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# A top-down model for Neuronal Synchronisation

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Synchronisation between neurons in the visual system [Gray et al., 1989; Eckhorn et al., 1988] has been suggested to be a mechanism for binding together features of a visual scene, a pre-requisite for the recognition of complex objects. In this paper we show that synchronisation is an emergent property in a simplified multilayer model of visual information processing [Bugmann and Taylor, 1994a; 1994b], resulting from recognition in higher layers, and not causing it. We also show that the number and identity of the neurons synchronised in lower layers is determined by the conceptual level at which recognition takes place, or is pre-set to take place. This may solve one of the long-standing puzzles regarding feature linking via synchronization, namely how can low-level neurons know if the feature they are coding for belongs to a complex object or not.

The neural network model used in this study was initially designed to investigate visual latencies [Bugmann and Taylor, 1993; 1994b] and proved also useful for describing backward masking effects [Bugmann and Taylor, 1994a]. Accordingly, the model incorporates the basic components needed for feedforward information propagation: feedforward interlayer projections and feature-detecting neurons. Long-range lateral connections are not included, since they are assumed not to contribute to the responses with shortest latencies. Short-range lateral connections are not modelled explicitly but one of their possible effects, the production of the sustained firing [Douglas and Martin, 1991], is incorporated into the model of the neuron (which therefore actually represents a cluster of neurons). Interlayer feedback projections have been incorporated for the purpose of controlling the duration of the sustained firing.

The model is based 3 on hypotheses:

i) Neurons act as coincidence detectors and fire only in response to near-coincident input spikes. There is indirect evidence that visual neurons may operate in this mode. Attempts to reproduce the high frequency and high variability of cortical spike trains, have led [Softky and Koch, 1993] to concluded that neurons are operating as coincidence detectors. This is a possible function of biological neurons [Bugmann, 1991]. From the computational point of view, this function is well suited for feature detection because it makes the neuron very selective to the co-activation of input neurons. For simplicity, we assume perfect coincidence detection: a neuron fires only if one spike is produced by **all** its  $m$  inputs during a small time

window  $\Delta t$ . This facilitates the theoretical analysis of the model <sup>4</sup> [Bugmann and Taylor, 1994b] but is not critical for its behaviour. "Soft coincidence detection", e.g. a number  $m' < m$  of input spikes being able to generate an output spike, would lead to qualitatively the same behaviour.

ii) In response to coincidences, neurons enter in a mode of sustained random firing. It is known that cortical neurons are imbedded in a local network of excitatory interneurons which, if inhibition is disabled by injecting GABA agonists, causes prolonged sustained responses [Douglas and Martin, 1991]. However, there is no evidence that inhibition is disabled in the normal operation mode of the visual cortex. This feature of the model is not strongly supported by biological data and is nevertheless part of the model for several reasons. First, neurons operating as coincidence detectors have a very low firing frequency [Bugmann, 1991] and an amplification mechanism has to be assumed to explain the high firing frequency of cortical neurons. When the gain is very high, amplification results in prolonged self-sustained firing. This is one of the motivations behind hypothesis ii). Recently however, we have found that a neuron can produce high-frequency irregular spike trains without having to perform coincidence detection, if the potential of the membrane is partially reset after an output spike [unpublished results]. Therefore a mechanism for self-sustained firing is probably not needed to explain the high irregular firing rate of cortical neurons, but, as will be discussed later, it is essential for synchronisation. The second reason lies in the considerable jitter of the onset time of the responses of visual neurons [Levick, 1973, Richmond et al., 1987]. If the responses of some neurons is very short, these may have stopped firing before other neurons have even started. This can cause a temporal fragmentation of a visual scene which prevents the totality of its components to be simultaneously available for analysis. If visual neurons have a short-term memory property (self-sustained firing) or show prolonged input-driven responses, neurons in a given layer will eventually be active simultaneously. So, sustained firing is one of the possible responses to the fragmentation problem. One may note that, while fragmentation caused by jitter is statistical effect, fragmentation due to intensity-dependent retinal latencies is deterministic and can be exploited [Burgi and Pun, 1994].

iii) Feedback from higher areas has an inhibitory effect which interrupts the sustained firing. This feature is present for consistency reasons, because hypothesis ii) requires some mechanism to control the duration of the sustained firing. It also allows minimisation of the duration of the sustained firing while guaranteeing information propagation [Bugmann and Taylor, 1994a]. Anatomically, it is known that a large fraction of inter-area feedback projections connect to inhibitory interneurons. Therefore, feedback can theoretically control the duration of sustained firing.

We have implemented these ideas in a simple pyramidal neural network model shown in figure 1. The 64 neurons in the first layer (layer 0) represent a subset of neurons in the Lateral Geniculate Nucleus which are activated by a given complex visual pattern. Neurons in layer 1 detect elementary patterns made of 4 active neurons in layer 0. Neurons in layer 2 respond to more complex patterns coded by 4 active neurons in layer 1. The neuron in layer 3 responds to the complete complex pattern. Neurons operate in discrete time steps  $\Delta t$  as coincidence detectors and enter in a state of sustained firing after a coincidence of  $m=4$  input spikes has been detected. At the same time, neurons send an inhibitory feedback to their  $m$  input neurons in the previous layer, in order to stop the sustained firing, because it is no longer needed. The inhibitory signal prevents any firing of a neuron during the following  $t_{inh}$  time steps. The sustained firing is produced by setting a neuron to fire a spike with probability  $p_1$  at each time step. The first layer (layer 0) represents an aggregate of the retina and the lateral geniculate nucleus. The retinal jitter [Levick, 1973] is produced by starting input neurons with a low firing probability  $p_0 < p_1$ . As soon as the first spike is produced, the neuron is switched to a sustained firing with firing probability  $p_1$ . Therefore, the only role of  $p_0$  is to generate jitter.

Figure 2a shows the sequence of spikes produced by all neurons in each layer. At approximately time step 60 all neurons in the layer 0 become synchronised. As the only link between these neurons is the indirect feedback from the last layer, synchronization starts after the last layer neuron has produced its first spike.

Figure 2b shows the corresponding post-stimulus histogram averaged over 100 runs. These show temporal patterns similar to those observed in visual neurons [Richmond et al., 1987]. As synchronization does not occur with the same phase during all runs, the oscillations are cancelled in the averaging process.

Figure 3 shows a simulation where the last neuron is disabled. Now layer 2 represents the highest possible conceptual level (patterns of 16 active neurons in layer 0) at which recognition can take place. One can see that the neurons sending information to these neurons are synchronised with different phases of the oscillations.

Regarding the mechanism for synchronisation in this model, synchronization is caused by the inhibitory feedback which stops the firing of all  $m$  input neurons at the same time. During the inhibitory period, the inputs to these  $m$  neurons have time to start firing. Therefore, when the inhibitory effect disappears, some of the jitter has been cancelled, and most  $m$  input neurons have input conditions allowing them to start firing immediately. As inhibition ends

simultaneously in these neurons, they start firing synchronously. Thereby, they inhibit synchronously their input neurons in the previous layer, and inhibition propagated backwards to a larger number of neurons. We may note that the sustained firing has to be disabled in the last active layer to prevent a permanent inhibition of the previous layer. This is necessary to allow synchronised activity.

The period of the synchronous oscillation is the sum of the duration of the inhibition, the feedforward and feedback propagation time and the average firing time needed before a coincidence occurs. In the present model, each spike produced by the target neuron initiates a new inhibitory period in its  $m$  inputs neurons, which extends the duration of the effect of previous inhibitory feedback spikes. Therefore, the duration of the sustained firing in the target neuron affects also the period of the oscillations, as can be seen by comparing the periods in the figures 2a and 3. It is possible to modify the model in order to trigger the feedback inhibition only in response to coincidences. This would remove the dependence of the period of the oscillation on the level at which recognition takes place. At the present stage of our knowledge, there is no reason to chose one or the other model. There may however be a support for variable oscillation frequencies in experimental results on quantified reaction times [Deheane, 1993]. These data indicate that sensory information available for pattern discrimination arrive in packets at discrete intervals (10 to 40 ms), the length of the intervals being larger when higher cortical layers are involved.

A prediction of our model is that synchronization should be observable in all visual layers, starting with the lateral geniculate nucleus (layer 0 in the model), up to the layer where recognition takes place. This is partially confirmed. Synchronization has been observed in the area 18 [Eckhorn et al., 1988], area 17 [Gray et al., 1989] and recently in the lateral geniculate nucleus, where it has as been shown that synchronisation was caused by feedbacks from area 17 [Sillito et al., 1994]. However, the LGN has no local mechanism for producing sustained firing. It only relays prolonged spike trains produced by retinal ganglion cells [Levick, 1973]. The role of feedback has not been shown for other layers.

Regarding the phase of the oscillations, we may note a progressive shift to later times of the peak of firing probability from lower layers to higher layers (figure 1). Such an effect is observed in the auditory system [Ribary et al., 1991].

Regarding latencies, due to the jitter in the first layer (reproducing the retinal jitter), the average response latency of a neuron in layer 1 is much larger than the spike propagation time. This may explain the long response latencies observed in V1 with visual stimuli, compared to latencies measured with electrical stimulations [Maunsell and Gibson, 1992]. The factors

affecting the latencies are analysed in [Bugmann and Taylor, 1994b]. The model predicts that an experimental manipulation of the retinal jitter may lead to strong observable effects. For instance, a reduction in jitter may increase the speed of visual information processing.

As a general comment, all models of synchronisation proposed so far have made use of a "spike producing engine" which was then subjected to external synchronising influence. Such engines were either a local oscillator or integrate-and-fire neurons with a more or less continuous input current from an external "background" source [Nischwitz et al., 1992; and references therein]. Our model makes no exception, the local network which produces spike trains in a self-sustained way is such an engine. Without it, for instance if the firing of the neurons in the model was purely caused by feedforward input, there would be no synchronisation. Two main differences between our and other models are: 1) the top-down nature of the synchronising message and 2) synchronisation is not required for pattern recognition. It appears only when the pattern recognition process is completed (by pattern we understand here a selection of 64 active visual neurons).

Although a number of models have described synchronization as an effect of lateral interactions between neurons in the same layer [Nischwitz et al., 1992; and references therein], there is no experimental evidence that horizontal connections participate in feature linking via synchronization. Even evidence for the role of callosal projections for interhemispheric synchronization does not allow one to draw a clear cut conclusion for horizontal connections [Engel et al., 1991]. This is because callosal projections comprise also feedforward and feedback projections. Beside that, horizontal connections link mainly neurons tuned to similar visual patterns, at least in V1 [Gilbert, 1992]. These are therefore not good candidates for feature linking via synchronization, because a complex visual stimulus is usually made from a set of dissimilar subpatterns. On the other hand, there is clear evidence for the role of feedback projections [Sillitto et al., 1994]. Further, it is conceptually more satisfactory to see synchronization as a top-down process. An example is the book/title problem: when one is looking at the front page of a book, the neurons coding for all of the front page should be synchronised when one is evaluating the general layout. However, when one is reading the title, only the neurons coding for the characters in the title need to be synchronised. Therefore, the binding problem should actually be solved before synchronisation may start. Another model suggests that thalamocortical projections operate the selection of neurons to be synchronised [Niebur et al., 1993]. Such a model only displaces the problem of deciding what elementary features belong to a complex pattern. Suggestions as to how that might be achieved have been proposed recently in terms of competition on working memory sites [Taylor, 1994].

If the hypothesis on which the model is based are confirmed, our results suggest that synchronization is an intrinsic property of the visual system and is not required for the recognition of complex patterns. However it results in multi-resolution feature linking which could be exploited at further stages of neural information processing. For instance, if we observe the organisation of visual areas along the surface of the cortex and the reciprocal thalamic connections with all these areas, one may conceive of a mechanism by which a thalamic signal defines in which area recognition is to take place, depending on the task one is involved in, and then collects information on the recognised complex pattern at various levels of details, i.e. from lower visual areas (layers in our model). The synchronization among all neurons coding for the object may also prove useful for sending information to extravisual areas, for instance in the frontal lobe. More simply, synchronisation may signal that the visual information has been recognised and allow eye movements towards a new fixation point. The model suggests also that synchronisation among neurons should only occur if the task requires the recognition of the complex visual pattern which they code for. Thereby, experiments could be designed to generate synchronisation in a controlled way between neurons far apart on the cortical surface.

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## Figure Captions:

### Figure 1:

The network used in the simulations is a pyramidal network representing the subset of visual neurons needed to activate the last neuron in the pyramid. Neurons operate in discrete time steps. Each neuron has  $m=4$  inputs and produces a spike when a coincidence of  $m$  input spikes is detected within the same time step. From the next time step on, it produces a random spike train with probability  $p_I$  of having a spike at each time step. Also, an inhibitory signal prevents all its  $m$  input neurons to fire during  $t_{inh}$  time steps. After the end of the inhibitory period, a neuron has to detect a new coincidence before re-entering into a sustained firing mode. The first layer (layer 0) represents an aggregate of the retina and the lateral geniculate nucleus. The retinal jitter [Levick, 1973] is produced by starting input neurons with a low firing probability  $p_0 < p_I$ . As soon as the first spike is produced, the neuron is switched to a sustained firing with firing probability  $p_I$ . Therefore, the only role of  $p_0$  is to generate jitter. Neurons in the lateral geniculate nucleus are supposed to relay the spike train from a single ganglion cell. The feedback from area V1 is supposed to inhibit the transmission of the retinal spikes during a time  $t_{inh}$ . At the end of the inhibition, transmission is resumed and neurons in layer 0 resume their firing with probability  $p_I$ .

### Figure 2

**a)** Spike trains all neurons in each layer during a single run of 200 time steps. There are 64 neurons in layer 0, 16 in layer 1, 4 in layer 2 and a single neuron in layer 3. At time step 1, all neurons in layer 0 start firing with a probability  $p_0 = 0.08$ . After their first spike, they enter in a state of sustained firing with probability  $p_I = 0.8$ . The duration of the feedback inhibition is  $t_{inh} = 10$  time steps. The propagation time from one layer to the next is  $t = 1$  time step. After the last neuron in the pyramid has started firing, the inhibitory feedback synchronises the neurons in the lower layers. Due to the synchronization, the initial jitter is cancelled and neurons need only to fire short burst of spikes before a coincidence is detected in the next layer. The sustained firing of the neuron in the last layer is disabled so that it does not exert a permanent inhibition of neurons in layer 2. It fires only in response to coincidences.

**b)** Time-Histograms of the response of one neuron in each layer, averaged over 100 runs. The simulation conditions are the same as in figure 2a. One may observe that the interlayer latencies are much longer than the propagation time of single spikes. That is due to the retinal jitter in layer 0. The continuous line is the theoretical firing probability in the case without feedback inhibition. Once neurons have started firing, they keep firing with a probability  $p_I = 0.8$ . Therefore, after the initial jitter period, the average firing probability is  $p_I$ .

### Figure 3.

Spike trains produced under the same conditions as in figure 2a, except that the neuron in layer 3 has been disabled and the neurons in layer 2 do not enter in sustained mode. Synchronization occurs now with different phases in the 4 subsets of neurons corresponding to the 4 neurons in layer 2.

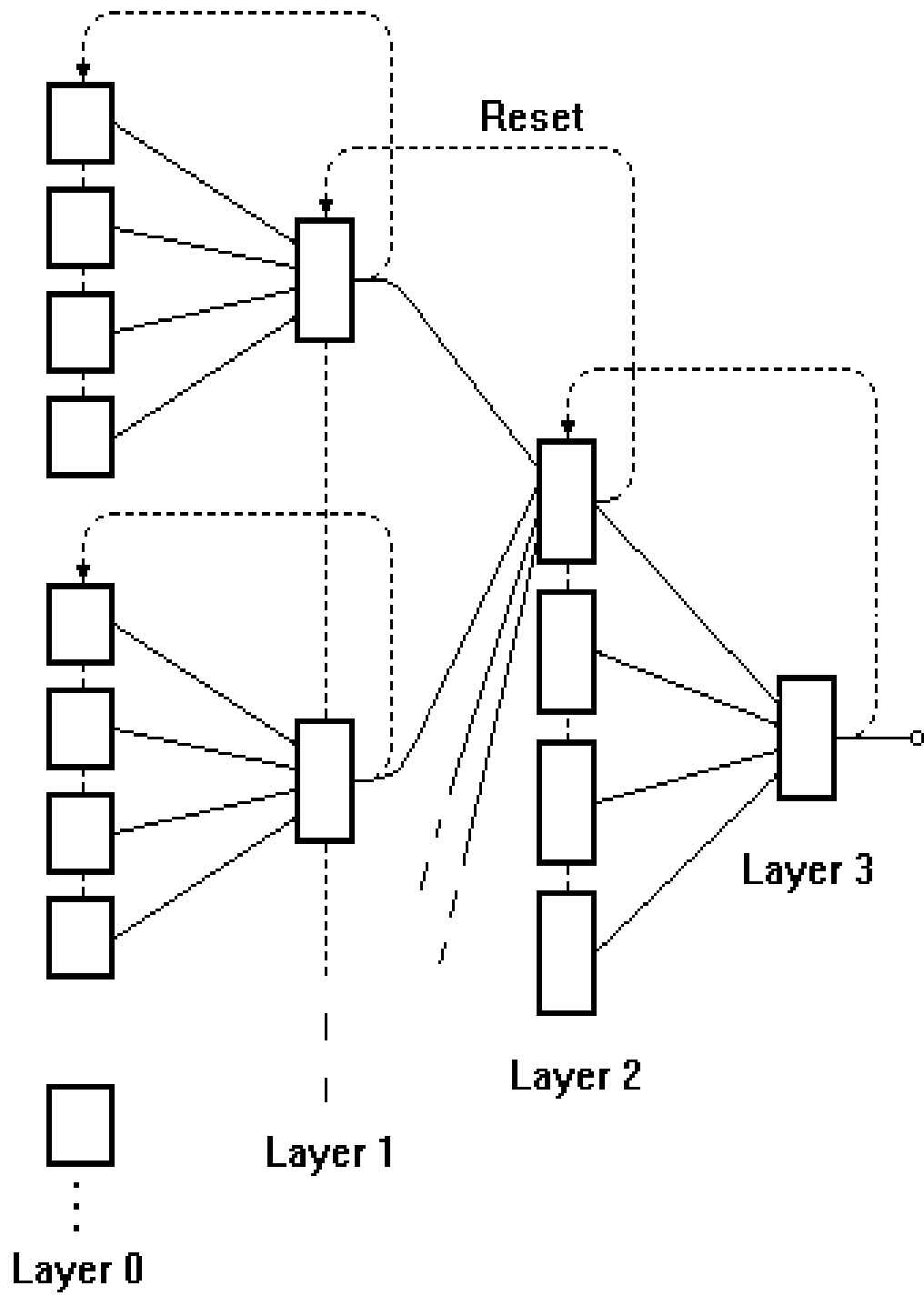


Figure 1

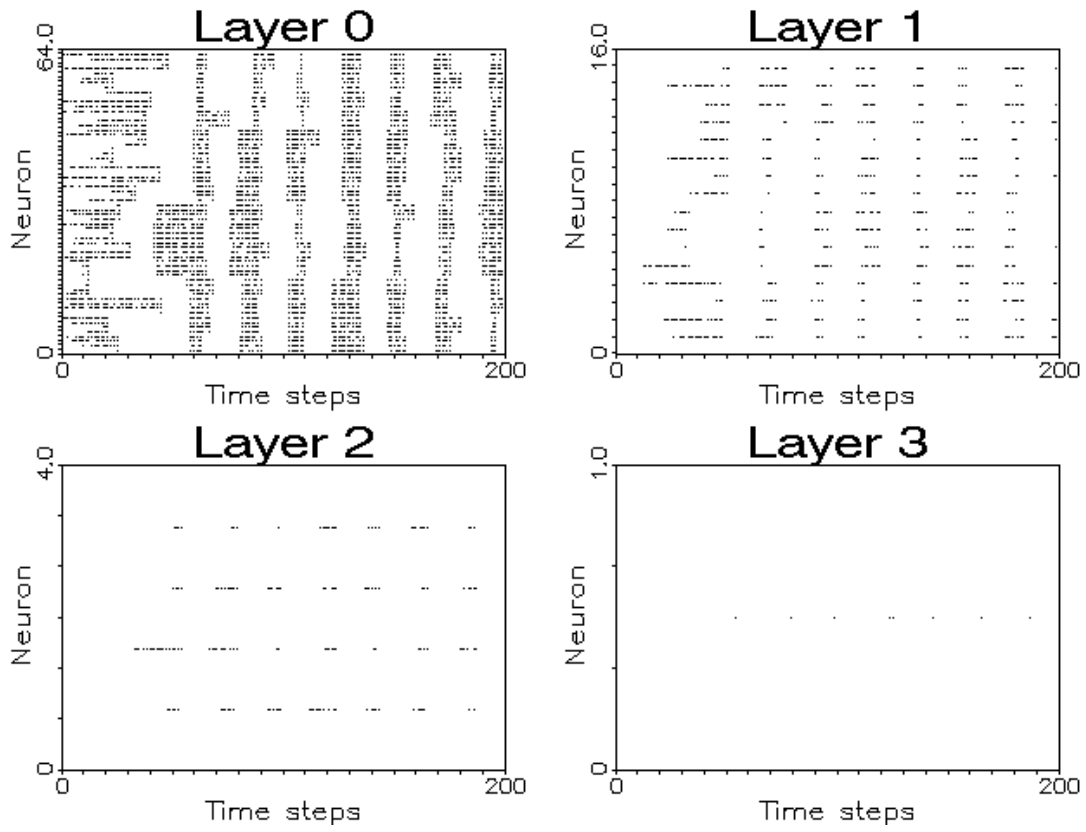


Fig. 2a

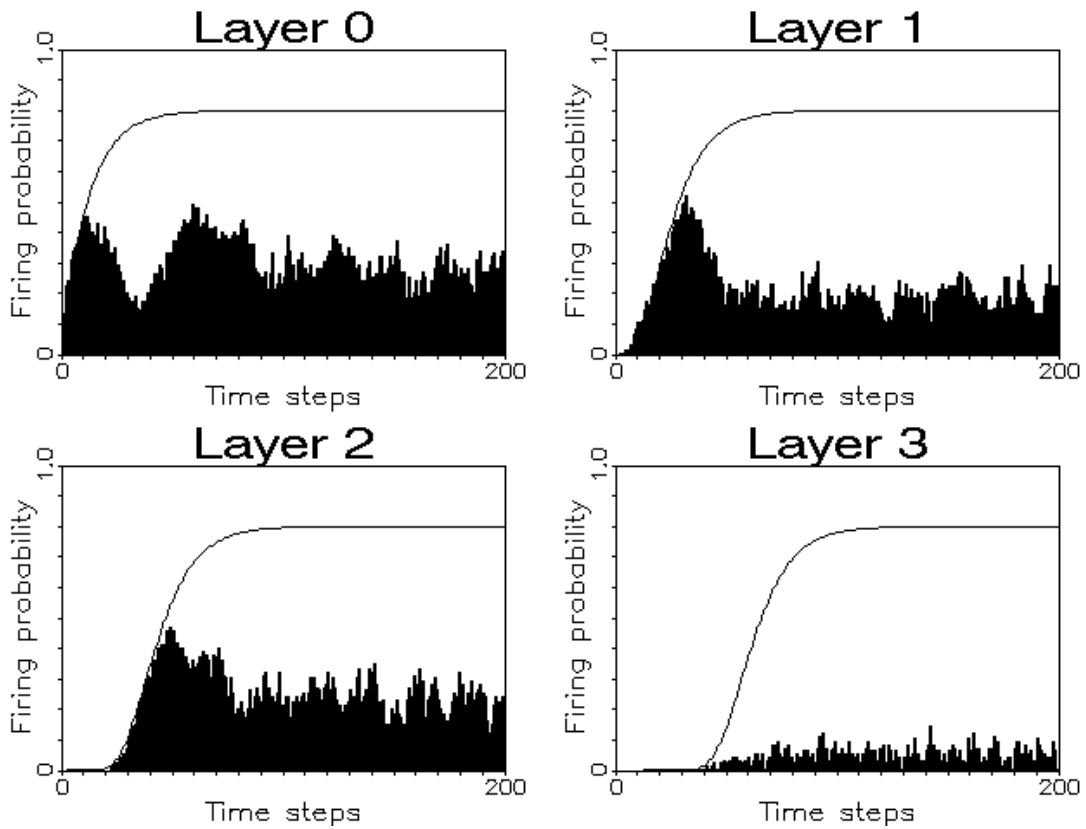


Fig 2b

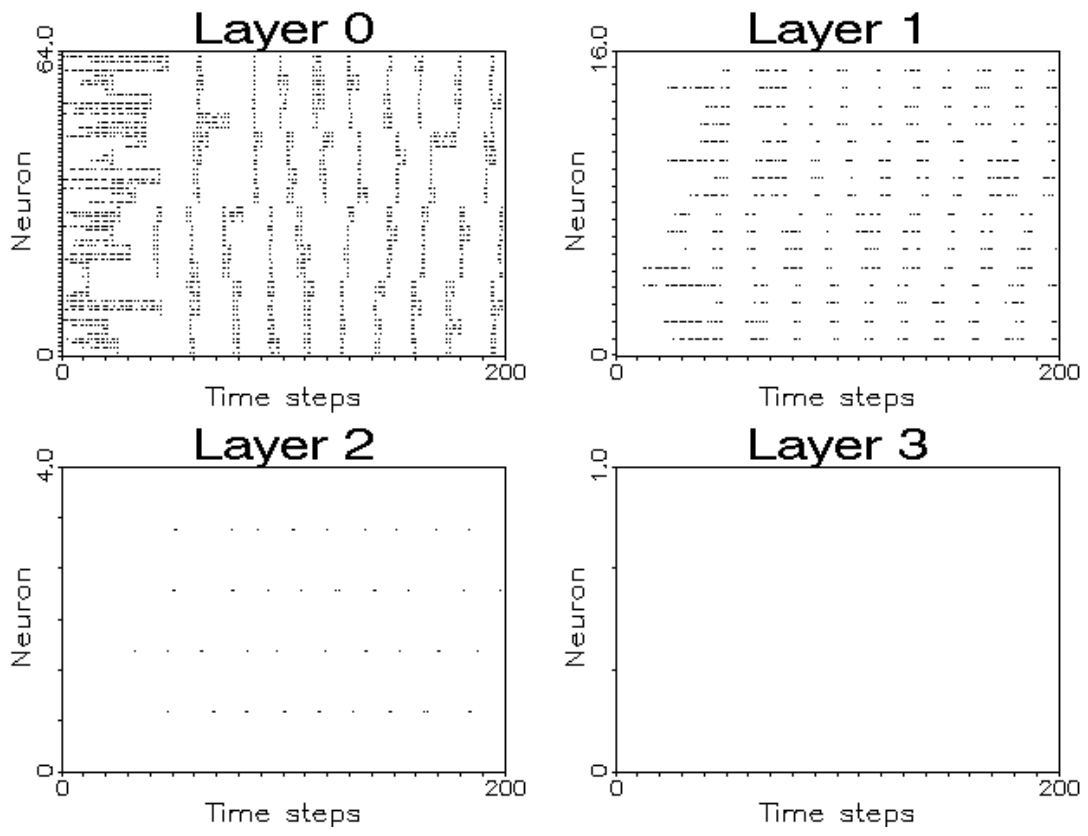


Fig. 3