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Oscillatory response in a sensory network of ON and OFF cells with instantaneous and delayed recurrent connections

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A neural field model with multiple cell-to-cell feedback connections is investigated. Our model incorporates populations of ON and OFF cells, receiving sensory inputs with direct and inverted polarity, respectively. Oscillatory responses to spatially localized stimuli are found to occur via Andronov–Hopf bifurcations of stationary activity. We explore the impact of multiple delayed feedback components as well as additional excitatory and/or inhibitory non-delayed recurrent signals on the instability threshold. Paradoxically, instantaneous excitatory recurrent terms are found to enhance network responsiveness by reducing the oscillatory response threshold, allowing smaller inputs to trigger oscillatory activity. Instantaneous inhibitory components do the opposite. The frequency of these response oscillations is further shaped by the polarity of the non-delayed terms.

Keywords: neural field; delayed feedback; sensory inputs; oscillations; ON and OFF cells

1. Introduction

Rhythmic activity in the brain is commonly associated with the processing of neural information. Such oscillatory patterns are ubiquitous in many areas of the cortex, where they take part in higher brain functions and memory, displaying a vast range of frequencies. They are found in the thalamus, the thalamo-cortical system and in many sensory pathways such as vision (Gray & Singer 1989; Engel *et al.* 1992; Lumer *et al.* 1997), electroreception (Doiron *et al.* 2004) and auditory processing (Galazyuk & Feng 2001). Oscillatory behaviour in sensory systems has been proposed to be one of the basic mechanisms of input selection and detection, where oscillatory activity is triggered on the basis of stimulus properties. Specifically, oscillatory response has been observed in various sensory networks under spatially non-homogeneous stimulation. Excitatory populations are known to enter states of rhythmic activity when the input shows sufficient spatial contiguity ('binding stimulus'; Engel *et al.* 1992; Wang 1999; Marinazzo *et al.* 2007; Borgers *et al.* 2008), or is noisy but shows sufficient spatial correlation (Doiron *et al.* 2004).

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One contribution of 13 to a Theme Issue 'Delayed complex systems'.

Aside from sensory stimuli structure, specific circuit geometry plays a crucial role in the presence of rhythmic activity. Network oscillations in sensory systems typically refer to synchronous states achieved by the means of Andronov–Hopf-type instabilities commonly observed in inhibitory networks (Campbell *et al.* 1995; Dhamala *et al.* 2004; Roxin *et al.* 2005). However, the effect of multiple recurrent connections blurs the notion of what causes oscillatory behaviour, as the combined actions of local and global signals are poorly understood. Models in electroreception commonly incorporate global, i.e. all-to-all, recurrent connections. In vision, models introduce an elaborate mixture of global and local recurrent circuitry to mimic sensory information processes and exhibit oscillatory activity, a feature which can be amplified by feedback connections (Lumer *et al.* 1997). Generically, sensory pathways incorporate sets of recurrent connections with distinct polarities, i.e. either excitatory or inhibitory, where these are associated with excitatory and inhibitory synaptic connections, respectively (Wilson & Cowan 1972; Golomb & Ermentrout 2001; Blomquist *et al.* 2005; Laing & Coombes 2006). For example, Laing & Longtin (2003) studied oscillation thresholds for paired excitatory and inhibitory delayed feedback, where delays were either fixed or distributed. Further, Hahnloser *et al.* (1999) suggested that combined positive and negative feedback may describe attention modulation in cortical networks.

Most sensory systems exhibiting oscillatory activity also involve ON and OFF cells (Kandel & Schwarz 1983; Robin & Royer 1987; Fields *et al.* 1995). While the connection between rhythms and sensory inputs has been partially established, there is currently no consideration of the distinct ON and OFF cells' behaviours in the treatment of sensory information and the genesis of temporal activity oscillations. We now question how these populations might behave in a feedback system under stimulation: can oscillations still be observed? Does the system have the same oscillation threshold?

In our previous work (Lefebvre *et al.* 2009), precise conditions on which oscillatory input responses are seen in a general ON/OFF system with a unique global inhibitory delayed feedback were established, along with a study of network responses to periodic forcing as well as the gain of the system in the equilibrium regime. Here, we want to investigate the more generic case of a mixture of local and global recurrent connections, and investigate how this change in the network architecture influences the genesis of oscillatory activity. Our aim is to understand generic properties beyond those studied for the standardly studied equivalent ON cell system, where local circuitry reinforces global oscillations (Wang 1999) or vice versa (Lumer *et al.* 1997). To do so, we will first present our model in §2, and review in §3 the conditions on which oscillatory instabilities occur in a model with delayed inhibitory feedback components and how the interplay between ON and OFF populations input responses results in oscillatory activity. In §4, we introduce a mixture of instantaneous and delayed recurrent connections and demonstrate how the mixed feedback profile alters the instability threshold and the response frequency to spatially localized pulses.

2. Model

Our analysis is particularly motivated by electroreception, but also applies to other senses. The architecture considered in figure 1 is inspired by the physiology of the electrosensory lateral lobe (ELL) found in the brains of the weakly electric
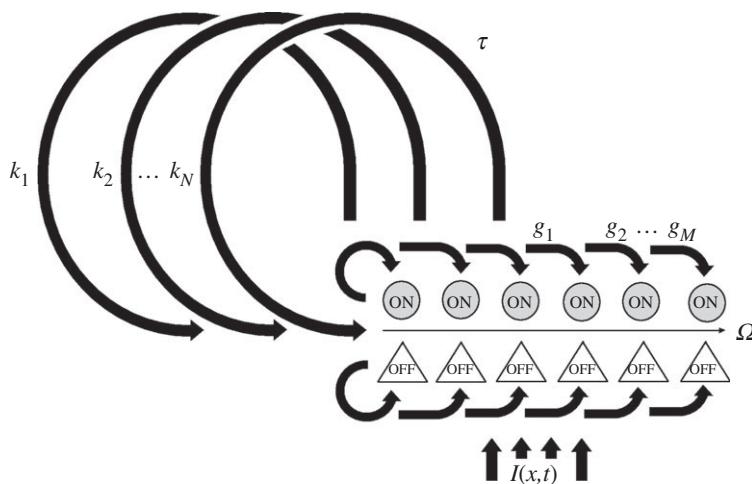
Figure 1. Schematic of the multi-loop feedback circuit. The system consists of a layer of ON and OFF pyramidal cells. These integrate spatio-temporal inputs $I(x,t)$ and project their output activity to higher brain centres, which process and feedback the signal via multiple feedback loops, after some time delay τ and with polarity k_i. Instantaneous, i.e. non-delayed, feedback loops mimic local connectivity with polarities g_j.

fish *Apteronotus leptorhynchus*, acting as the primary operator in stimuli encoding (for an exhaustive physiological discussion see Berman & Maler (1999)). The sensory layer is populated by ON and OFF pyramidal cells that feed-forward their activity vertically to higher brain centres; these in turn integrate ON and OFF activity and feed it back to the sensory layer via delayed interactions of different polarities. Here, these higher brain centres do not contribute to spatial encoding, but merely act as activity accumulators. This fact distinguishes our approach from typical neural field models that usually exhibit spatial connectivity profiles (Pinto & Ermentrout 2001; Bressloff *et al.* 2003; Hutt *et al.* 2003; Coombes & Owen 2004, 2005; Folias & Bressloff 2005; Hutt & Atay 2005). Non-delayed recurrent connections are nevertheless added to mimic local anatomy, connections which are weak in the ELL of the electric fish. As there are very few lateral connections between units in the sensory layer in electrosensory systems, these connections are typically neglected, the dynamics of the system being described using delayed feedback components.

As in many sensory pathways, spatio-temporal inputs are processed through the interplay of ON and OFF neural populations. The distinct input response mechanism between these cell types is mainly because of the presence of extra preprocessing within the OFF pathway, where an intermediate cellular body called an *interneuron* transfers an inverted image of received inputs to the OFF cells, while ON cells receive the input directly, with preserved polarity. Thus, when the input stimulus increases, ON cell activity increases while that of OFF cells decreases. Given the synaptic response functions η_{on} and η_{off} and some applied pre-synaptic input $I(x,t)$, the post-synaptic potentials PSP_j for $j = \mathrm{ON}, \mathrm{OFF}$ at the sensory layer are given by

$$\mathrm{PSP}_{\mathrm{on}}(x,t) = \eta_{\mathrm{on}} * I(x,t)$$

and

$$\text{PSP}_{\text{off}}(x, t) = \eta_{\text{off}} * \mathcal{I}[I(x, t)],$$

where $*$ is a temporal convolution and $\mathcal{I}$ stands for the interneuronal process. We make the hypothesis that the operator $\mathcal{I}$ is linear to first order such that it may be approximated by $\mathcal{I}(u) \approx -u$. Thus, for simplicity, we consider the situation where, without sensory inputs $I(x, t) = 0$ and in open loop, stationary activity states correspond to both dormant ON and OFF populations $\bar{u}_{\text{on}} = \bar{u}_{\text{off}} \approx 0$.

The system is composed of N distinct feedback loops where the delay $\tau > 0$ accounts for processing and axonal conduction times and is assumed to be identical for all delayed circuits. The mean somatic membrane potentials, or *activities*, $u_{\text{on}}(x, t)$ and $u_{\text{off}}(x, t)$, at the sensory layer obey the following dynamics:

$$\left.\begin{array}{l} (1 + a_{\text{on}}^{-1}\partial_t)u_{\text{on}}(x, t) = \displaystyle\sum_{i=1}^{N} k_i S(u_{\text{on}}, u_{\text{off}}, t - \tau) + \sum_{j=1}^{M} g_j S(u_{\text{on}}, u_{\text{off}}, t) + I(x, t) \\[4mm] \text{and } (1 + a_{\text{off}}^{-1}\partial_t)u_{\text{off}}(x, t) = \displaystyle\sum_{i=1}^{N} k_i S(u_{\text{on}}, u_{\text{off}}, t - \tau) + \sum_{j=1}^{M} g_j S(u_{\text{on}}, u_{\text{off}}, t) - I(x, t), \end{array}\right\} \tag{2.1}$$

where we chose exponential synapses, i.e. $\eta_p(s) = a_p e^{-a_p s}$, $p = \text{ON, OFF}$. We use k for delayed feedback strengh, and g for non-delayed or instantaneous feedback strength. Polarities of the recurrent connections are individually weighed by $k_i, g_j > 0$ for excitatory and $k_i, g_j < 0$ for inhibitory feedback, where $i = [1, N]$ and $j = [1, M]$. A spatio-temporal stimulus $I(x, t)$ with arbitrary polarity (either excitatory or inhibitory) is presented with inverted polarity to the OFF layer, while ON cells receive the input directly. The recurrent term

$$S(u_{\text{on}}, u_{\text{off}}, t) = \int_{\Omega} \mathrm{d}y[\alpha_{\text{on}} f_{\text{on}}(u_{\text{on}}(y, t)) + \alpha_{\text{off}} f_{\text{off}}(u_{\text{off}}(y, t))] \tag{2.2}$$

corresponds to global, i.e. all-to-all, coupling, for which $f_j(u) \equiv (1 + e^{-\beta(u-h_j)})^{-1}$ $(j = \text{ON,OFF})$ is a smooth sigmoidal firing rate function with threshold h_j and gain β. The finite spatial domain is Ω, while α_j is the relative proportion of j-type cells in the population. ON and OFF populations project evenly to all cells in the system via the multiple feedback connections, irrespective of their polarity, which might be either excitatory or inhibitory, or both.

3. Oscillatory activity and stimulation

Let us first consider the non-stimulated case, i.e. $I(x, t) = 0$, and the regions in parameter space where global oscillations may be found. We will neglect all non-delayed recurrent signals, i.e. $g_j = 0$, $\forall j$, and describe the evolution of activity in the context of multiple delayed loops. Oscillatory activity is typically characterized by determining Andronov–Hopf instability thresholds.
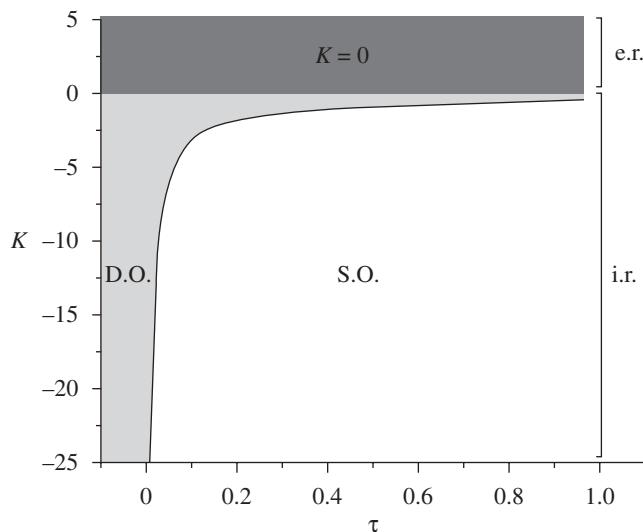
Figure 2. Andronov–Hopf curve in (K, τ) parameter space. The horizontal line $K = 0$ separates the parameter space between excitatory and inhibitory regimes. The bifurcation curve delimits regions of damped oscillations and regions where global oscillations are stable. As the number of inhibitory delayed components increases (K decreases), smaller delays are needed to stabilize oscillatory solutions, reducing the instability threshold.

The solutions $\bar{u}_{\mathrm{on}}$ and $\bar{u}_{\mathrm{off}}$ of equation (2.1) for $g_j = 0$ are spatially uniform and can be implicitly written as

$$\left.\begin{aligned} \bar{u}_{\mathrm{on}} &= K\frac{\Omega}{2}[f(\bar{u}_{\mathrm{on}}) + f(\bar{u}_{\mathrm{off}})] \\ \bar{u}_{\mathrm{off}} &= K\frac{\Omega}{2}[f(\bar{u}_{\mathrm{on}}) + f(\bar{u}_{\mathrm{off}})], \end{aligned}\right\} \tag{3.1}$$

and

where $K \equiv \sum_{i=1}^{N} k_i$. For simplicity, we chose $\alpha_{\mathrm{on}} = \alpha_{\mathrm{off}} = 1/2$, $a_{\mathrm{on}} = a_{\mathrm{off}} = 1$ and $h_{\mathrm{on}} = h_{\mathrm{off}} \equiv h$. We further fixed the response gain $\beta = 25$, so that the firing rate function f is smooth.

Since all the delays in equation (2.1) are identical, the multiple feedback components of figure 1 are analogous to the single delayed connection case with gain K. In figure 2, whenever $K > 0$, no oscillatory solutions are possible, as excitatory connections dominate the dynamics and bring the system to a regime of multistability. However, if $K < 0$, linearizing the system around equation (3.1) indicates that a supercritical Andronov–Hopf bifurcation occurs for smaller values of the delay as K decreases, meaning that a dominant number of inhibitory components versus excitatory components first makes oscillatory activity possible, and further encourages the stability of global oscillations by decreasing the magnitude of the critical delay. Consequently, additional delayed feedback components with identical delays but different polarities do not alter the dynamics qualitatively, if the condition $K < 0$ is fulfilled.

The stimulated case, i.e. $I(x, t) \neq 0$, can be analysed in a similar fashion, to determine the effect of distributed input on the genesis of rhythmic activity. We will assume from now on that a single inhibitory delayed connection is

present, weighed at $K = k_1 = -1$, which we now know is analogous to the case of several delayed feedback connections dominated by inhibition, treated previously. A spatially distributed stimulus of the form $I(x, t) = I(x)$ induces a non-homogeneous solution, determined from equation (2.1) by

$$\left.\begin{array}{l} \bar{u}_{\mathrm{on}}(x) = S(\bar{u}_{\mathrm{on}}, \bar{u}_{\mathrm{off}}) + I(x) \\ \bar{u}_{\mathrm{off}}(x) = \bar{u}_{\mathrm{on}}(x) - 2I(x). \end{array}\right\} \tag{3.2}$$

and

Oscillatory response corresponds to an input-triggered supercritical Andronov–Hopf bifurcation. We can isolate the instability and specify the input response threshold by linearizing equation (2.1) around equation (3.2) for $\bar{u}_{\mathrm{on,off}}(x, t) = \bar{u}_{\mathrm{on,off}}(x) + u_\lambda(x)e^{\lambda t}$, $\lambda \in \mathbb{C}$. This particular choice of ansatz restricts our stability analysis to spatially homogeneous modes. We obtain the characteristic equation

$$\lambda + 1 + Re^{\lambda\tau} = 0. \tag{3.3}$$

An input is expected to cause an Andronov–Hopf bifurcation if $Re(\lambda) = 0$ for $\lambda = a + iw$, $w \neq 0$, which occurs whenever the parameter R satisfies

$$\tan(\omega(R)\tau) + \omega(R) = 0, \tag{3.4}$$

where $\omega(R) = \sqrt{R^2 - 1}$ is the frequency at the bifurcation. The parameter R is defined by

$$R = \left[\alpha_{\mathrm{on}} \int_\Omega \mathrm{d}y f'(\bar{u}_{\mathrm{on}}(y)) + \alpha_{\mathrm{off}} \int_\Omega \mathrm{d}y f'(\bar{u}_{\mathrm{off}}(y))\right]. \tag{3.5}$$

The parameter R arises from linear stability considerations, and is an integral over the solutions $\bar{u}_{\mathrm{on}}(x)$ and $\bar{u}_{\mathrm{off}}(x)$, measuring how close these are to the feedback activation threshold h. Spatially distributed inputs $I(x, t)$ are expected to bring the solutions either closer to or away from h, subsequently changing the value of R and triggering oscillatory solutions via Andronov–Hopf instabilities whenever $R = R_c$, where R_c satisfies equation (3.4). As opposed to the non-stimulated case where an increase in the delay τ caused the oscillations for $K < 0$, spatially profiled stimulation alone triggered oscillatory activity by balancing local excitation and recurrent inhibition at some critical feedback amplitude, specified by h, which will be fixed throughout the analysis. Lefebvre et al. (2009) studied the exact dynamical impact of a modification of h.

For concreteness, we numerically test these results with a pulse stimulus defined by $I(x, t) = I_o$ for $x \in \Delta = [x_1, x_2]$ and $t_o < t < t_1$ while $I(x, t) = 0$ otherwise. The width of the pulse is defined by $\Delta = |x_1 - x_2|$. This input distribution is ideal for separating local and global dynamics and identifying feedback effects, and is coherent with many stimulation patterns studied experimentally in spatially extended systems. From figure 3, stationary uniform activity states $\bar{u}_{\mathrm{on}}$ and $\bar{u}_{\mathrm{off}}$ are stable on the basis of well-chosen parameters until $t = t_o$. The equilibrium (3.2) becomes unstable for the duration of the pulse and recovers stability at the offset of stimulation, delimiting the oscillatory response time of the combined ON and OFF population. Figure 4 illustrates the condition equation (3.4) fulfilled at the onset of the stimulus $t = t_o$ and again at the offset $t = t_1$ for $R_c \approx 1.823$ and $\tau = 2$, where the eigenvalues cross back and forth the imaginary axis.
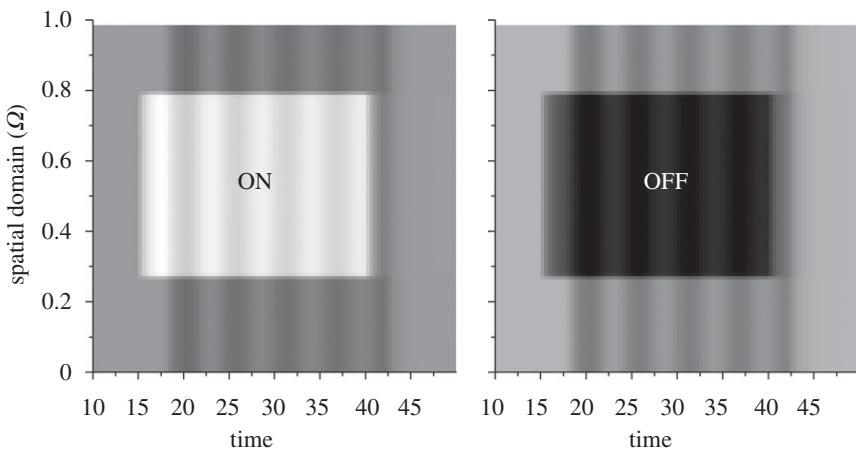
Figure 3. ON/OFF network oscillatory response to a localized pulse. Parameters are $\tau = 2$, $\Omega = 1$ and $h = 0.25$. The input has the amplitude $I_o = 0.4$ between $x_1 = 0.25$ and $x_2 = 0.75$, and 0 otherwise for $15 < t < 40$.
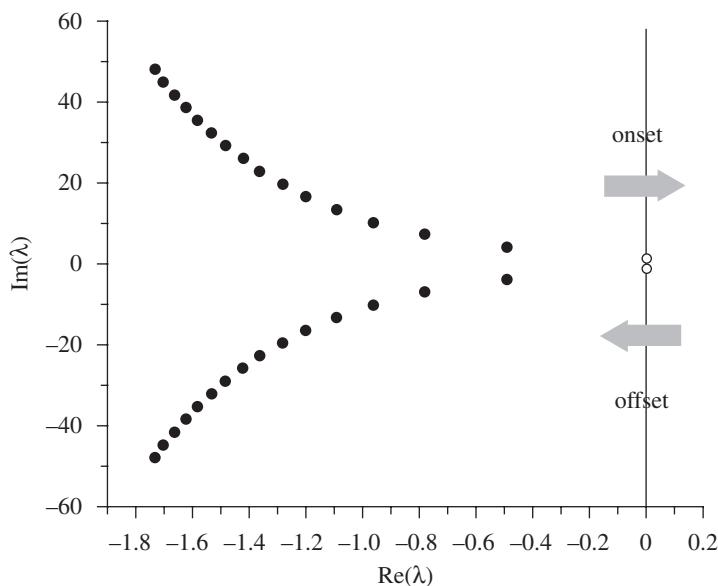

Figure 4. Eigenvalues crossing the imaginary axis as the critical parameter R_c is met. At the onset of the pulse stimulus, the Andronov–Hopf curve (3.4) is crossed for the chosen delay $\tau = 2$, where the parameters are such that the solutions enter a regime of stable oscillations. Unstable eigenvalues cross the imaginary axis accordingly. At the offset of the bump, the opposite process takes place and the stationary activity states recover their stability and the oscillations disappear at the same time as the stimulus.

This behaviour is coherent with many findings on recurrent neural networks, where a spatially localized pulse generates global oscillations when the input width is sufficiently large (Borgers *et al.* 2008), even though no delay is present. Further findings also seem to agree for stochastic integrate-and-fire models with

delayed feedback, where the input spatial correlation must meet a critical value to trigger an oscillatory response (Doiron *et al.* 2004), or require the use of dynamic synapses to establish the required level of non-linearity (Marinazzo *et al.* 2007). Our results incorporate distinct ON/OFF population responses, and indicate that oscillatory activity as a response mechanism is possible even when individual cell responses to external inputs are not purely excitatory. The dynamic distinctiveness and sensitivity of ON/OFF networks when compared with the purely excitatory case, i.e. ON/ON networks, are studied elsewhere (Lefebvre *et al.* 2009).

4. Instantaneous and delayed feedback dynamics

Although delayed feedback connections have been studied extensively (Campbell *et al.* 1995; Chacron *et al.* 2003; Meyer *et al.* 2008 and references therein), little is known about *mixed* feedback profiles, where non-delayed ('local') and delayed ('global') recurrent terms are combined. This set-up is further complicated by the presence of distinct ON and OFF populations. This raises an important question as to how robust are the dynamics seen in a delayed feedback system when additional recurrent terms are considered. *Non-delayed* or *instantaneous recurrent* components account for local signals, mimicking local spatial connectivity and lateral activity propagation. Eventually, we would like to understand the role of spatial connectivity profiles (which greatly complicates the analysis), but this knowledge will build on the simpler all-to-all instantaneous plus delayed coupling studied here.

Of particular interest is how delayed and non-delayed components combine and alter the oscillatory activity threshold. For simplicity, we set $M = 1$ and look at the case where a single non-delayed recurrent component of polarity g is present. Equation (2.1) becomes

$$\left.\begin{aligned} (1 + a_{\mathrm{on}}^{-1}\partial_t)u_{\mathrm{on}}(x,t) &= -S(u_{\mathrm{on}}, u_{\mathrm{off}}, t - \tau) + gS(u_{\mathrm{on}}, u_{\mathrm{off}}, t) + I(x,t) \\ \text{and} \quad (1 + a_{\mathrm{off}}^{-1}\partial_t)u_{\mathrm{off}}(x,t) &= -S(u_{\mathrm{on}}, u_{\mathrm{off}}, t - \tau) + gS(u_{\mathrm{on}}, u_{\mathrm{off}}, t) - I(x,t), \end{aligned}\right\} \quad (4.1)$$

where we set $\alpha_{\mathrm{on}} = \alpha_{\mathrm{off}} = 1/2$, $a_{\mathrm{on}} = a_{\mathrm{off}} = 1$, $h_{\mathrm{on}} = h_{\mathrm{off}} \equiv h$ and $\beta = 25$. Note, the first terms on the right-hand side are delayed, while the second ones are not. As before, we assumed here that we have a predominantly inhibitory feedback loop, weighted by $K = k = -1$. Fixed points of equation (4.1) are now given by

$$\left.\begin{aligned} \bar{u}_{\mathrm{on}}(x) &= (g - 1)S(\bar{u}_{\mathrm{on}}, \bar{u}_{\mathrm{off}}) + I(x) \\ \text{and} \quad \bar{u}_{\mathrm{off}}(x) &= \bar{u}_{\mathrm{on}}(x) - 2I(x); \end{aligned}\right\} \quad (4.2)$$

similarly, for the purely delayed case above, linearizing the system around equation (4.2) for the ansatz $\bar{u}_{\mathrm{on,off}}(x,t) = \bar{u}_{\mathrm{on,off}}(x) + u_\lambda(x)e^{\lambda t}$, $\lambda \in \mathbb{C}$, yields a perturbed version of the previous eigenvalue problem
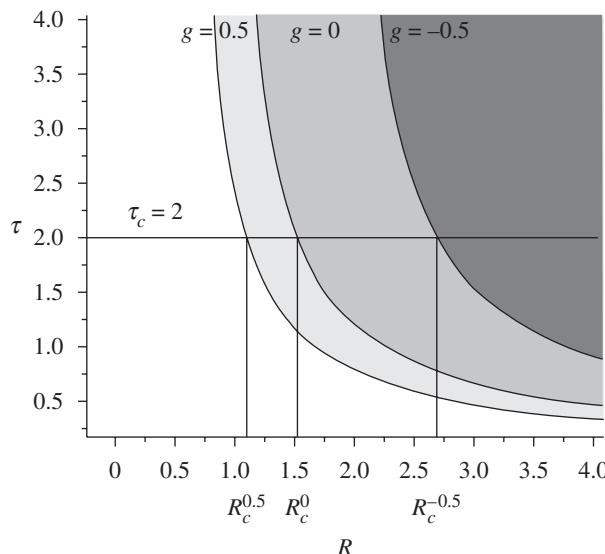
$$\lambda + 1 + Re^{\lambda\tau} - gR = 0, \quad (4.3)$$

Figure 5. Andronov–Hopf curve (4.4) for $g = 0.5$, 0 and -0.5. Shaded regions correspond to parameter sets where oscillatory solutions are stable. These regions are delimited by Andronov–Hopf curves as in equation (4.4) for different values of g. The instability thresholds for $\tau = 2$ are such that $R_c^{0.5} < R_c^0 < R_c^{-0.5}$, indicating that the additional non-delayed excitatory component ($g = 0.5$) increases the 'oscillatory' sensitivity of the system, promoting oscillatory responses to pulse inputs.

where R is given in equation (3.5). The instantaneous recurrent term is expected to shift the spectrum, according to the magnitude of g. Oscillatory solutions are stable in parameter space in a region delimited by the curve

$$w(R)(-\cos(w(R)\tau) + g) = \sin(w(R)\tau), \qquad (4.4)$$

where the frequency is now given by $w(R, g) = \sqrt{(R^2 - 1 + 2Rg - R^2 g^2)}$.

The parameter R can be treated as a function of the instantaneous recurrent strength, i.e. $R = R(g)$, so that we may identify the oscillatory response threshold by solving equation (4.4) for $R_c(g) \equiv R_c^g$. Surprisingly, the response threshold is found to be inversely proportional to g, indicating that increasingly excitatory non-delayed components decrease the value of the threshold R_c^g and facilitate the genesis of oscillation. Figure 5 shows this by comparing the values of $R_c^{-0.5}$, $R_c^{0.5}$ and R_c^0, the last value corresponding to the purely delayed case, i.e. without any instantaneous recurrent term. Excitatory non-delayed interactions ($g = 0.5$) reduce the oscillatory response threshold, so that $R_c^{0.5} < R_c^0$. The opposite occurs for inhibitory non-delayed interactions ($g = -0.5$), where $R_c^{-0.5} > R_c^0$. This implies that minimal input distribution requirements are relaxed when $g > 0$, increasing the system sensitivity to pulse inputs that cause oscillations. In the case of a localized pulse (figure 6), the minimal pulse spatial width $\Delta = |x_1 - x_2|$ causing oscillations is significantly smaller, while the interval of amplitudes I_o generating oscillations is greatly enlarged. We also note the characteristic symmetry between excitatory ($I_o > 0$) and inhibitory inputs ($I_o < 0$), owing to combined ON and OFF responses, indicating that evenly distributed inputs of opposed polarity will generate the same network response.
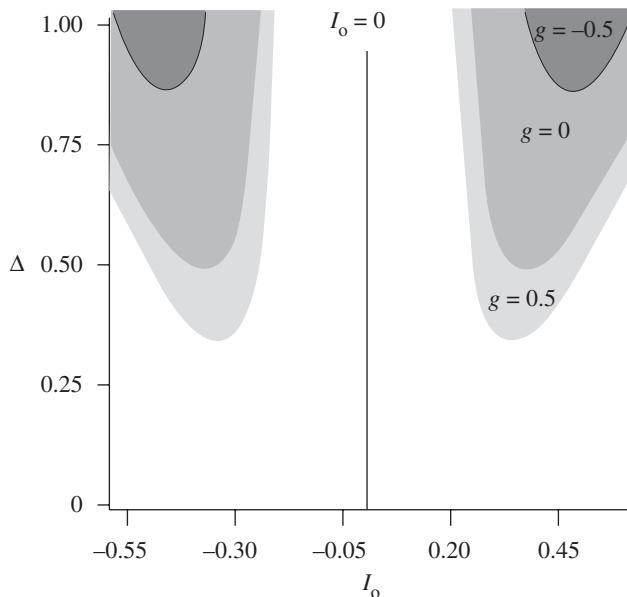
Figure 6. Pulse widths Δ and amplitudes I_{o} generating oscillatory responses. Shaded regions correspond to the input configurations where oscillatory responses to a localized pulse are observed, for $g = -0.5$, 0 or 0.5. The response threshold changes induced by additional non-delayed connections, on top of the global delayed inhibitory feedback, alter the criteria imposed on the input in order to trigger an Andronov–Hopf instability in the system. Parameters are $\Omega = 1$, $\tau = 2$ and $h = 0.25$.

In order to test this prediction, we stimulate the network response in figure 7 with a pulse-shaped stimulus of different strengths, i.e. $g = -0.5$, 0 and 0.5. The system exhibits small damped oscillations for $g = -0.5$, indicating that the input width and amplitude are not sufficient to trigger stable oscillations. When g is increased to 0, damped oscillations are still observed, although with longer decay rate, indicating that the system is closer to the oscillation threshold. When $g = 0.5$, the input triggers stable oscillations. In all these cases, the same input distribution was used. The extension to multiple instantaneous feedback connections may be done in a similar way to that of delayed connections, setting $G = \sum_{j=1}^{M} g_j$, yielding similar quantitative results (not shown).

We can identify the values of R satisfying equation (4.4) and consider how the response frequency $w(R_c, g)$ varies as a function of g, at the threshold. As figure 8a shows, an increasing instantaneous recurrent strength g decreases the response frequency, indicating that local signals shape oscillatory patterns, even in the case where global inhibitory delayed connections are present. Throughout this work, we restricted our analysis to the strength interval $g \in [-1, g_{\mathrm{SN}}]$. For $g < -1$, the frequency $w(R, g)$ becomes imaginary and oscillatory activity disappears inside the associated region of parameter space. At g_{SN}, a saddle-node bifurcation occurs, as shown in figure 8b. At this point, network oscillations collide with the basin of attraction of the new fixed points, and multistability is observed. The saddle-node bifurcation point is determined by the firing rate threshold h and response gain β, fixed earlier.
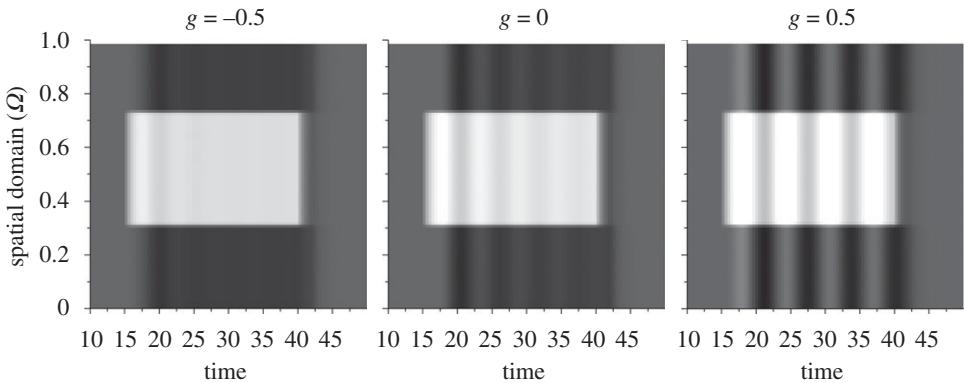
Figure 7. ON population responses to a localized pulse when $g = -0.5$, 0 and 0.5. Parameters in equation (4.1) are $\Omega = 1$, $I_{\mathrm{o}} = 0.3$, $\Delta = 0.4$, $h = 0.25$ and $\tau = 2$.
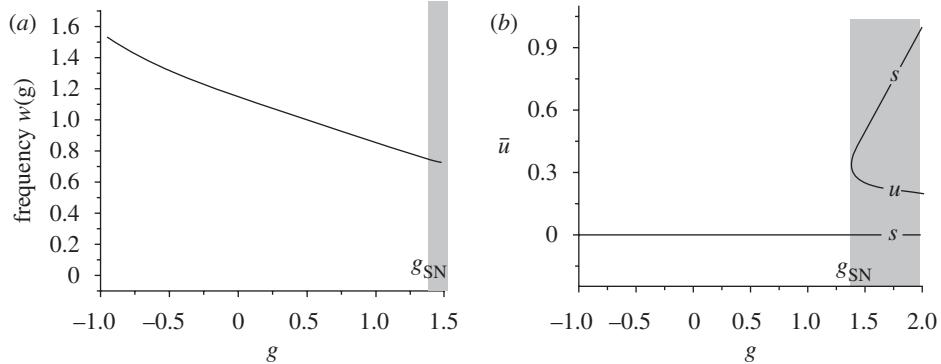

Figure 8. (*a*) Input response frequency as a function of the instantaneous recurrent signal polarity g. The input response frequency at the threshold decreases as the non-delayed recurrent signal becomes more and more excitatory. (*b*) Saddle-node bifurcation occurring at $g_{\mathrm{SN}} \approx 1.375$, delimiting the region investigated. Parameters $\tau = 2$ and $h = 0.25$.

5. Conclusion

In this paper, we first demonstrated how oscillations appear in a delayed feedback network of ON and OFF cells with external stimuli, and investigated the issue of multiple delayed feedback loops. We then analysed the effects of a mixture of delayed and non-delayed recurrent connections and demonstrated how the stability of the input-induced oscillations depends on the strength of non-delayed connections. When a delayed inhibitory term is present, instantaneous excitatory connections increase the network oscillatory responsiveness by decreasing the response threshold and allowing a greater range of pulse inputs to trigger oscillatory activity. Non-delayed inhibitory connections do the opposite by increasing the oscillatory response threshold. Further, the response frequency decreases when g increases.

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