

Robust Feedforward Processing in Synfire Chains

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Abstract

The rapidity of time-constrained visual identification suggests a feedforward process in which neural activity is propagated through a number of cortical stages. The process is modelled by using a synfire chain, leading to a neural-network model which involves propagating activation waves through a sequence of layers. Theory and analysis of the model's behaviour, especially in the presence of noise, predict enhancement of wave propagation for a range of noise intensities. Simulation studies confirm this prediction. The results are discussed in terms of (spatio-temporal) stochastic resonance. It is concluded that feedforward processes such as time-constrained visual identification may benefit from moderate levels of noise.

1 Introduction

Confronted with an unexpected picture, the human visual system is nevertheless capable of identifying its contents within 100 ms [1]. Neurophysiological studies show that visual signals entering the retina are propagated through a number of parallel pathways (see, e.g., [2]). One such pathway runs from the primary visual cortex (V1), through several intermediate areas, to the inferior temporal (IT) cortex where identification is assumed to take place (see, e.g., [3]). Upon presentation of an image, cells fire in sequence along the identification pathway indicating the propagation of activity associated with the image [4]. At the IT level, cells differentially sensitive to object identity already start firing 100 ms after stimulus onset; all this is consistent with a rapid feedforward process [1] [5]. Nerve cells, however, are intrinsically noisy [6], and therefore accurate feedforward processing requires an adequate signal-to-noise ratio. While feedback processes are normally expected to enhance the signal-to-noise ratio (see, e.g., [7]), they cannot provide the dominant

contribution to the initial identification, given the 100 ms time constraint. Thus, the question is: how can a feedforward system with noisy elements perform as well as the identification pathway does?

Our strategy for answering this question is to focus on the propagation of uniformly patterned stimuli. We reduce the identification task to a detection task, enabling us to concentrate upon the propagation process, which remains a prerequisite for identification. An example of such a detection task is the presentation of a brief flash of light onto the retina whence the resulting activity is propagated. In Section 2 a synfire-chain model [8], consistent with feedforward propagation of activity through pathways, is described. In Section 3, we analyse the robustness of this model. Whilst one might expect noise to have increasingly detrimental effects on the propagation of patterns, we predict by this analysis that some levels of noise will actually *enhance* the propagation process. Results from simulation studies confirm the noise-enhancing effect and show how the enhancement changes with input strength. Finally, Section 4 discusses the behaviour of our model, relating it to stochastic resonance [9] in excitable media [10]. In addition, it discusses the extension of the model to allow for more realistic identification tasks. The article concludes that some levels of noise have beneficial effects on feedforward neural processing.

2 Model Description

Abeles [8] proposed the synfire chain as a biologically plausible model of cortical processing. Our interest in time-constrained visual processing in the identification pathway led us to employ a synfire chain with only feedforward connections.

2.1 Model Structure

Figure 1 shows the structure of our model. It consists of $L + 1$ layers: one input layer and L propagation layers. Each of these layers may be equated with a cortical level in the identification pathway. The *chain width* N is defined as the number of neurons per layer. The input layer (retina), $l = 0$, holds the input signal. Each propagation layer l , with $l \in \{1, 2, \dots, L - 1\}$, is fully connected with its successor layer $l + 1$. The last propagation layer, L , serves as the output layer and may be equated with the level of the inferotemporal areas.

Our synfire chain is *complete* in that each neuron p of layer $l \in \{1, 2, \dots, L\}$, denoted $n_l(p)$, receives its input $(i_l(p, t))$ at time t from *all* neurons $n_{l-1}(q)$, with $p, q \in \{1, 2, \dots, N\}$. The input is given by

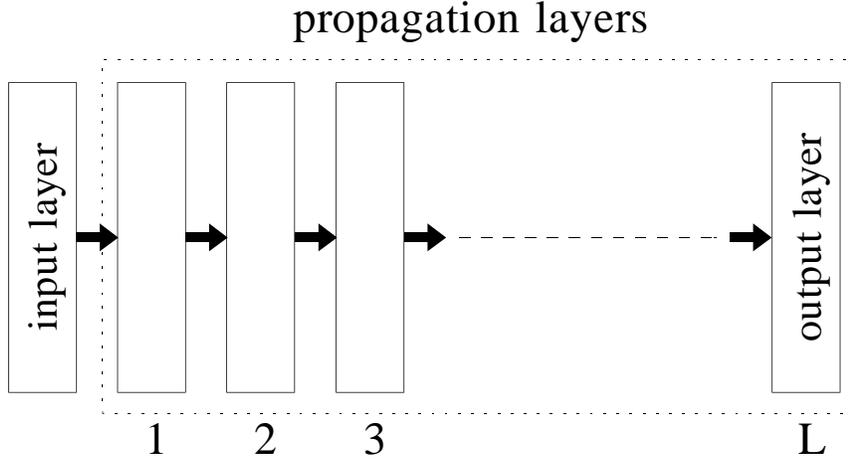


Figure 1: The structure of the model.

$$i_l(p, t) = \sum_{q=1}^N w_l \theta(V_{l-1}(q, t) - 1), \quad (1)$$

where w_l is the weight of the connections from layer $l - 1$ to l . The Heaviside step function θ models the conditional spiking of the neuron; when the potential V exceeds the threshold value θ 's output is set to 1. We take a threshold value of 1. Hence, $\theta(V - 1) = 1$ if $V > 1$ and $\theta(V - 1) = 0$ otherwise. The neural dynamics, describing the change of the membrane potential V over time, are defined as (cf. [11])

$$\frac{dV_l(p, t)}{dt} = -\frac{V_l(p, t)}{\tau} + i_l(p, t - t_{delay}), \quad (2)$$

with τ a time constant specifying the decay of the membrane potential. A refractory period is incorporated by setting $V_l(p, t + t_{spike}) = 0$ when $V_l(p, t) = 1$, where t_{spike} is the spike duration. The potential remains zero for a time interval equal to the spike duration. Setting $t_{spike} = t_{delay} = 1$, integration of equation 2 over the delay time t_{delay} leads to the following discrete approximation of the potential dynamics [11]:

$$V_l(p, t + 1) = [\alpha V_l(p, t) + i_l(p, t) + \nu(p, t)] \theta(1 - V_l(p, t)), \quad (3)$$

where $\alpha = \exp(-\frac{1}{\tau})$ and we have added a Gaussian random variable $\nu(p, t)$ distributed around zero with standard deviation σ .

2.2 Activation Waves

The presentation of an input pattern is defined by the synchronous spiking of *all* neurons (i.e., a brief flash of light) in the input layer at $t = 0$. If the strength of the input is sufficient, it leads to the spiking of neurons in the next (propagation) layer which, in turn, may suffice to produce synchronous firing of neurons in the subsequent layer, and so on. This propagation of synchronous firing, i.e., the *activation wave*, provides a crude approximation to the propagation of activity along the visual pathway in response to a stimulus. A single wave of simultaneously firing neurons, which represents a stimulus pattern in our model, is of course insufficient for visual identification. Pattern information may well be carried in the relative timing of individual spikes propagating together through the identification pathway [12] [13]. The simplification is, however, sufficient to allow us to study the robustness of wave propagation in the presence of noise.

3 Performance with and without Noise

We have investigated the robustness of wave propagation by analysis and simulation studies. To quantify the robustness of our model to the intrinsic-noise strength σ , we have defined a performance measure $P_{survival}$, being the probability of arrival of an activation wave at the output layer in response to the presentation of an input pattern.

3.1 Wave Propagation

The zero-noise case. After presentation of an input at $t = 0$ to the input layer, the potential of the p -th element of the first propagation layer ($l = 1$) at $t = 1$ is

$$V_1(p, 1) = \sum_{q=1}^N w_1. \tag{4}$$

As soon as $w_1 > \frac{1}{N}$, the potential exceeds the threshold and the element will emit a spike. Similarly, for $w_l > \frac{1}{N}$, $l \in \{2, 3, \dots, L\}$, the elements in layer l will spike at $t = l$. So, provided that $w = w_l > \frac{1}{N}$ for all $l \in \{1, 2, \dots, L\}$, presentation of an input pattern leads to the propagation of an activation wave through the synfire chain.

The noise case. In the presence of noise, the p -th element of the first propagation layer has the following potential when $V(p, 0) \leq 1$:

$$V_1(p, 1) = \alpha\nu(p, 0) + \sum_{q=1}^N w_1 + \nu(p, 1) \quad (5)$$

and $V_1(p, 1) = 0$ when $V(p, 0) > 1$. The latter case refers to the p -th element emitting a spike at $t = 0$, leading to a reset at $t = 1$. In the first case (no reset), the condition for spiking at $t = 1$ is given by $V_1(p, 1) > 1$ or $\alpha\nu(p, 0) + \sum_{q=1}^N w_1 + \nu(p, 1) > 1$. For weight values $w_1 \leq \frac{1}{N}$, the propagation element may nevertheless fire, when the noise contributions are sufficient to bridge the gap between the signal and threshold, i.e., when $V_1(p, 1) = \alpha\nu(p, 0) + \nu(p, 1) > 1 - Nw_1$. Using this expression we computed the probability of firing of an element in the first propagation layer as a function of σ for the *subthreshold* value $w_1 = 0.99/N$. The results are shown in Figure 2a. A clear noise-induced enhancement is observed. The maximal spiking probability falls within the range $0.3 < \sigma < 0.4$.

To analyse the propagation of activation waves in the presence of noise we define $F_l(t)$ as the fraction of firing elements in layer l at time t . We focus on the potentials of the elements in layers 2 to L and define $w_l = w$ for $l \in \{2, 3, \dots, L\}$:

$$V_l(p, t) = \alpha V_l(p, t-1) + \sum_{q=1}^N w \theta(V_{l-1}(q, t-1)) + \nu(p, l), \quad (6)$$

which leads to the following condition for spiking: $\nu(p, l) > 1 - NF_{l-1}(l-1)w - \alpha V_l(p, t-1)$. Figure 2b shows the survival rates $P_{survival}$ (i.e., the probability of this condition being met for layer L) as a function of σ for $L = 10$, $w_1 = 0.99/N$, and $w = 2/N$. (The latter value allows for the recovery of the impaired activation wave at the first propagation layer.) These rates are obtained by first computing the spiking probability for the first propagation layer using the data of Figure 2a, and then using the results so obtained to compute the probability for the second layer, and so on.

Our analysis leads to the prediction, that (i) a moderate noise level will maintain the propagation of signals which would otherwise die out before reaching the output layer, and that (ii) the enhancement will be relatively insensitive to changes in the noise intensity over a wide range ($0.1 < \sigma < 0.4$).

3.2 Simulations and Results

To verify the predictions of the analysis, we performed simulation studies of wave propagation in our synfire model with $L = N = 10$. The weights were set to the values used in the

analysis (i.e., $w_1N = 0.99$ and $wN = 2$). Initially, at $t = 0$, all neurons in the input layer are set to $V_0(p, 0) > 1$ for $p \in \{1, 2, \dots, N\}$, and set to zero for $t > 0$. The noise intensity of the neurons in the input layer is set to zero, while for all other neurons it is set to a fixed value σ . At each time step $t > 0$ all neurons in the propagation layers are updated according to equation 3.

Figure 3 shows the proportion of fully propagated activation waves $P_{survival}$ (averaged over 10,000 runs) as a function of the intrinsic noise parameter σ . The close fit of the simulation results with the predicted survival rate (continuous line) confirms our analysis.

Results of additional simulations in which we varied the value w_1N in the subthreshold interval $0.5 < w_1N < 1.0$ illustrate how the input strength affects the shape of the propagation curve. Figure 4 displays the six curves associated with (from top to bottom) $w_1N = 0.99, 0.9, 0.8, 0.7, 0.6$ and 0.5 . As the input decreases, the magnitude of the enhancement decreases too. The value of σ at which the maximum survival rate is obtained increases with smaller values of w_1 .

Finally, in Figure 5, the behaviour of our model for subthreshold ($w_1N = 0.99$, bottom curve), and superthreshold ($w_1N = 1.01$, top curve) inputs is illustrated. (The middle curve shows the results for $w_1N = 1.0$.) The effect of noise differs for these two regimes. Whereas noise enhances wave propagation in the subthreshold case, it suppresses propagation in the superthreshold case.

4 Discussion and Conclusions

Noise enhances the propagation of activation waves in complete synfire chains; we have found a range of noise levels for which patterns may be propagated. Such noise-dependent behaviour is characteristic of *stochastic resonance*, where nonlinear systems exhibit a noise-enhanced detection of subthreshold signals (see, e.g., [9]). Jung and Mayer-Kress's [10] excitable-media model resembles our model, in being based on threshold elements with a reset mechanism, but theirs is a lattice rather than a layered structure. They also observed (spatio-temporal) stochastic resonance, i.e., the noise-enhanced propagation of activation waves (and other spatio-temporal patterns).

We have focussed on the effects of intrinsic noise on the propagation of activation waves in a synfire chain. Our study is inspired by the time-constrained visual identification process which has to take place as a feedforward pass through the identification pathway. For simplicity, we reduced the identification task to a detection task by defining the input signal as an activation wave of synchronously spiking elements. Although our results show that noise enhances the propagation of such waves, it is not clear if the same counts for waves representing visual pictures.

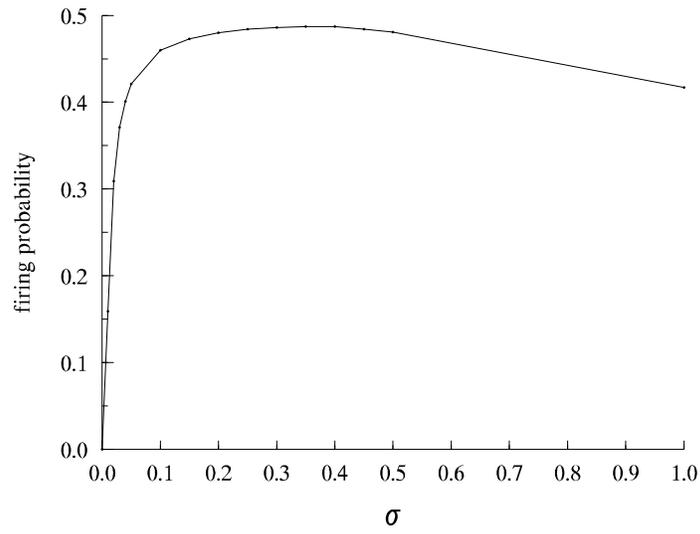
Hopfield [13] proposed that spike timing may be used as an encoding mechanism for perceptual processing. Combining Hopfield's coding proposal with our model implies a departure from the synchrony required in synfire chains. In this more realistic model, patterns are represented by the relative timings of action potentials. Each processing element has synapses with differential delays and processing in each layer involves the transformation of an incoming spatio-temporal pattern into a new spatio-temporal pattern. Upon reaching the output layer, the transformed spatio-temporal activation pattern maps directly onto a subset of elements which represent its identity. The question whether such a model would also benefit from intrinsic noise is a matter of further study.

In conclusion, we have found stochastic resonance in a noisy feedforward processing system. As neural elements are intrinsically noisy [6], we are pleased to discover that such noise is beneficial, rather than requiring suppression, for some types of rapid processing the brain probably employs.

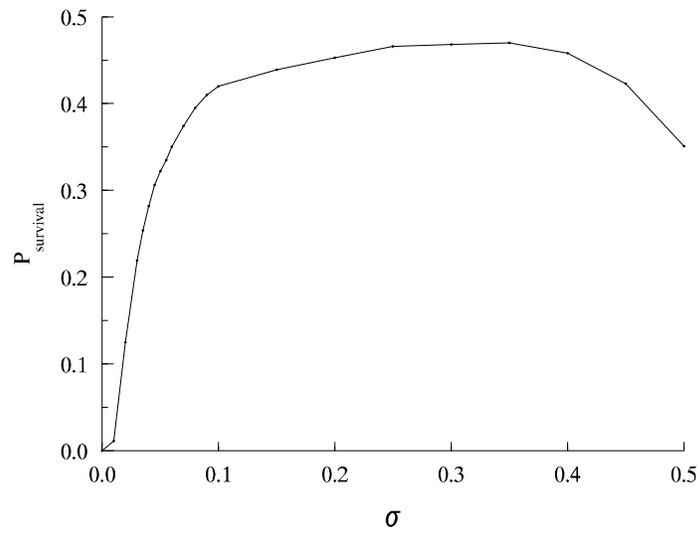
References

- [1] Thorpe, S.J. and Imbert, M. (1988). Biological constraints on connectionist modelling. In R. Pfeifer, Z. Schreter, F. Fogelman-Soulié, and L. Steels (Eds.), *Connectionism in Perspective*, pp. 63-92. Amsterdam: Elsevier Science Publishers B.V. (North-Holland).
- [2] Felleman, D.J. and Van Essen, D.C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1, 1-47.
- [3] Young, M.P. (1995). Open questions about the neural mechanisms of visual pattern recognition. In M.S. Gazzaniga (Ed.), *The Cognitive Neurosciences*, pp. 463-474. Cambridge, MA: MIT Press.
- [4] Desimone, R., Moran, J., and Spitzer, H. (1989). Neural mechanisms of attention in extrastriate cortex of monkeys. In M.A. Arbib and S. Amari (Eds.), *Dynamic interactions in neural networks: Models and data*, pp. 169-182. New York: Springer.
- [5] Cotterill, R. (1994). *Autism, intelligence and consciousness*. Biologiske Skrifter, 45. The Royal Danish Academy of Sciences and Letters. Copenhagen: Munksgaard.
- [6] Stevens, C.F. (1994). What form should a cortical theory take. In C. Koch and J.L. Davis (Eds.), *Large-Scale Neuronal Theories of the Brain*, pp. 239-255. Cambridge, MA: MIT Press.
- [7] Douglas, R.J. and Martin, K.A.C. (1990). Neocortex. In G.M. Shepherd (Ed.), *The Synaptic Organization of the Brain*, pp. 389-438. Oxford: Oxford University Press.

- [8] Abeles, M. (1991). *Corticonics. Neural circuits of the cerebral cortex*. Cambridge: Cambridge University Press.
- [9] Moss, F., Pierson, D., and O’Gorman, D. (1994). Stochastic resonance: Tutorial and update. *International Journal of Bifurcation and Chaos*, 4, 1383-1397.
- [10] Jung, P. and Mayer-Kress, G. (1995). Spatio-temporal stochastic resonance in excitable media. *Physical Review Letters*, 74(11), 2130-2133.
- [11] Usher, M., Stemmler, M., Koch, C., and Olami, Z. (1994). Network amplification of local fluctuations causes high spike rate variability, fractal firing patterns and oscillatory local field potentials. *Neural Computation*, 6, 795-836.
- [12] Thorpe, S.J. (1990). Spike arrival times: A highly efficient coding scheme for neural networks. In R. Eckmiller, G. Hartmann, and G. Hauske (Eds.), *Parallel processing in neural systems and computers*, pp. 91-94. Amsterdam: Elsevier Science Publishers B.V.
- [13] Hopfield, J.J. (1995). Pattern recognition computation using action potential timing for stimulus presentation. *Nature*, 376, 33-36.



(a)



(b)

Figure 2: (a) The probability of firing of an element in the first propagation layer as a function of σ . (b) The predicted survival rate ($P_{survival}$) as a function of noise intensity (σ).

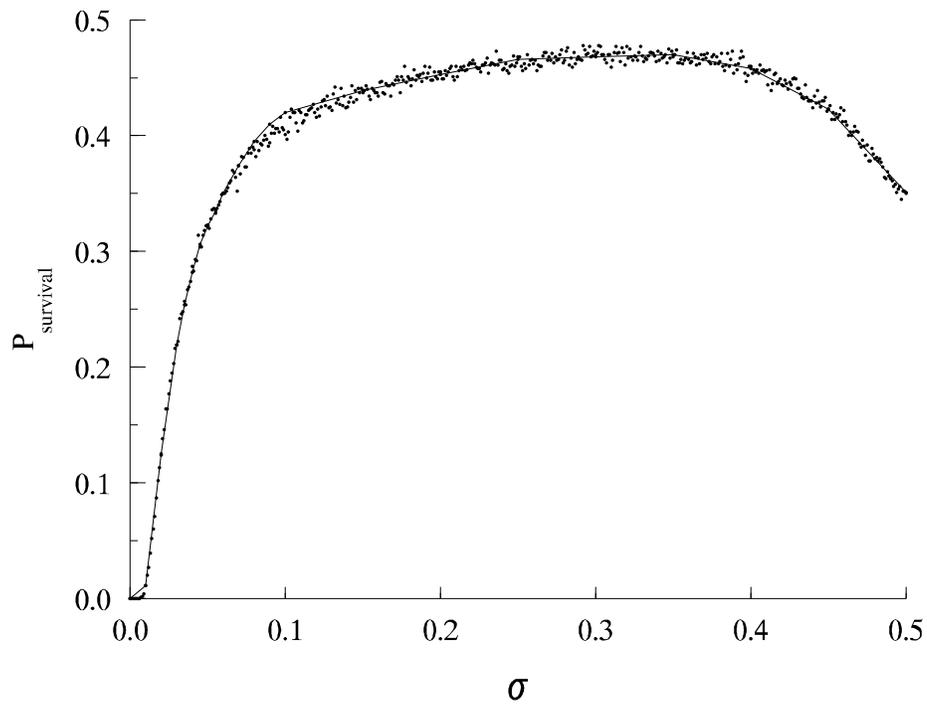


Figure 3: The survival rate (P_{survival}) as a function of noise intensity (σ). The dots are the simulation results. The drawn curve corresponds to the curve in Figure 2b.

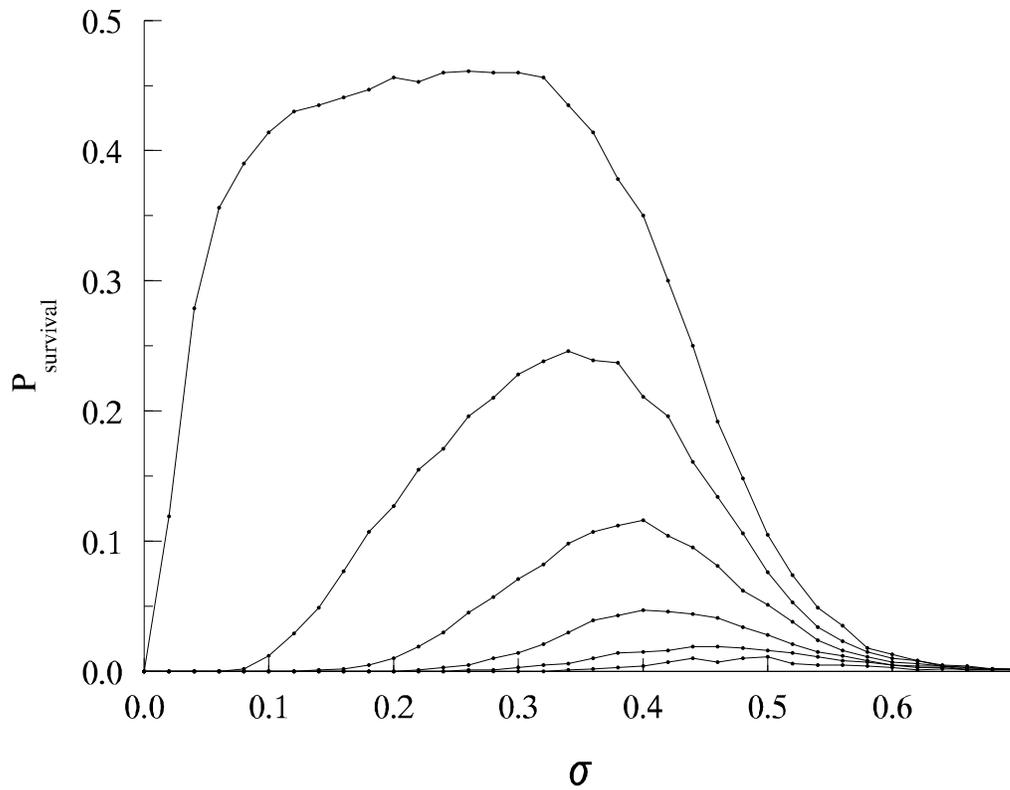


Figure 4: The survival rate (P_{survival}) as a function of noise intensity (σ) for several sub-threshold values of $w_1 N$. The curves show the results for (from top to bottom) $w_1 = 0.99, 0.9, 0.8, 0.7, 0.6$ and 0.5 .

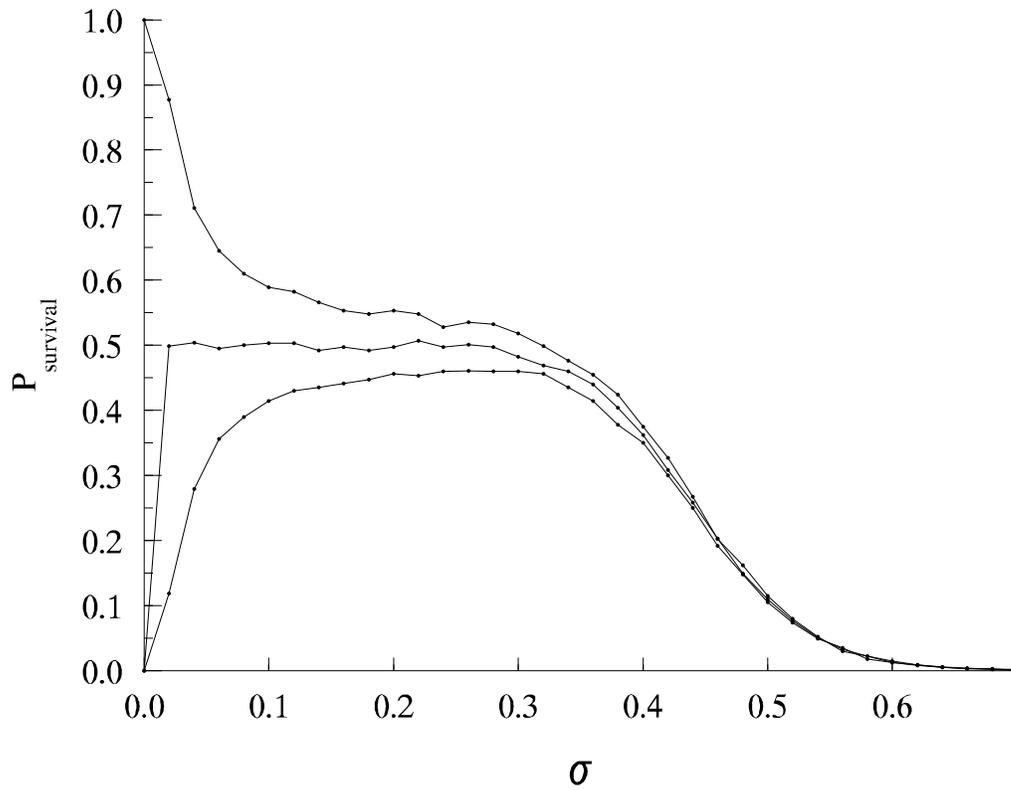


Figure 5: The survival rate ($P_{survival}$) as a function of noise for subthreshold input ($w_1N = 0.99$, lower curve), threshold input ($w_1N = 1.0$, middle curve) and superthreshold input ($w_1N = 1.01$, top curve).