Spatio-temporal information coding in the cuneate nucleus

J. Navarro[1], A. Canedo[1] and E. Sánchez[2]

[1]Departamento de Fisioloxía, Facultade de Medicina.
Universidade de Santiago de Compostela
15782 Santiago de Compostela, Spain
fsjna@usc.es, fsancala@usc.es
[2]Grupo de Sistemas Intelixentes (GSI)
Departamento de Electrónica e Ciencias da Computación, Facultade de Física.
Universidade de Santiago de Compostela
15782 Santiago de Compostela, Spain
eduardos@usc.es

Abstract

The dorsal column nuclei, cuneatus and gracilis, receive somesthetic information impinging on projection cells and local inhibitory interneurons. The presence of these interneurons allows spatio-temporal progressive coding of information that can be modelled (Sánchez et al., 2004) using their known synaptic connections with projection cells (Mariño et al., 1999; Aguilar et al., 2002, 2003). Here we explore the dependency of the processing time required to complete the progressive coding with regard to cutaneous stimuli varying in size and contras.

Keywords: Dorsal Column nuclei, Somatosensory System, Computational Models, Information Coding

1. Introduction

The dorsal middle region of the dorsal column nuclei (DCN) is constituted for two classes of neurons, glutamatergic cells projecting into the contralateral medial lemniscus and local interneurons releasing GABA, glycine or both neurotransmitters (Popratiloff et al., 1996). The cat's DCN receive cortical input from the primary somatosensory cortex (Chambers and Liu, 1957; Walberg, 1957; Rustioni and Hayes, 1981; Martinez et al., 1995) and primary glutamatergic afferents topographically aligned (Berkley et al., 1986; Conti et al., 1989; Rustioni and Weinberg, 1989; Kharazia et al., 1996).
Recent studies using intracellular as well as extracellular recording combined with microiontophoresis have revealed that: i) the cuneate neurons projecting to the medial lemniscus present a center-surround antagonism (Canedo and Aguilar, 2000), ii) the internal circuitry of the cutaneous sector of the cat's cuneate nucleus is such that the projecting cells with matched receptive fields monosynaptically activate each other through recurrent collaterals re-entering the nucleus, while inhibiting other projection neurons with different RFs (Aguilar et al., 2002), and iii) the cortico-cuneate cells (Aguilar et al., 2003) and primary afferents (Soto et al., 2004) with matched RFs activate and disinhibit aligned cuneo-lemniscal neurons and inhibit other neighbouring projection neurons with unmatched RFs. The activation at the centre of the RF is produced through NMDA and non-NMDA glutamate receptors, the lateral inhibition is produced through GABAergic interneurons and the disinhibition is mediated by serial glycinergic-GABAergic-projection cells interactions (Aguilar et al., 2002,2003; Soto et al., 2004).
The above results are the basis to determine the influences over each projecting neuron and were used to develop a computational model for the cuneate nucleus (Sánchez et al., 2004). Both projection neurons and interneurons are represented as MacCulloch-Pits processing units. Concretely, the activity of the processing units representing the projection neurons is under the modulating influence of primary afferent, collateral recurrent and corticocuneate inputs affecting these cells as described above. The different weight values w_{ji} model the synaptic interactions among the distinct classes of neurons and are grouped into matrixes whose values allow for adjusting the contribution of each neuronal class to the network representing the cuneate nucleus.

2. Methods

In this work we explore the behaviour of the computational model proposed by Sanchez et al. (2004). The model consists of 40,000 units distributed over three main layers representing: (1) projection or cuneolemniscal (CL) neurons, (2) GABaergic recurrent interneurons, and (3) glycinergic interneurons. CL units show an excitatory centre - inhibitory surround afferent 3x3 RF, as well as recurrent inhibition mediated through GABaergic interneurons. These units have a 7x7 ring-shaped RF derived from CL cells

that are second-order neighbours. Finally, the glycinergic interneurons present a fully excitatory 9x9 RF deriving from CL cells with overlapped RFs. The RF´s sizes were selected such that their combination gives the more stable results. In addition, the interneurons produce shunting inhibition on CL neurons thus achieving robust edge detection against stimulus intensity. The computational simulations initially update units in layer 1 and 2, then units in layer 3, and finally those located in layer 4. Each stage in the update process is called iteration.

Experiments were performed with stimuli of different forms, sizes and textures over a white background. Both stimulus and output intensity are represented in grey scale, thus taking values from 0 to 255. Stimulus textures are obtained from .bmp files produced with GIMP, a Linux image-processing application. Quasi-random frames with a repetitive pattern of hexagonal tiles were generated, and then combined to build a mosaic. The GIMP function *gaussian blur* has been used to modify the degree of stimulus contrast. Network responses were characterized based on two main features: robustness of the edge detection process and processing time required to reach a stationary state.

3. Results

In general, when a stimulus is presented to the network, three main elements in the output are clearly observed: (1) stimulus edge detection through the excitatory centre - inhibitory surround generated by primary afferents, (2) an oscillatory response reaching a stable state and determined by recurrent inhibition, and (3) a progressive coding starting from higher contrast regions and finishing with lower contrast ones and that is induced by the inhibitory action of glycinergic interneurons over GABAergic interneurons. This last element could be viewed as a type of fill-in effect.

We have initially tested the model with a non-blurred stimulus composed by hexagonal tiles. Figure 1 shows the stimulus (first image) as well as the network output corresponding to iterations 1, 3, 6 and 9. The edges, the oscillatory response and the fill-in progressive coding of some tiles can be observed. The fill-in process is fast and the stationary state is reached at iteration number 6.

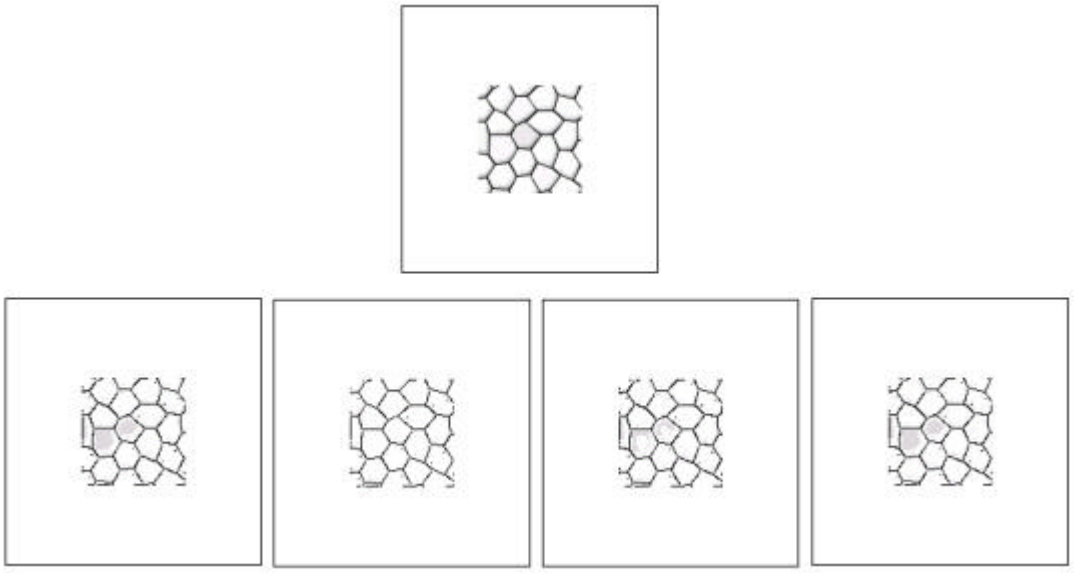

Figure 1. Fill-in effect for non-blurred stimulus. The stimulus (first image) is made up of hexagonal tiles of size 20. The rest of images show the network output for iterations 1, 3, 6 and 9.

In order to study the relationship between stimulus contrast and processing time of the fill-in effect, we have repeated the previous experiments with the same input, but different degrees of gaussian blur. When this parameter was set to 5 (moderate blur), the stationary state is reached later, at iteration number 18. Figure 2 shows the stimulus (first image) and the network responses at iterations 1, 3, 6, 9, 12, 15, 18 and 21. Due to the blur transformation, the fill-in effect affects a larger area, thus probably demanding more computational power, i.e processing time, to complete the effect. This trend is stressed when the gaussian blur parameter is set to 16 (high blur), as shown in Figure 3. The stimulus (first image) now requires 30 iterations to reach the stationary state. The fill-in effect now covers the whole area of the stimulus and progressive coding is much slower than in previous cases. The last example is presented in Figure 4, where the stimulus is a square with uniform texture and same size as before. The first image illustrates the stimulus while the other ones represent the output at iterations 1, 3, 6, 9, 12, 15, 21 and 25. The stationary state is reached after iteration 30. Although the stimulus is far simpler than those used in previous figures,

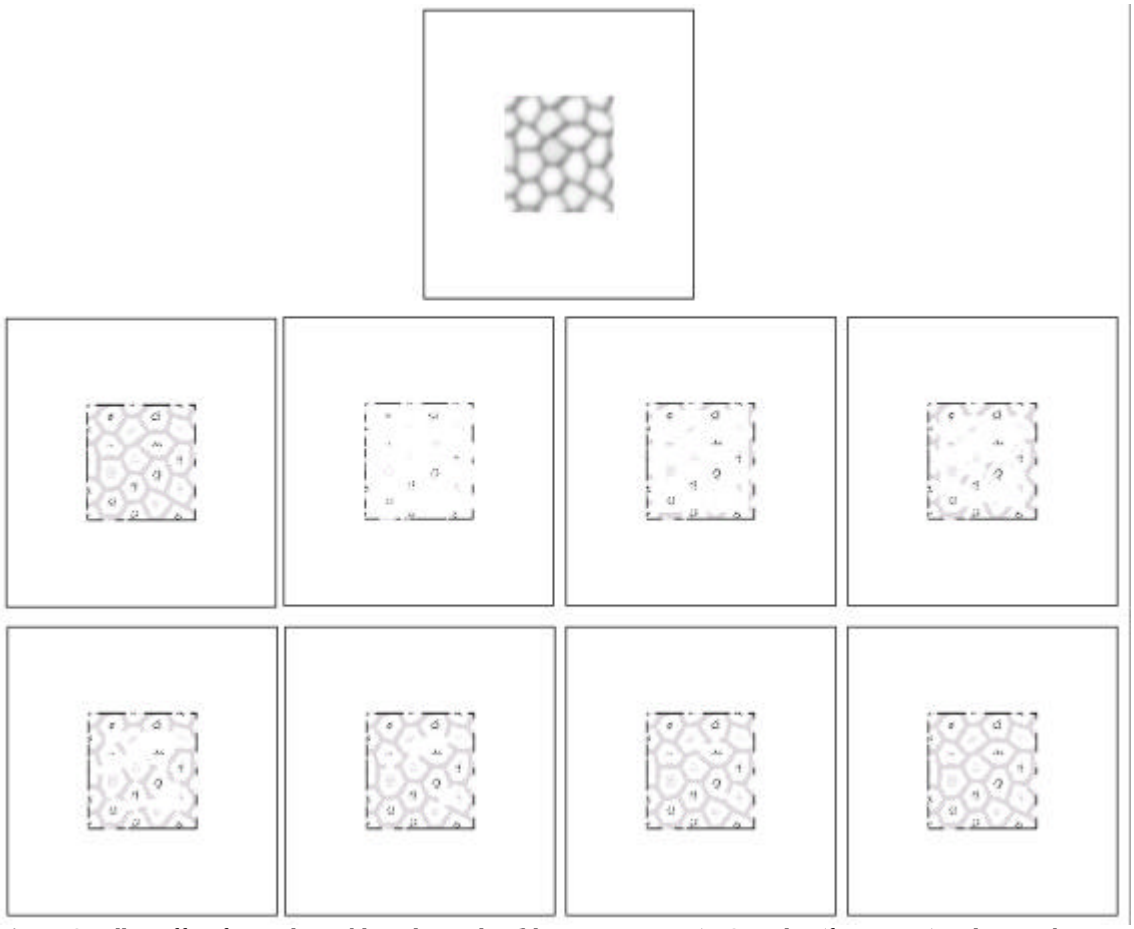

Figure 2. Fill-in effect for moderate blurred stimulus (blur parameter = 5). Stimulus (first image) and network output (following images) for iterations 1, 3, 6, 9, 12, 15, 18, and 21, is shown.

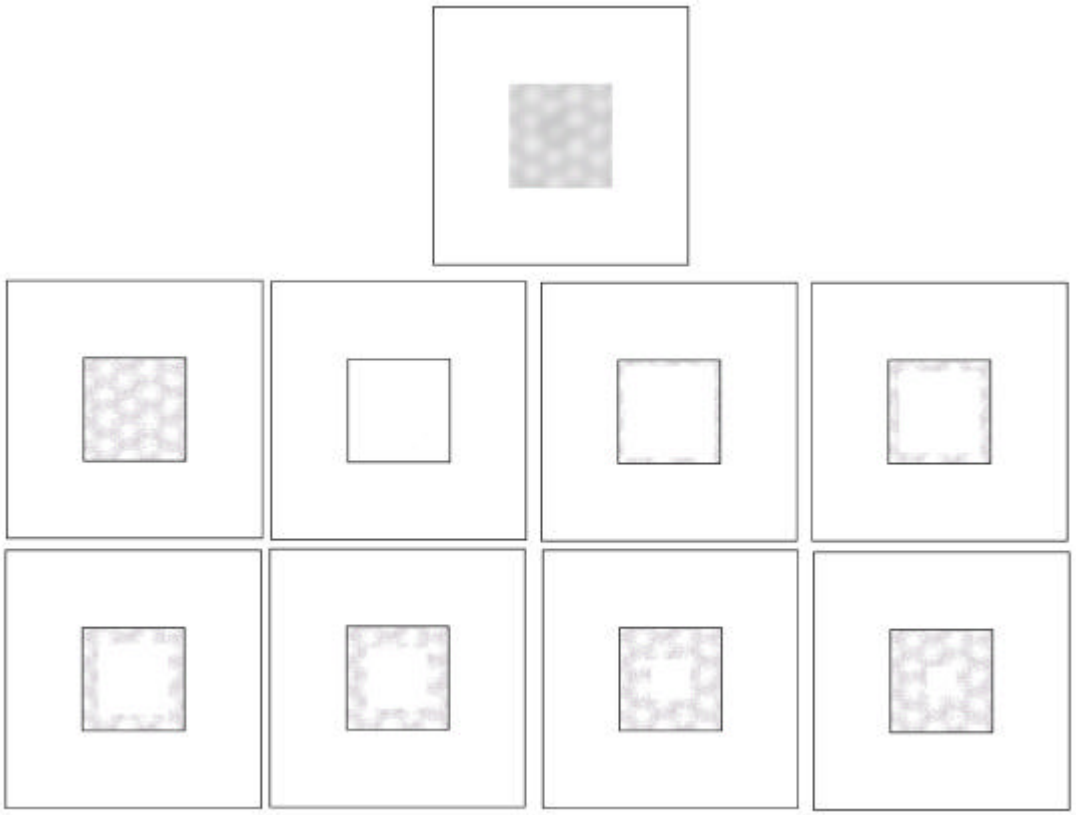

Figure 3. Fill-in effect for high blurred stimulus (blur parameter = 16). Stimulus (first image) and network output (following images) for iterations 1, 3, 6, 9, 12, 15, 21 and 24, is shown.

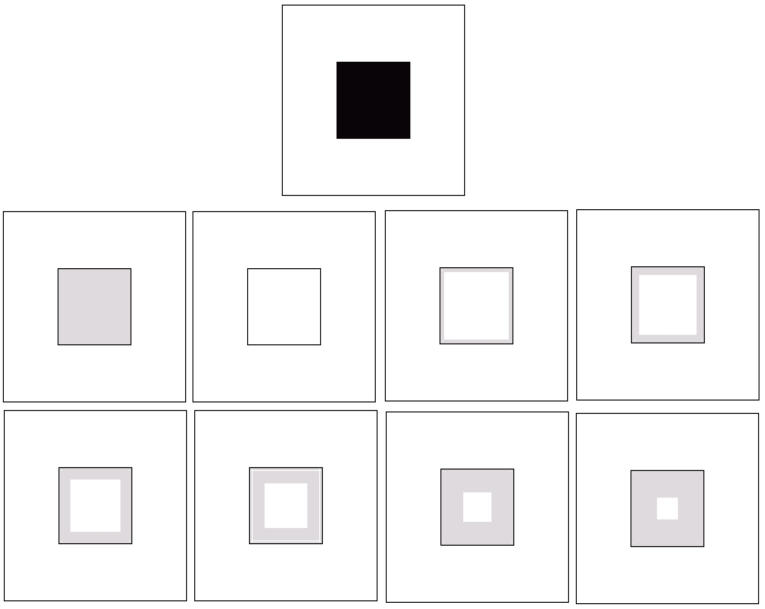

Figure 4. Fill-in effect for non-blurred stimulus with uniform texture. Stimulus (first image) and network output (following images) for iterations 1, 3, 6, 9, 12, 15, 21 and 25, is shown.

the main output elements are again presented: edge detection, oscillatory response and progressive fill-in coding.

A comparison between the previous experiments is shown in Figure 5. Two parameters, named "number of zeros" and "global output", are introduced to characterize the progressive coding on each iteration. The first one represents the number of neurons that are excited by the stimulus but that do not reach threshold and hence do not fire. The second one is the sum of the activation function at those units receiving afferent excitation. Both parameters show an oscillatory pattern that decreases in amplitude over time,

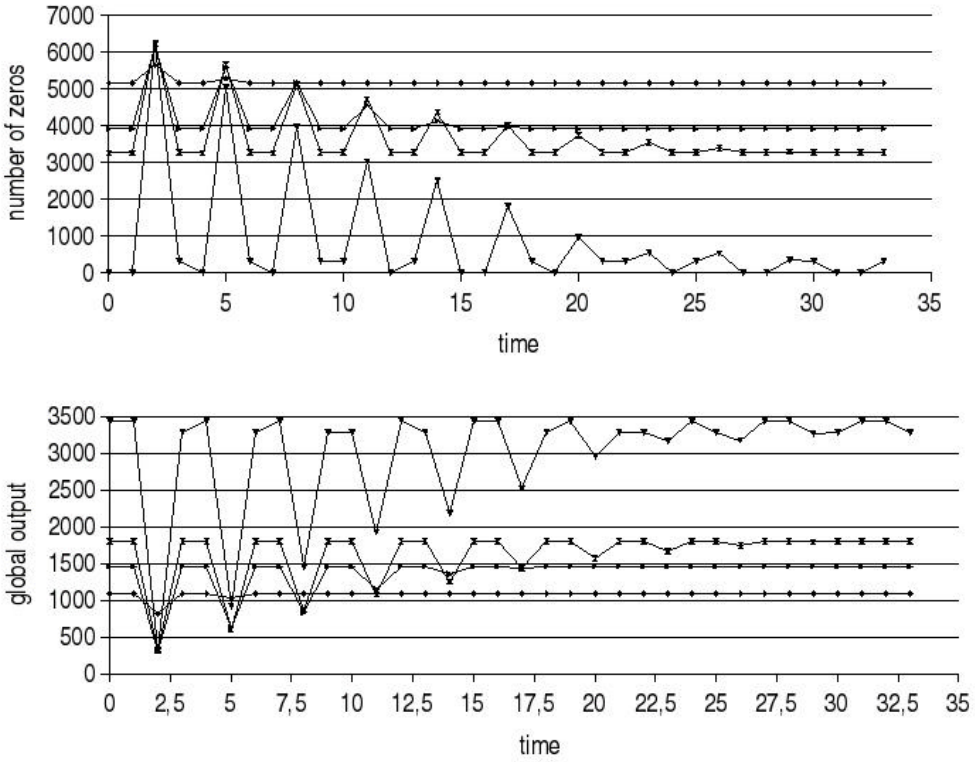

Figure 5. Parameters "number of zeros" and "global output" represented over time. In the top plot, the first trace describes the network response to the stimulus shown in Figure 1. The rest of traces correspond to figures 2, 3 and 4, respectively. In the bottom plot, the ordering is just the inverse. In both plots, the degree of stimulus contrast determines the oscillatory duration, the oscillatory amplitude and the residual oscillations at the stationary state. All stimuli have the same size and form.

meaning that the stationary state is reached in all cases. The degree of stimulus contrast determines the evolution of the parameters over time. Lower contrast implies: (1) longer duration of the fill-in effect before reaching the stationary state, (2) larger amplitudes of the oscillatory patterns during the fill-in effect, and (3) larger amplitudes of the residual oscillations when the stationary state is reached. The opposite can be applied for higher contrast. In the Discussion section, we provide a possible interpretation of these findings.

Additional experiments were performed with stimulus with textures made up with different tile sizes. Figure 6 confirms that the relationship between stimulus contrast and processing time is maintained. In all cases, the required processing time increases when contrast decreases (gaussian blur increases).

To complete this section, we have analyzed the fill-in effect dependency upon stimulus size and processing time. Results are shown in Figure 7 with round-shaped stimulus and uniform textures. Again, edge detection and fill-in progressive coding is observed. The plot illustrates that the processing time linearly increases with the stimulus size, expressed in terms of the stimulus diameter.

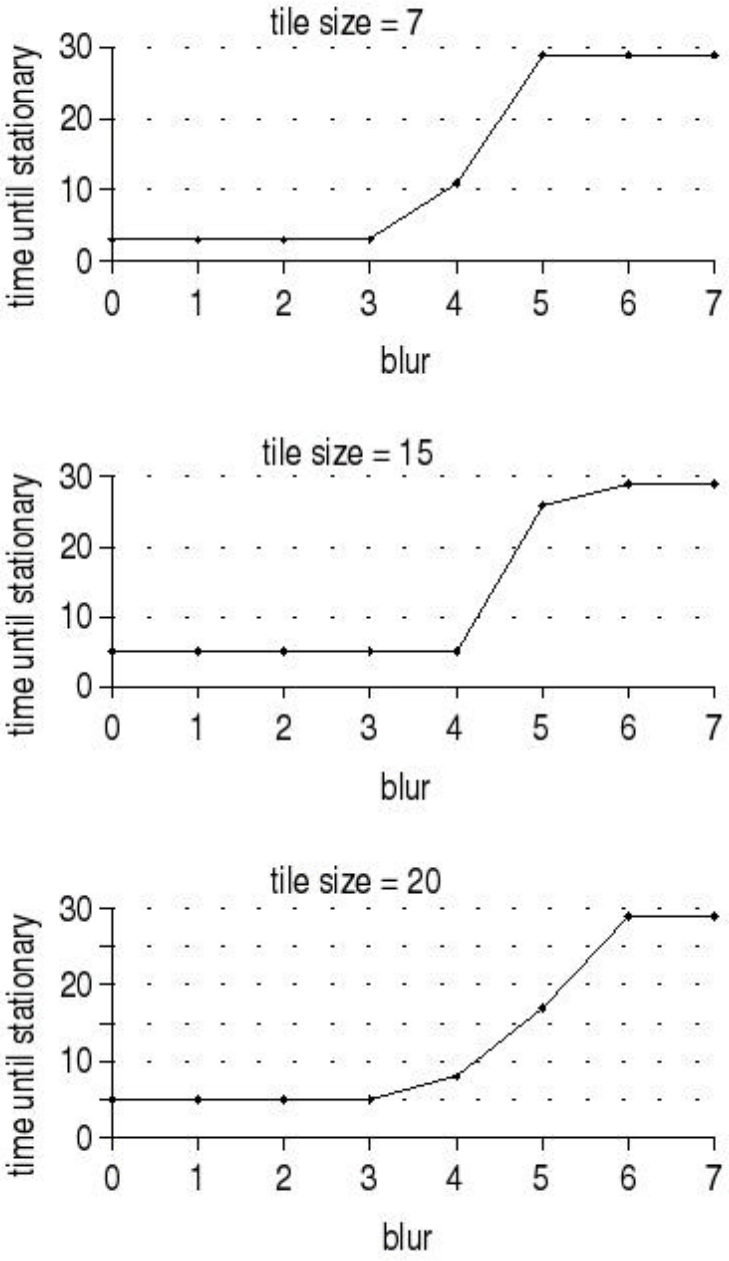

Figure 6. Relationship between processing time, degree of blur and stimulus tile size. For each tile size, the relationship between processing time and the degree of blur is shown. A sigmoid-like function describes the dependency of processing time and the degree of blur.

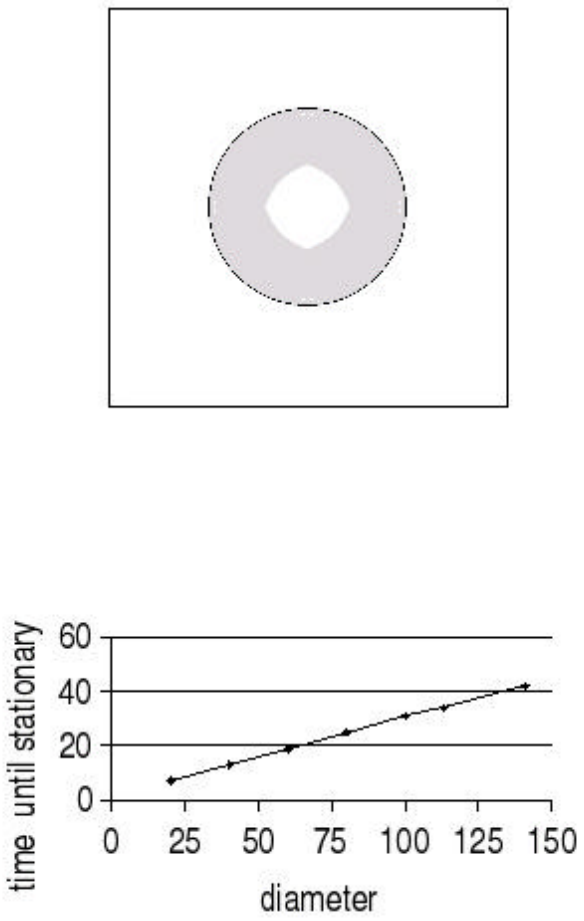

Figure 7. Relationship between stimulus size and processing time. Network output at iteration 21 after the presentation of a round-shaped stimulus with uniform texture (top). The relationship between processing time, until reaching the stationary state, and stimulus diameter follows a linear function (bottom).

4. Discussion

Based on the results, the network behaviour is robust as it performs edge detection and fill-in progressive coding under a variety of presented stimuli. However, the network processing varies depending on the stimulus contrast and size. According to the results, this processing seems highly predictable and in some cases can be easily quantified. The explanation of this complex behaviour lies on the network architecture, which was constructed based on experimental data obtained from projection neurons of the cat's cuneate nucleus. The interplay between excitatory and inhibitory influences is the key to explain the oscillatory response and the fill-in effect.

On the other hand, the model is consistent with the behaviour expected for a structure, like the cuneate nucleus, where the first processing of somatosensory information is performed. The function of tactile and pressure receptors in the skin is intended to get all possible information from the outside world. Such information is determined by the texture and size of objects around us. When the skin contacts surfaces of reduced size or highly-contrasted, the information is rapidly processed and compactly transmitted over time to higher processing areas, like the Thalamus, which also receives an "end of transmission" signal as the network reaches its stationary state. Furthermore, bigger or blur stimulus, i.e low-contrasted surfaces, induce either longer duration of the fill-in effect (longer oscillatory patterns) or residual oscillations when the stationary state is reached. Such coding can be understood as the need to further accomplish exploratory motor actions. The detection and classification of these encoded signals would require specific decoders, like the local oscillators proposed by Ahissar and Vaadia (1990), at higher cognitive structures.

The combination of the fill-in progressive coding discussed in this paper with appropriate decoders would allow the nervous system to evaluate the result of an exploratory action, to choose the best perception strategy, and broadly speaking, to manage its computational resources in a more efficient way.

References

Aguilar, J., Rivadulla, C., Soto, C. & Canedo, A. (2003) New corticocuneate cellular mechanisms underlying the modulation of cutaneous ascending transmission in anesthetized cats. *J. Neurophysiol*., **89**: 3328-3339.

Aguilar, J., Soto, C., Rivadulla, C. & Canedo, A. (2002) The lemniscal-cuneate recurrent excitation is suppressed by strychnine and enhancedd by $GABA_A$ antagonists in the anesthetized cat. *Eur. J. Neurosci*., **16**, 1697-1704.

Ahissar, E. $ Vaadia EE. (1990). Oscillatory activity of single units in a somatosensory cortex of an awake monkey and their possible role in texture analysis. *Proc. Natl. Acad. Sci*., **87**, 8935-8939.

Berkley, K.J., Budell, R.J., Blomqvist, A. & Bull, M. (1986) Output systems of the dorsal column nuclei in the cat. *Brain Res. Rev.*, **11**, 199-225.

Canedo, A & Aguilar, J. (2000) Spatial and cortical influences exerted on cuneothalamic and thalamocortical neurons of the cat. *Eur. J. Neurosci*., **12**, 2515-2533.

Chambers, WW. & Liu, CN. (1957) Cortico-spinal tract of the cat. An attempt to correlate the pattern of degeneration with deficits in reflex activity following neocortical lesions. *J. Comp. Neurol.*, **108**, 23-55.

Conti, F., De Felipe, J., Fariñas, I. & Manzoni, T. (1989) Glutamate-positive neurons and axon terminals in cat sensory cortex: a correlative light and electron microscopio study. *J. Comp. Neurol.*, **290**, 141-153.

Kharazia, V.N., Phend, K.D., Weinberg, R.J. & Rustioni, A. (1996) Excitatory amino acids in corticofugal projections: microscopic evidence. In: *Excitatory amino acids and the cerebral cortex*. Conti, F., Hicks, T.P. (eds). Cambridge, MA: MIT Press/Bradford Books, pp. 127-135.

Mariño, J., Martinez, L. & Canedo, A. (1999) Sensorimotor integration at the dorsal column nuclei. *NIPS* **14**, 231-237.

Martinez, L., Lamas, JA.& Canedo, A. (1995) Pyramidal tract and corticospinal neurons with branching axons to the dorsal column nuclei of the cat. *Neuroscience*, **68**, 195-206.

Popratiloff, A., Valtschanoff, J.G., Rustioni, A. & Weinberg, R.J. (1996) Colocalization of GABA and glycine in the rat dorsal column nuclei. *Brain Res*., **706**, 308-312.

Rustioni, A. & Hayes, NL., (1981) Corticospinal tract collaterals to the dorsal column nuclei of cats. *Exp. Brain Res.*, **43**, 237-245.

Rustioni, A. & Weinberg, R.J. (1989) The somatosensory system. In Björklund, A., Hökfelt, T. & Swanson, L.W. (eds), *Handbook of Chemical Neuroanatmy: Integrated Systems of the CNS.* Elsevier, Amsterdam, pp. 219-321.

Sánchez, E., Aguilar, J., Rivadulla, C. & Canedo, A. (2004) The role of Glycinergic Interneurons in the Dorsal Column Nuclei. *Neurocomputing*. (To appear in June 2004).

Soto, C., Aguilar, J., Martín-Cora, F., Rivadulla, C. & Canedo, A. (2004) Intracuneate mechanisms underlying primary afferent cutaneous processing in anesthetized cats. *Eur. J. Neurosci.* **19**, (in press).

Walberg, F. (1957) Corticofugal fibres to the nuclei of the dorsal columns. An experimental study in the cat. *Brain*, **80**, 273-287.