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► To cite this version:

Jérémy Fix. A computational approach to the control of voluntary saccadic eye movements.. The 1st International Conference on Cognitive Neurodynamics : ICCN 2007, 2007, Shanghai, China. inria-00166540

HAL Id: inria-00166540

<https://inria.hal.science/inria-00166540>

Submitted on 7 Aug 2007

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A computational approach to the control of voluntary saccadic eye movements

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Abstract. We present a computational model of how the several areas involved in the control of voluntary saccadic eye movements might cooperate. This model is based on anatomical considerations and lays the emphasis on the temporal evolution of the activities in each of these areas, and their potential functional role in the control of saccades.

1 Introduction

From the early work of [1], re-examined by [2], we know that the visual information is processed along two pathways : the ventral stream provides visual information for object recognition whereas the dorsal stream provides information necessary for the the control of action. In the rest of the article, we will exclusively focus on the control of voluntary saccadic eye movements involving a cortical pathway throughout several brain areas. A subcortical pathway also exist and might be involved in reflexive saccades. If we follow the pathway from a visual stimulation to the production of a saccade, we can identify several structures involved directly or indirectly in the control of these movements. In the case of voluntary saccadic eye movements, the main areas include the superior colliculus (SC), the frontal eye fields (FEF), the supplementary eye fields (SEF), the dorsolateral prefrontal cortex (dlPFC), the lateral intraparietal sulcus (LIP) and the visual cortex ([3, 4]).

In the last few years, several studies have led to a better understanding of the representation of the spatial representation of visual information in LIP. Both experimental measurements and computational models have shed the light on an eye centered representation ([5, 6]). The neurons in LIP are also strongly modulated by the position of the eye, head and body parts. Andersen et al [5] have shown, for example, that the activity of the neurons in this area depends on the eccentricity of the eye, while always exhibiting a maximal response at a given retinal position. Computational modelings [7] have provided strong results that indicate that the representation of the information in a common eye-centered representation, modulated by the position of the eye, head and body parts, can be decoded in several frames of reference, namely eye-, head- and body-centered.

The neurons in FEF receive strong topographically organized projections from the posterior parietal cortex. Umeno et Al [8] distinguish three types of

neurons in FEF. *Visual neurons* respond to visual stimuli but not to the initiation of a saccade. On the opposite, *movement related neurons* fire before and during saccades, whether or not the saccade is triggered by a visual stimulus. *Visuomovement neurons* have both visual and movement-related activity. Among these three types of cells, only ones related to movement project to the superior colliculus and to the caudate nucleus [3]. The first projection carries the target of the saccade while the second determines when the movement is executed.

An enhanced activity in the supplementary eye field (SEF) is recorded when the selection of a target (among several possible stimuli) for a saccadic eye movement is based on internal factors such as motivation or reward expectation [9, 10]. The SEF has been thought to represent the targets of saccadic eye movements in a craniocentric frame of reference [11]. More recently, [12] have shown that the encoding in SEF is much more complex than a simple craniocentric representation and that there coexists a continuum of eye-, head- and space/body-centered representations for gaze coding. Finally, [13] have provided evidences for the role of the dorsolateral prefrontal cortex in spatial working memory.

While more and more is known about the different structures involved in the control of saccadic eye movements, the way these areas cooperate to select the relevant stimuli, to decide which of them is the next target to focus on, to memorize these targets when the task at hand requires it is still unclear. We propose in the next section a neural network architecture relying on the previously introduced anatomical considerations and illustrate its functioning with a classical double-step task.

2 Architecture of the model

The model we propose, depicted on figure 1, is based on the Continuum Neural Field Theory ([14, 15]), a framework of dynamical lateral interactions within a neural map. It consists in several two dimensional sets of units, each of them characterised by an activity denoted $u_M(x, t)$ (for a unit at position x , in the map M) that follows the ordinary differential equation 1.

$$\begin{aligned} u_M(x, t + 1) &= u_M(x, t) + \tau \cdot \delta u_M(x, t) \\ \delta u_M(x, t) &= \sum_{y \in M} w_{xy} \cdot u_M(y, t) + I(u_{M'}(y, t), y \in M', M' \neq M) \end{aligned} \quad (1)$$

where M and M' are maps of units, w_{xy} a *mexican-hat* lateral-weight function and $I(u_{M'}(y, t), M' \neq M)$ a function computing the influence of input units. We distinguish two kinds of function for the integration of the inputs : the classical weighted sum and a weighted sum of the product of inputs' activity. We have shown in [16] that these sigma-pi integrations provide an efficient way to remap a visual information across saccadic eye movements.

After this brief introduction of the computational bases, we will describe the global architecture of the model and the functional role of each map. The visual input feeds the LIP map. This map represents the visual information in

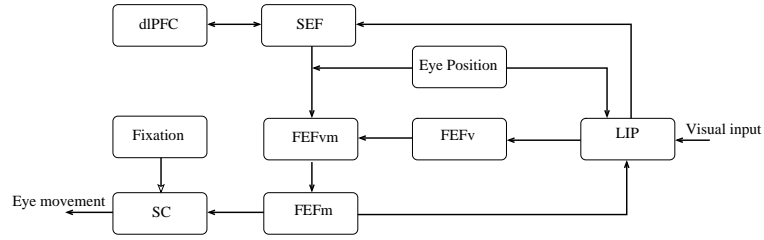


Fig. 1. A possible architecture of how the major brain areas involved in the control of voluntary saccadic eye movements might cooperate.(Refer to the text for details)

an eye-centered frame of reference, its units being modulated by the position of the eye. The LIP map then projects to the FEFV and SEF maps. The pathway from FEFV to FEFM selects one target for a saccadic eye movement among the presented stimuli. These maps represent the visual information in an eye centered frame of reference (FR). While FEFVM represents all the potential targets for a saccadic eye movement, a local excitatory - global inhibitory pattern of lateral connections in FEFM provides a competition among these targets, so that only one stimulus can emerge in FEFM : the target of the next saccade. This target then reenters LIP; this reentry signal represents the spatial attention bias observed in physiological recordings. The SEF map encodes the positions of the eye in the orbit (in a craniocentric or head-centered FR) that center each stimulus on the retina. As detailed in the introduction, the distributed representation in LIP (in an eye centered FR, modulated by the proprioception) allows to decode the information in such a frame of reference. The recurrent circuit formed by SEF and DLPFC forms a craniocentric memory of the stimuli, used when the task requires to memorize their position. This memory has the advantage to be independent on the position of the eye and provides the FEFVM map with the positions of the stimuli relative to the current position of the eye, this transformation being realised by the sigma-pi combination of the SEF and EYE POSITION maps (we cannot explain in detail this transformation but the same principle is detailed in [16]). The projections from FEFM to SC carry the position of the target for the eye movement. SC is strongly inhibited by FIXATION units so that the saccade is executed only if these neurons release their inhibition. This inhibition might represent the inhibitory projections from the FEF to SC, going through the basal ganglia, reported in anatomical studies.

3 Discussion

The presented architecture was successfully applied to a classical double-step task¹. The aim of the model was not to reproduce all the physiological prop-

¹ A video showing the temporal evolution of the model is available at <http://www.loria.fr/~fix/demo.php?demo=iccn>

erties gathered on the areas involved in the control of voluntary saccadic eye movements. Rather, we wanted to test a possible way in which these areas might cooperate emphasizing the functional role of each of them. One of the limitations of this model is that the selection of the target of the saccade emerges from lateral competition in the FEFM map, giving the opportunity to all the potential stimuli to be selected while one may desire to avoid selecting a previously focused one. A bias toward non previously focused stimuli may be achieved by adjoining a working memory to the FEF maps as illustrated in [16].

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