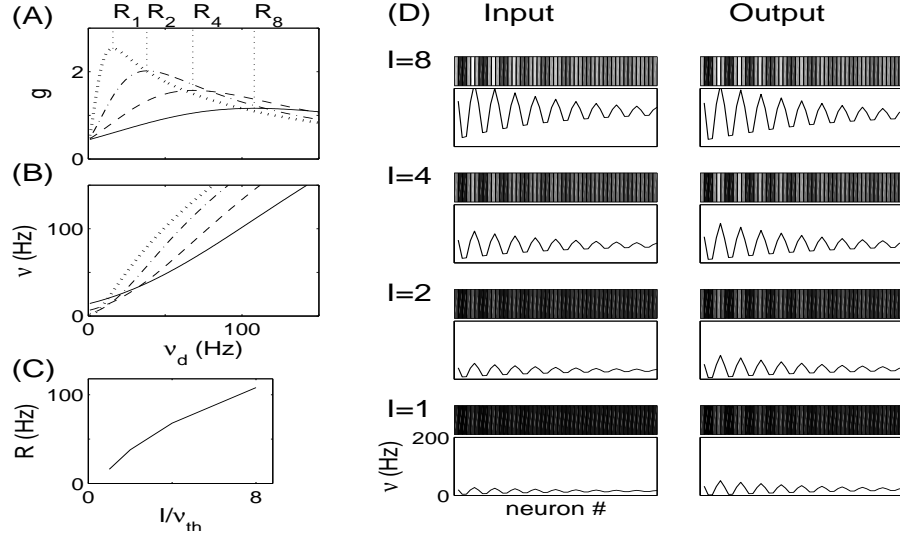
Figure 2: The gain (A) and output firing rate (B) as a function of the driving rate for $I = \{1, 2, 4, 8\} \times \nu_{\text{th}}$ (key as for Fig.1). (C) The dynamic range, R, as a function of intensity I. (D) Exponentially decaying sinusoidal contrast gratings before (left) and after (right) neural processing as a function mean intensity $I = \{1, 2, 4, 8\} \times \nu_{\text{th}}$ (rows 1-4)

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duced into just one neuron in the network, so that 200 of its synapses received an external driving input with mean rate ν_{d} (instead of $\nu_{\text{x}} = I$) while the remaining synapses received the same mean rates of external or recurrent inputs as the other neurons in the network. Since this one neuron contributes insignificantly to the level of background activity, this allows the drive to the neuron and the background activity to be varied independently though ν_{d} and ν_{x}, respectively. The results of this manipulation are shown in Fig.2 for a ratio of inhibition to recurrent excitation of $r = 2$, corresponding to a choice that is well within the range that is consistent with experimental data on background activity (see Fig.1). This value gives results that are typical of values in this range. Fig.2B shows the driven output rates as a function of driving input rates for the four levels of intensity, and Fig.2A shows the corresponding gain. For the lowest level of diving input ($\nu_{\text{d}} \approx 0$ Hz) the gain is nearly independent of the level of background activity and so there is no gain modulation. However, as the driving input rate increases so does the gain in a way that is strongly dependent on the overall intensity, I. This modulation of the gain is mediated by the level of background activity, which is directly set by the overall

intensity (see Fig.1B). The gain peaks at a value of ν_d that is also dependent on I, after which is declines to an asymptotic value that is independent of I.

There are three noteworthy aspects of this gain modulation that are consistent with it acting as a form of dynamically adjustable contrast enhancement. To see this, consider now a more general situation in which the stimulus varies across some parameter-dimension (such as space) and this is represented by a range of values of ν_d across the input fibres. Specifically consider a sparse representation in which a relatively small number, N_d, of neurons receive a driving input that may vary from neuron to neuron but (for simplicity) not synapse to synapse, $\nu_{\mathrm{d},j}^k = \xi_j$ for $k = 1, \ldots, 200$, and also receive a lower background level $\nu_{\mathrm{x},j}^k = \nu_\mathrm{th}$ for $k = 201, \ldots, C_\mathrm{x}$ on the remaining synapses. The other N_b neurons receive the background rate $\nu_{\mathrm{x},j}^k = \nu_\mathrm{th}$ on all their synapses. It is supposed that changes in the intensity of the stimulus by a factor α result in a multiplicative change, $\alpha\nu_{\mathrm{x},j}^k$ in the external input for all neurons and synapses. In the context of this scenario, the first thing to notice in Fig.2A is that strong features of the stimulus (i.e., relatively large values of ξ_j) will be amplified relative to weak features of the stimulus, so long as the value of ξ_j lies in the dynamic range, R, of the neuron, defined here as the monotone increasing portion of the gain curve. The result of this processing is an enhancement of contrast. The second noteworthy aspect of Fig.2A is that the dynamic range scales with the overall intensity in an approximately linear way, as illustrated in Fig.2C. This means that the dynamic range of the neuron will be tuned in proportion to I so as to cover the range of values of $\nu_\mathrm{d} = \alpha\xi_j$ expected from a stimulus with intensity I. The neurons thus remain sensitive to contrast over a range of intensities. The final point to note from Fig.2A is that the maximal gain is greatest for the lowest intensity input patterns. This means that an input pattern that is presented at low intensity will have its peak features amplified more than if it was presented at high intensity. This could increase the perceptibility of the features of weak stimuli. As a concrete illustration of this dynamic contrast enhancement, Fig.2D illustrates the output of the driven neurons in the network when the driving input, ξ_j, is an exponentially modulated sinusoidal grating. The input rate $\nu_{\mathrm{d},j}$ is shown in the left column and the output rate ν_j is shown in the right column, in graphical and in gray-scale formats. The contrast enhancement is evident, particularly for weak input patterns, as expected from the above discussion.

4 Conclusions

Using a model of cortical background activity that is supported by experimental evidence, we have confirmed that such activity alters the integrative properties of neurons in such a way as to leads to a form of gain modulation whereby neurons remain sensitive to contrast within an input pattern over at least an order of magnitude in input pattern intensity.

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