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Classification of somatosensory stimuli on the basis of the temporal coding at the cuneate nucleus

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ABSTRACT

The present study explores the capacity of a temporal code generated by the projection neurons of a realistic computational model of the cuneate nucleus to classify somesthetic stimuli. Four classification experiments were carried out with a feedforward network trained under a supervised learning algorithm in which the input is a vector including the sequence of outputs of the cuneate nucleus. The number of correct responses on each classification task varied with the complexity of the experiment, but a decrease in the number of errors was observed when presenting the optimal length of the input vector. This suggests that the cuneate nucleus might (1) transmit the appropriate information required for input classification, and (2) function as an information processing center and not merely as a relay or filtering stage.

1. Introduction

Our interest focuses on the information processing of the middle zone of the cuneate nucleus (CN), which is located at the dorsal column nuclei and receives input from primary afferents transmitting tactile information from cutaneous receptives located in the upper trunk. The types of cells found in the cuneate circuitry are the following [2,7]: projection or cuneothalamic cells (CT), gabaergic interneurons (GAB), and glycinergic interneurons (GLY). To date, only the structure of the receptive fields (RFs) of CT cells is known [5]. Their RFs, determined by the somatotopic organization of the afferent cells, are made up of an excitatory center as well as an inhibitory surround mediated by GAB interneurons coming from adjacent areas. Further experiments [1] suggested that CT cells also receive: (1) recurrent lateral inhibition induced by GAB interneurons, which are excited from CT cells located at non-adjacent receptive fields, and (2) recurrent disinhibition, or facilitation, mediated by GLY interneurons inhibiting GAB interneurons. After being transformed by the cuneate nucleus, the somesthetic information passes to the ventro-postero-lateral (VPL) nucleus of the thalamus [6] before reaching the primary somatosensory cortex.

The functional role of the CN is hard to assess experimentally because of some important methodological limitations: firstly, the complexity of carrying out intracellular recordings of CN cells in awaking animals, and secondly, the difficulty of setting and controlling the stimulation parameters with the required spatial and temporal accuracy. To overcome these limitations, a realistic computational model of the CN based on experimental findings was developed [14]. A scheme of the model describing the different types of neurons as well as both afferent and recurrent connections is shown in the left inset of Fig. 1. The neuron's RFs described above are also depicted in the right inset. In a previous work [9], it has been shown that this circuitry produces a spatio-temporal progressive coding that starts signaling regions with lower regularity (higher intensity contrast), and progressively covers regions with an increasing degree of regularity (lower intensity contrast) until the stimulus is filled. In order to visually explore this code evolving over time, a global output variable has been chosen. It might represent the activity of a single feature detector integrating the output of CT neurons at any given time. The temporal series of this variable reveals an oscillatory pattern showing a repeated behavior in which the oscillation's amplitude diminishes with time until a stationary state, corresponding with the end of the fill-in process, is reached. The analysis of this behavior discovered positive correlations [9] between the degree of regularity of the stimuli and some parameters of the oscillatory pattern such as (1) the duration of the fill-in effect, (2) the amplitude of the oscillatory patterns during the fill-in effect, and

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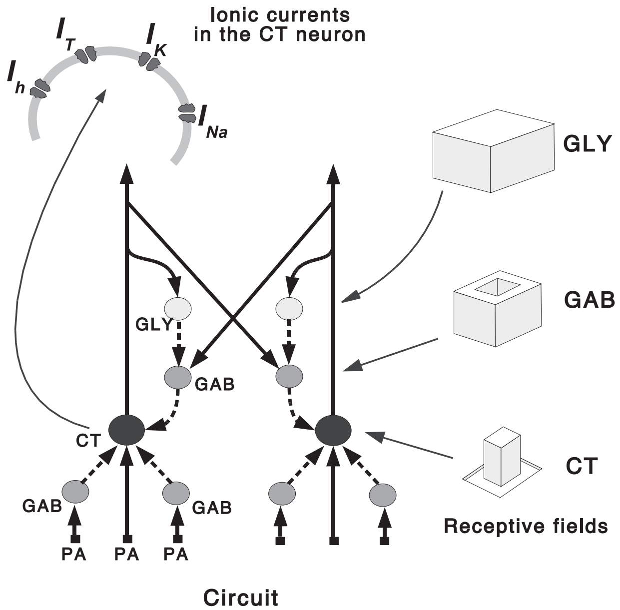

Fig. 1. Realistic model of the cuneate nucleus based on experimental findings in the cat. PA: primary afferents, CT: cuneothalamic cells, GAB: gabergic interneurons and GLY: glycinergic interneurons. Solid and dashed arrows represent excitatory and inhibitory synapses, respectively. The shape of RFs for CT, GAB and GLY cells is also shown.

(3) the amplitude of the residual oscillations when the stationary state is reached. Similar correlations were found between the size of the stimuli and the mentioned parameters of the oscillatory pattern. These findings might suggest that (1) the progressive coding built at the CN seems to encode salient features of the stimuli (such as the degree of regularity and size), and (2) the oscillatory patterns could be useful to decode and classify incoming somesthetic stimuli. This paper is aimed at testing the later hypothesis.

2. Methods

2.1. Model of cuneate nucleus

Each CT neuron n_j has been modeled in a realistic way with the following firing condition $y_j(t) = 1$ if $v_j(t) > \Theta_{spike}$, where $v_j(t)$ is the membrane potential at time t and Θ_{spike} a positive threshold value. The membrane potential is updated as follows: $v_j(t) = v_j(t-1) + I_j^{total}(t) - I_j^{ionic}(t)$, where the total afferent input $I_j^{total}(t)$ being computed by multiplying every input I_i inside its receptive field by its corresponding synaptic weight w_{ij}. The ionic current term I_j^{ionic} is a linear combination of the contributions of a sodium current, a potassium current, a hyperpolarization-activated cationic current, and a low-threshold calcium current, all currents being supported by experimental evidence [4,11,12]. The interneurons have been characterized as simple McCulloch–Pitts units, in which the output of the jth neuron is $y_j = \Psi(\sum w_{ji} x_i)$ with activation function Ψ being of the threshold type, and the strength of the synapse between neuron ith and neuron jth being described by the weight w_{ji}. As regards the circuitry, the key aspect is the recurrent loop around the cuneothalamic neurons, whose state at time t is determined by the output of other CT neurons at time $t-1$. These recurrent connections are responsible for the generation of the temporal progressive code observed as the output of CT neurons. Further details of the model and its temporal code can be found in Navarro et al. (2007) [10].

2.2. Preprocessing the oscillatory pattern of the global output variable

As described in the Introduction section, a single global output variable was initially chosen to visualize the progressive coding generated by the CN over time. The positive correlations found between some parameters of the global output oscillatory pattern (see Fig. 2 and panels B1 and B2 of Fig. 3) and salient features of the stimuli might suggest that this way of coding could be useful to classify the stimuli at later processing stages. As the oscillatory pattern of the global output presents doublets, which are repeated peak values to probably provide a robust postsynaptic response at the VPL, as well as points of time in which the CN output is silent, preprocessing was carried out in a two-stage process: the first one aimed at removing null values and repetitions of the first peak value, the second one to normalize the data. Panels C1 and C2 of Fig. 3 show two examples of this transformation.

2.3. Classification with a feedforward network and supervised learning

Our hypothesis is that the oscillatory patterns could be useful to classify incoming somesthetic stimuli. To test this idea we have been inspired by the concept of ideal observer introduced by Britten et al. (1992) [3]. In their work, an observer has to predict the motion directions in a two-alternative forced choice task on the bases of ROC curves derived from behavioral experiments with monkeys. They found that the observer could perform the discrimination tasks with a similar accuracy that the monkey did. Our

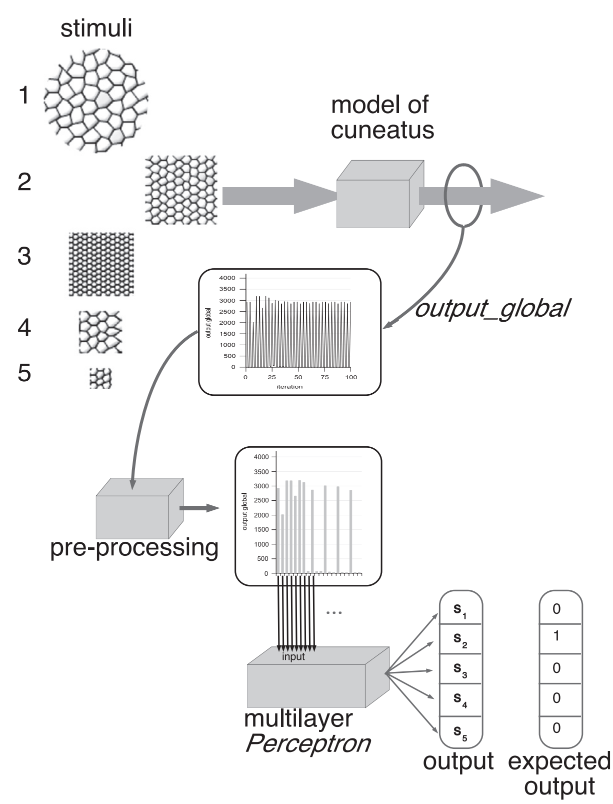

Fig. 2. Classification experiments to test the encoding capabilities of the temporal oscillatory pattern. The oscillatory pattern made up of the *output_global* variable evolving over time is pre-processed by removing zeros as well as the repeated first value. The resulting series is the input vector of the classifier. The expected output (size 2 in this example) is extracted from the training set in order to both compute the classification error and modify the appropriate learning weights. Arrows indicate the flow of data in the classification experiments.