TRANSFORMATION OF CONTROL SIGNALS FOR SACCADIC EYE MOVEMENTS

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Abstract

The topography of extrapersonal space is reflected in the functional organization of various neural structures. A model example is the eye-movement control regions in brain stem and cortex. Parameters of a saccade are here represented in spatial distribution of activity in topographically arranged population of neurons. The transformation of this spatial code into the commands for extraocular muscles remains an open question. In the following paper a first step in this transformation is suggested: a neural wiring scheme for computation of the horizontal and vertical component of the movement from the motor map. This scheme is an implementation of existing black-box models into a physiologically plausible neural circuitry. Results of computer simulations are compared with experimental data to confirm the plausibility of the model.

1 Introduction

In spite of a long history of enquiry, today the understanding of complex human behavior seems to be far away. In such situation the most powerful (and perhaps the only possible) approach is to reduce the global question into well defined and analyzable parts, taking into account that the whole picture is broken and that the answers will be only partial. But that is the price to be paid. The analysis therefore could start with the situations where the task to be solved is well defined and there exists measurable parameters of the behavior.

One of the simplest behavioral task is orienting movement: the central nervous system directs attention to one among several objects detected by sensors, moves the eyes to that object and in some cases generates a limb movement to grasp it [21]. The movements of the eyes were described as saccades (from French "saccade" meaning jerk) and they are characterized by high-velocity change of eye position from one fixating point to another. Here, the sensorimotor transformation performed by our brain is easily to define: relative position of the object with respect to the fovea is transformed into the trajectory of eyes. The neural substrate for this transformation - the oculomotor system - has been an object of scientific interest for a long time. The most important parts of it has been identified and anatomically described. A major breakthrough in understanding the physiology of this system was made possible by single cell recording and stimulation in awake animals. The experiments of D. A. Robinson [12,14] revealed two very important control regions for eye movements: the cortical region called Frontal Eye Fields (FEF) and the brain stem structure superior colliculus (SC). Later experiments confirmed the importance of SC and FEF for the generation of eye movements: the combined lesion of both resulted in the lost of purposive movement control [15]. Robinson's experiments has shown, that microelectrode stimulation at any site in each of these structures reliably produces a saccade of particular size and direction, regardless of the initial position of the eye (fig 1a). In fig. 1b is a motor map in SC revealed by systematic stimulations through the whole region. It is evident that represented is contralateral oculomotor range: amplitudes from 2° to 50° and directions from -60° (down) to +60° (up).
Further experiments revealed a similar functional organization of both FEF and SC. Most of the results were obtained by single cell recording in awake animals performing saccadic eye movements. In both structures neurons were found that responds to visual stimuli (visual cells), neurons with the activity preceding movement (movement cells) or neurons with both types of activity (visuomovement cells). These results provide a strong evidence that FEF and SC are crucial structures in sensori-motor transformation necessary for the control of purposive saccades.

In FEF the visual cells form a topographic map of the contralateral visual field with the gaussian receptive field of each cell. This means that each neuron responds most vigorously to a stimulus located at one particular point in the visual field and its response decreases with the distance of the stimulus from that point. The movement cells form a similar map; however the movement fields of the neurons are Gaussian in direction but log gaussian in amplitude. For visuomovement cells the sensorial and movement maps are aligned [2,6].

In SC the visual map is located in superficial layers, while visuomovement and movement cells are in the intermediate and deeper layers [8]. Besides the visual map, there are also somatosensory and auditory maps, each being topographically organized [17]. Movement fields in the SC were also Gaussian-like in shape, but with increasing distance from the central region the cells were tuned more broadly [16].

This organization suggests that the task to be solved in FEF and SC is to transform the position of a target detected by sensors into a motor error signal necessary for the generation of a saccade. The position of the target is encoded in the distribution of activity in the sensory maps and similar activity spread in the motor maps precedes each saccade. This spatial pattern of discharge encodes initial motor error, i.e. the amplitude and direction of a desired saccade [6,18]. In order to explain the next stages in the transformation of control signals we shall start at the endpoint - the extraocular muscles.

Eye muscles are arranged in three pairs aligned in almost perpendicular planes, each pair being responsible for one dimension [9]. The investigation in behavior of oculomotor neurons revealed that a saccade is preceded by a burst of activity proportional to the exerted muscle force. In the motoneurons innervating opposing muscle a decrease of activity was observed. If the movement was in the direction perpendicular to the plane of muscles, no activity change was noticed [13,3]. The parameters of a saccade in the pulling direction of the muscle are determined by the intensity and duration of motoneuron discharge burst.

Figure 1: a. Saccades produced by stimulation of one neuron in SC. Starting point of each arrowline is the initial position of the eye. b. Motor map in SC. Reprinted from [14].