Thalamocortical Feedback and Coupled Oscillators

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Abstract

Feedback systems are ubiquitous in neural systems and are a subject of intense theoretical and experimental analysis. Although there exists multiple hypotheses, there is little agreement on their exact function in neural systems. Looking at the thalamo-cortical feedback system as a model for studying feedback in general, I shall model such systems as coupled oscillators and ask if the feedback provides advantages to coding which could potentially be useful for survival. Issues such as synchronization of identically driven neurons and the role of noise in desynchronization will be explored. The goal of this project is to come up with hypotheses about the role of feedback which can immediately be tested in a suitable experimental system.

1 Thalamocortical feedback and potential roles

Most primary sensory stimuli are encoded through the use of **retinotopic maps** that extend throughout much of the primary sensory cortex and their corresponding thalamic nuclei. Information is transferred from “lower” sensory areas to “higher” sensory areas through the use of topographically arranged **feedforward pathways**. While it is clear what the role of the feedforward pathway is, it is also well established that there exists massive feedback and the role of this **feedback pathway** is less well understood.

Experiments done in monkeys in cats and rats have begun to shed light on the potential role of this feedback in sensory coding.

1. One potential role of the feedback could be to gate attentional mechanisms. It has been suggested that the feedback could be used to depolarize attended areas compared to unattended areas. A mechanism involving the **thalamic reticular nucleus** (TRN) has been suggested and evidence supporting this hypothesis has surfaced recently in experiments done on Macaque monkeys[1] which shows an increase in activity in attended areas and corresponding decrease in the activity in the TRN - consistent with the previously mentioned mechanism.

2. Alternative theories involving the ability of feedback to tune the receptive field of relay cells have been proposed. Temereanca et. al.[2], showed that enhancing the feedback through application of Bicuculline Methiodide (BMI) to layer 6 neurons enhances neural activity of thalamic barreloid nuclei corresponding to the principal whisker while suppressing activity in adjacent barreloid nuclei thus sharpening the receptive field of the Principal Whisker.

3. Another role of feedback could be in synchronizing all the neurons in the population corresponding to input stimulus. This should increase the SNR and thus be able to better drive the cortical neurons that receive input from the thalamus[4]. For example, Andolina et. al.[3], were able to reversibly inactivate the feedback layer (layer 6) in primary visual cortex and found that thalamic responses were less stimulus-modulated, less phase-restricted, and less reliable in response to drifting sinusoidal gratings in the absence of feedback as compared to its response in the presence of feedback.

I shall model the thalamocortical network as a circuit capable of synchronization, discuss potential coding advantages, discuss scenarios when synchronization is not necessarily a good idea and propose experiments which can potentially prove the above model.

2 A model for synchronizable networks

2.1 The minimal component

What is the minimal component necessary for synchronization in neural systems? Synchronization implies a mechanism by which oscillators are capable to interacting with one another. In the absence of interaction, the oscillators behave independently of each other and can never be expected to synchronize. It has previously been shown that reciprocal inhibitory connections are capable of synchronizing neurons (HW4). Moreover, reciprocal inhibitory connections are extremely common in most areas of the brain (although lateral inhibition has been proposed to subserve different purposes). However current intuition in circuit design[5] indicates that a different circuit is better able to provide tunability to the circuit. This design requires simultaneous positive and negative feedback onto the oscillator. Looking at the anatomy of the thalamocortical system, such a system is available through the use of the positive feedback from layer-6 neurons in the cortex and through the use of inhibitory feedback from the TRN onto **relay cells** in the thalamus. A schema of the known connectivity diagram containing the proposed minimal component is marked in **Figure 1.**

It is assumed hat both feedback components are required for proper synchronization to occur. Loss of any one is equivalent to loss of synchronizability. While it would be instructive to knock out the inhibitory feedback, current

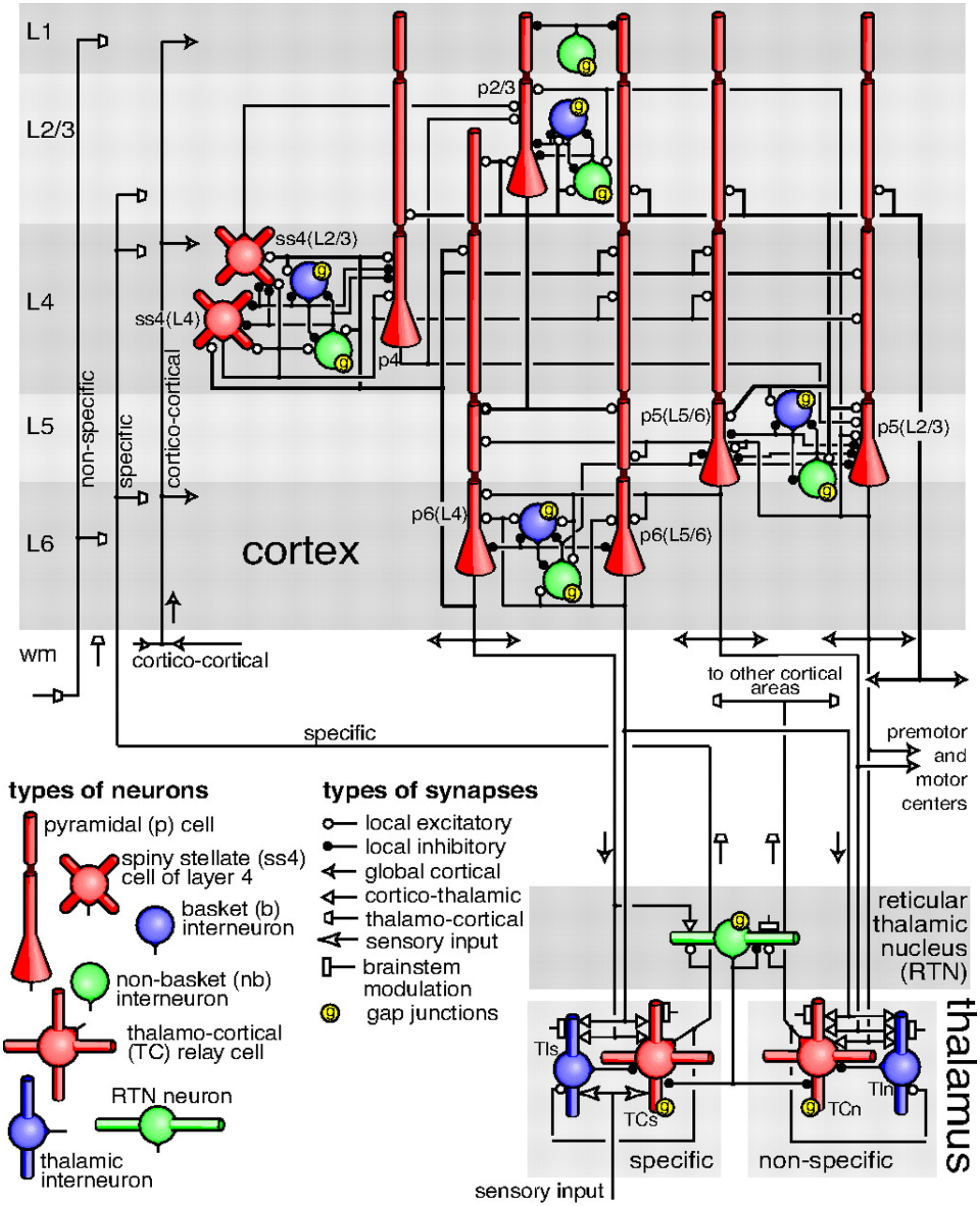


Figure 1: Minimal Thalamocortical component includes the feedforward component from thalamus to Cortex as well as the feedback from cortex to thalamus and the inhibitory connections from TRN to thalamus.

experimental technology allows us only to knock out the positive feedback coming from the cortex. While discussing an uncoupled oscillatory network, it is precisely this situation which is being discussed.

2.2 A mathematical formalism

Neurons will be assumed to be coupled phase oscillators. See the book "Weakly Connected Neural Networks"[7] for a discussion on the validity of the above assumption. The dynamics of phase oscillators is given by

$$\dot{\theta}_i = \rho_i + \sum_j a_{ij} sin(\theta_i - \theta_j); \;\; j = 1 \; to \; n$$

It is clear how the coupled phase oscillator is capable of showing synchronization. For the simple case of two oscillators having equal $\rho_i' s = \rho$, but having different starting phases $\theta_i(0) = \theta_0$, $\dot{\theta}_i$ will be different for both oscillators until $sin(\theta_i - \theta_j) = 0$ or until $(\theta_i - \theta_j) = n\pi$. Thus the two possible modes are $(\theta_i - \theta_j) = 2n\pi$ (in-phase) or $(\theta_i - \theta_j) = (2n+1)\pi$ (anti-phase). It is also intuitively clear that these modes are stable to noise in the input ρ_i as long as the noise is of the order of $\|a_{ij}\|$.

The nature of the dynamics in the presence of multiple connected oscillators is less clear. It has been shown[6] that for n identical coupled oscillators in a **ring** with **local connectivity** (each oscillator is influenced only by a subset of nearby oscillators), the only possible attracting states are "*q-twisted splay states*" where adjacent oscillators are phase shifted by a constant amount and all oscillators have the same final frequency. Here however, we study coupled oscillators in a line with local connectivity and possibly differing inputs.

3 Results

3.1 The rate of convergence to the attracting state is dependent on the coupling constants

Figure 2 shows the effect of coupling strength on the rate of convergence. We start 20 oscillators in a line with local connectivity (of 2) whose initial phases are randomly distributed in $(0 \;\; 2\pi)$. Coupling strength for all connections are identical although the result is not sensitive to differing coupling strengths. We see substantial interaction only when the coupling strength is comparable to the input strength. **Figure 3** shows the evolution of the state of the oscillator (as opposed to the phase evolution). We clearly see how, a system that makes use of coupling can use a higher SNR to identify the frequency of the oscillation (which correlates to the input strength). Infact, for sufficiently large networks getting identical inputs, the average of the strength of the output of all the oscillators is approximately constant while the same strength is definitely oscillatory for high coupling strengths.

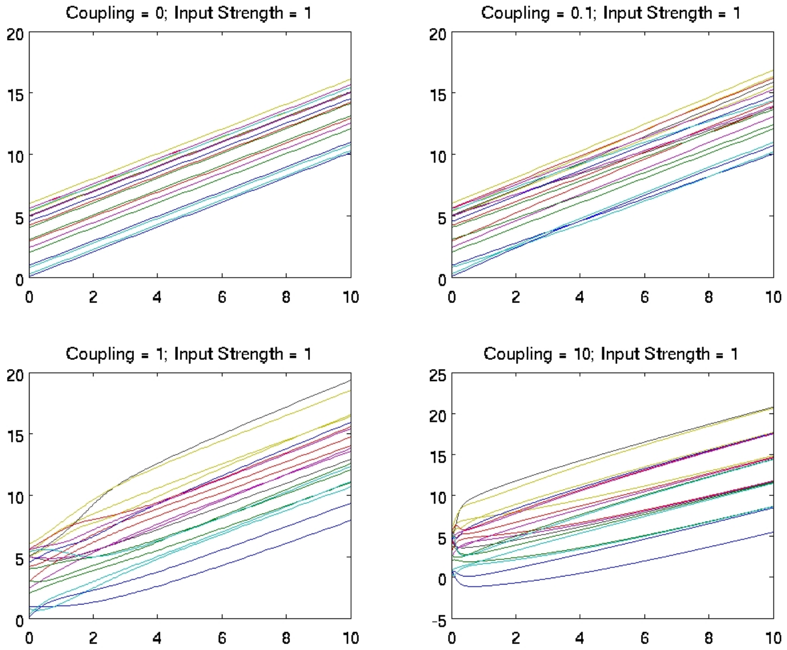


Figure 2: Convergence to the final attracting state depends on the coupling strength. Zero coupling leads to independent evolution of phases. High coupling (strength = 10) leads to states whose phases are separated by a multiple of π.

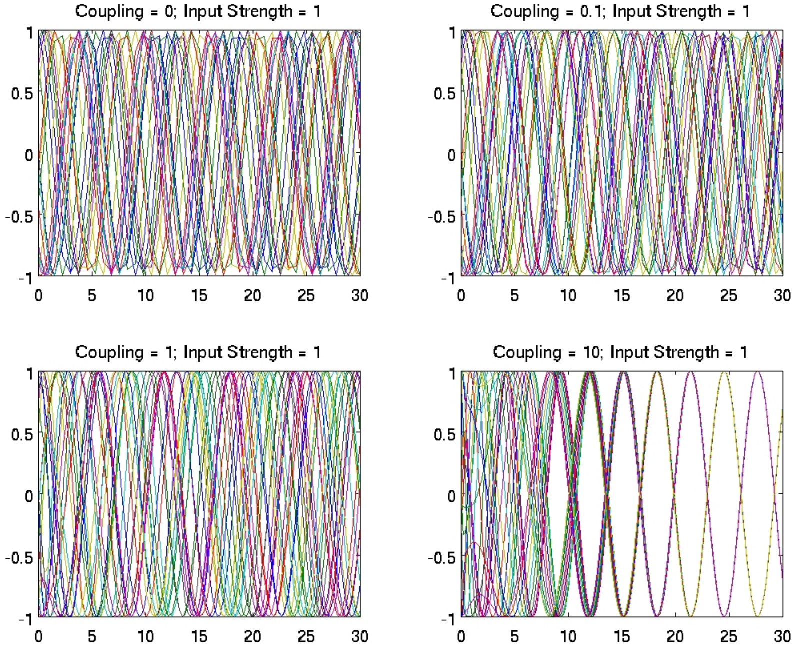


Figure 3: Evolution of Oscillator state. We see substantial synchronization only in the high coupling dynamics.

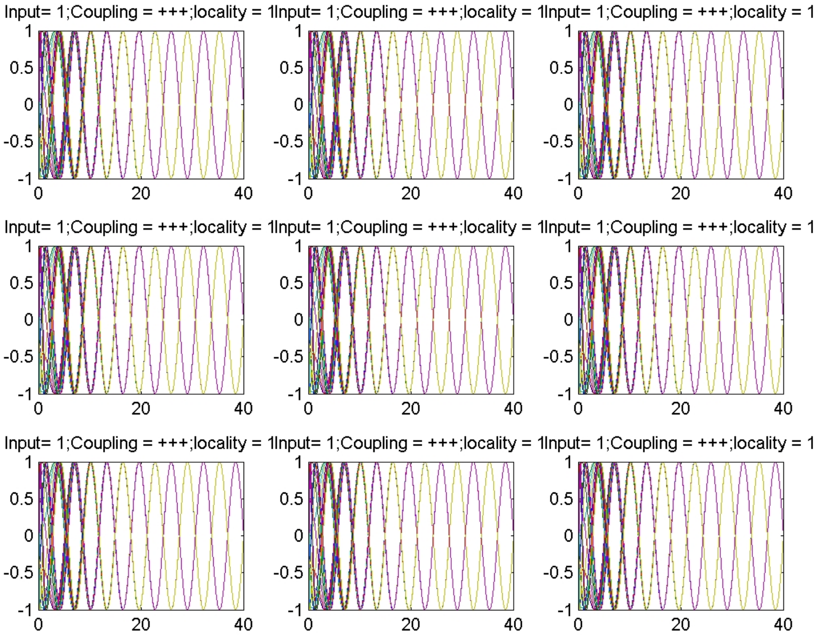


Figure 4: High coupling

3.2 Final state is robust to noise and initial conditions

Figure 4, 5, 6 show 9 different instantiations of the same oscillator starting out at different random initial phases and having internal noise in the input (1% of total input strength) but having different coupling strength. It is clear that the final state (synchronized / non-synchronized) is independent of both the initial condition and of the noise in the input.

3.3 Phase change with different inputs

Figure 7 shows the evolution of 20 oscillators in a line where 10 oscillators in the middle of the line receive a different input (strength = 10) compared to the other oscillators (strength = 1). The oscillators receiving high input are marked in red while those marked in grey receive background input. It is clear how the high input oscillators synchronize faster compared to the other oscillators. This means that an optimal detector downstream of this network can easily parse out the neurons that are more active compared to the others.

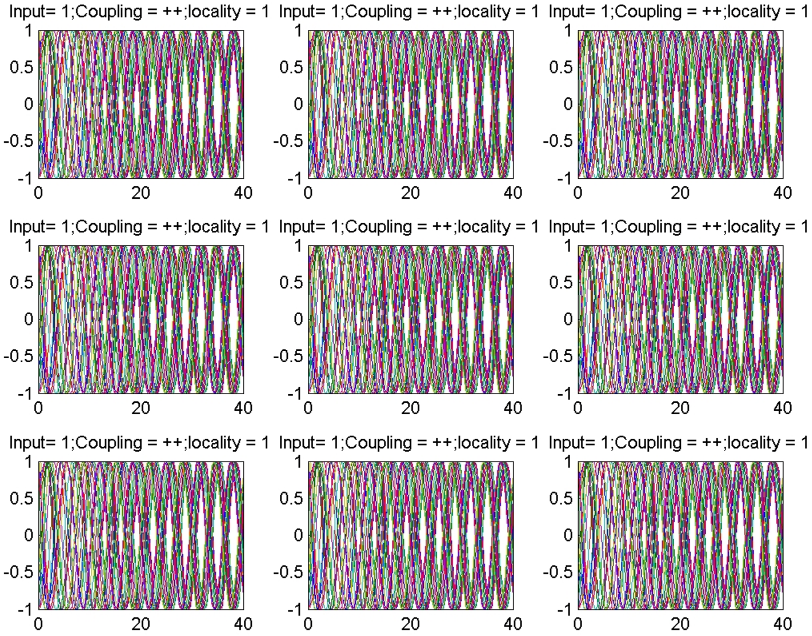


Figure 5: Medium coupling

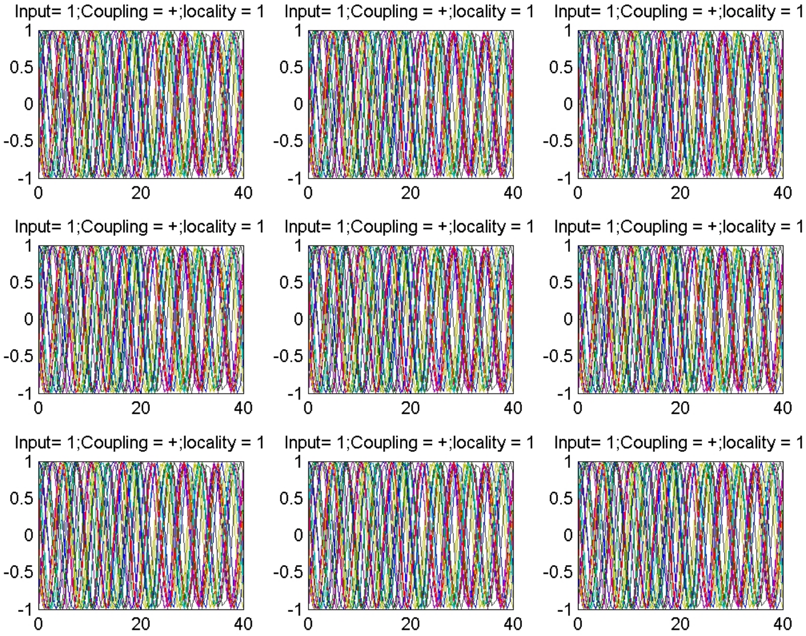


Figure 6: Low coupling

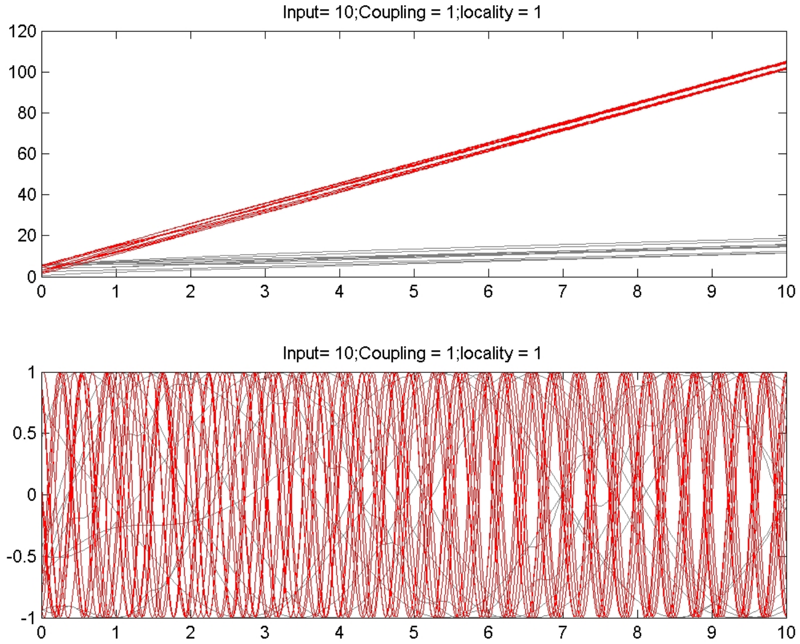
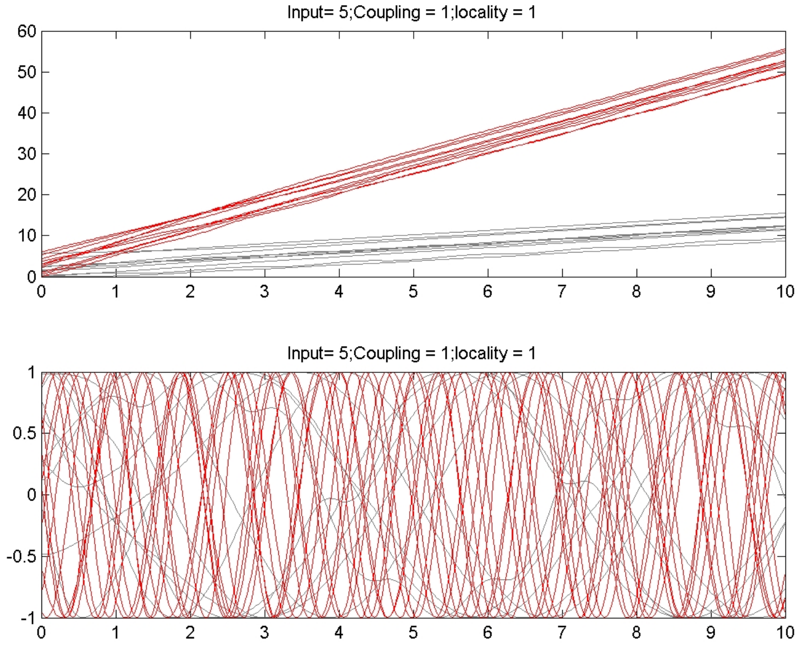


Figure 7: High Contrast. Input Strength = 10. Different inputs to 10 out of 20 neurons. Locality = 1. Same coupling for all oscillators. 1% noise in input



Input= 5;Coupling = 1;locality = 1

Input= 5;Coupling = 1;locality = 1

Figure 8: Medium Contrast. Input strength = 5. Different inputs to 10 out of 20 neurons. Locality = 1. Same coupling for all oscillators. 1% noise in input

3.4 Coupling depends on the contrast

Figures 7, 8 and 9 show that the rate of synchronization depends on the input strength. Synchronization is faster at higher contrasts compared to lower contrasts.

3.5 Coupling is not the optimal strategy for all scenarios

For low contrast signals, it may be a better strategy to use zero coupling strength to discriminate the object from the background. This is clear from **Figures 9 and 10**. While is possible to distinguish the higher contrast regions at lower time (≈ 5) in the zero coupling scenario(Fig 10), this is not possible even at higher times (≈ 9) in the coupled scenario (Fig 9). It is possible that at higher times the coupled oscillator is capable of giving a high SNR signal to reliably identify the higher contrast regions in the scene. However, encoding is only partly a matter of reliability. It is also a matter of speed. Extremely slow strategies, however reliable, are doomed to failure in the *game of life*.

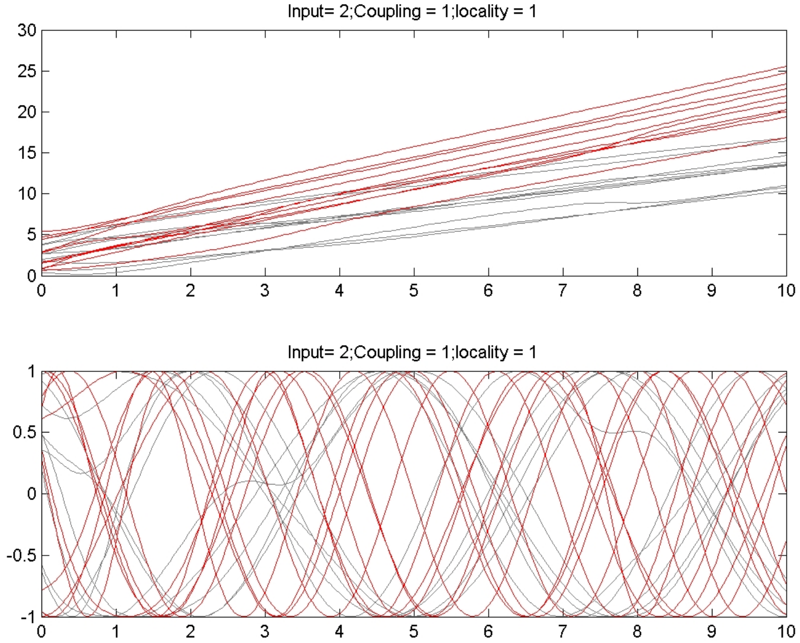


Figure 9: Low Contrast. Input strength = 2. Different inputs to 10 out of 20 neurons. Locality = 1. Same coupling for all oscillators. 1% noise in input

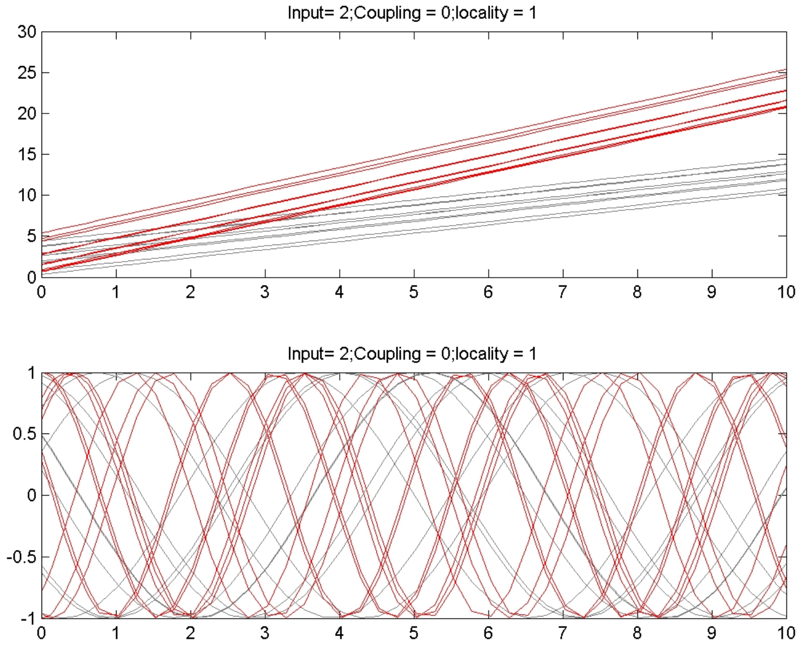


Figure 10: Zero coupling with low contrast

3.5.1 Hypothesis

If the neural system works as a coupled oscillator, then there should exist scenarios(when the contrast of the discriminandum in low) when the use of couling may be a suboptimal solution. An optimal neural system should be capable of modulating the extent of feedback based on task modality.

If there is no feedback modulation, artificially removing feedback should result in an increase in performance at low contrast only.

References

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