Subcortical saccadic selection processes: a model of the tecto-basal loops

Charles Thurat[1], Steve N'Guyen[2] and Benoît Girard[1] *

(1) Institut des Systèmes Intelligents et de Robotique, UMR 7222
CNRS - Université Pierre et Marie CURIE,
Paris, France
(2) Laboratoire de Physiologie de la Perception et de l'Action, UMR 7152
CNRS - Collège de France,
Paris, France

Abstract

Viewing a scene or searching for a target usually require an observer to make a series of saccades that quickly shift the orientation of the eyes. As many recent experimental studies highlighted the active role of the superior colliculus in saccade target selection, we here explore the possibility that the Superior Colliculus and Basal Ganglia interact in order to produce target selection in a purely subcortical network, within a new combined model of both structures. We propose a model linking together recent SC (Tabareau, Bennequin, Berthoz, Slotine, & Girard, 2007) and BG (Girard, Tabareau, Pham, Berthoz, & Slotine, 2008) models, and borrowing stochastic accumulation principle from a more abstract class of saccade selection models. We propose an explanation of experimental data gathered by (McPeek & Keller, 2004) regarding deficits in target selection after inactivation of the SC.

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1 Introduction

The generation and control of saccadic eye movements have been studied for a long time; they involve a large network of highly-interconnected cortical and subcortical structures (Moschovakis, Scudder, & Highstein, 1996). Microstimulation studies have shown that saccades can be generated by stimulating the superior colliculus, a multi-layered structure of the midbrain situated at the very middle of the various saccade-generation networks.

The SC is composed of several layers representing logarithmic retinotopic maps of the visual field (cf. (May, 2006; Isa, 2002; Isa & Hall, 2009), the most superficial receiving direct input from the retina as well as various projections from the cortex, and the deepest one controlling the generation of the motor command in the brainstem saccade generator.

Each layer of the SC is involved in loops with the basal ganglia (BG) (McHaffie, Stanford, Stein, Coizet, & Redgrave, 2005), a structure known for its ability to select between signals by decreasing its basal inhibitory output for the winning competitor and hyperinhibiting the losing competitors. The selection of the target of the upcoming saccade all the inputs of a given moment has long been thought to result from frontal eye fields (FEF) and basal ganglia interactions only. Since 2000, a number of experimental studies challenged this view by providing pieces of evidence suggesting that the SC is indeed involved in selection, for example (McPeek & Keller, 2004). Yet the most common hypothesis for this phenomenon relies purely on reciprocal lateral inhibitions within the SC layers to discriminate between competing stimuli, with no consideration for the functionnal loop between the SC and BG even though the BG are famed for their selection ability.

We propose a model of the SC-BG loop to test whether the selection processes occuring in the SC can result from subcortical SC-BG interactions. We propose a new interpretation for the activity profile of the Visuo-Motor prelude neurons recorded by (McPeek & Keller, 2002), seeing them as a stochastic integrators, which in turn bias the integration process, allowing the selection of a single target and the suppression of distractors.

2 Methods

The BG model is adapted from (Girard et al., 2008), with parameter modifications scaling it up to fit the dimensions of the SC retinotopic maps.

The SC model derives from that of (Tabareau et al., 2007) concerning the generation of saccadic motor commands from the activity of the motor map, onto which several new maps have been added. An integration map projects to the BG, which projects back toward the SC in two loops : an "upper"-one with shunting inhibition of the connexion between the input and integration layers, and a "downer"-one, with standard inhibition of the activity of each neuron in the buffer layer (cf. Fig. 1, left).

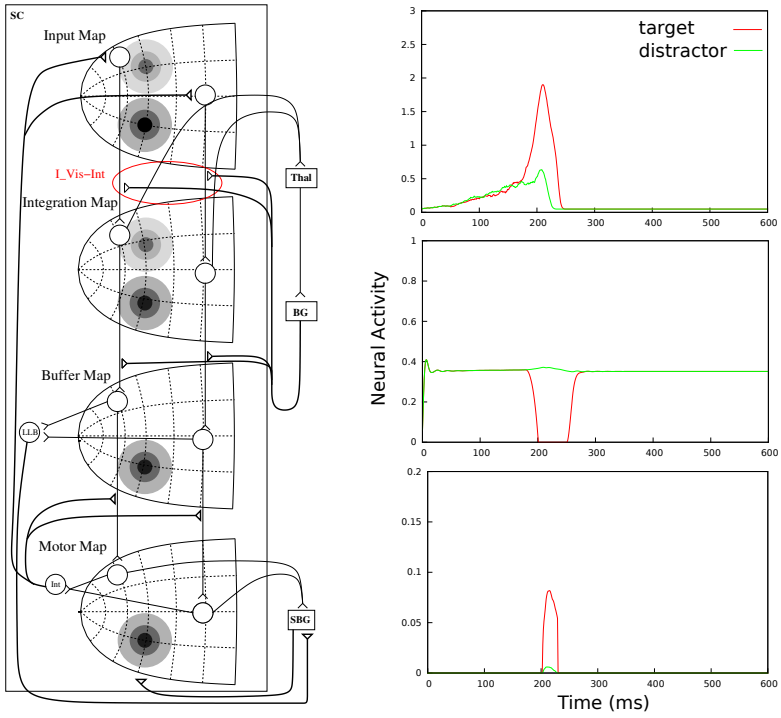

Figure 1: Left: architecture of the SC-BG model. Int: integrate-and-saturate neuron; LLB: long-lead burst neurons; SBG: saccade burst generators; Thal: Thalamus; $I_{Vis-Int}$: see eqn. 1. Right: activity of neurones coding for the center of two competing targets in several key maps of the model; Top: SC integration map activity fed to the BG; Middle: BG output fed back to the SC; Bottom: SC motor map activity.

The use of an integration map was guided by two considerations: first, feeding the BG circuit with two visual inputs of identical salience (i.e. two bumps of identical height) results in simultaneous selection of the two bumps, and in averaging saccades, while monkeys are able to select a target among

four identical ones; second, many high level saccadic selection models (Ludwig, Mildinhall, & Gilchrist, 2007) rely on stochastic accumulator races to take such decisions and accurately model many behavioral effects. Thus, it seemed interesting to investigate a possible neural substrate for such a mechanism. The most important part of our mechanism is the BG shunting inhibition that modulates the visual map input to the integration map ($IVisInt$, represented by a red ellipse on fig. 1, and thus modulates the rate of integration as follows:

$$I_{Vis-Int} = w_{Vis-Int} \times (\theta - BGOut(i,j)) \times Vis(i,j) \quad (1)$$

where Vis is the visual map, $BGOut$ the output of the BG, (i,j) the coordinates of the considered neuron, and θ a threshold higher than the BG output at rest, when no selection is done. Hence, integration occurs in the presence of visual inputs even when the BG haven't yet selected a target. When a target begins to be selected, the BG output decreases for neurons coding for this target and increases for the others, so that the integration rate is boosted for the winning site and almost cancelled for the others.

Fig. 1, Right shows how the model selects between two target of identical saliences: top shows the race-like integration of saliences occuring in the integration map, with accumulation of noise leading to one random target being enhanced by the BG ; middle shows the disinhibition output of the BG, with one channel clearly selected, and the other very lightly further inhibited, and bottom shows activity for only the winning target on the motor map, that will drive the saccade generators of the brainstem.

We tested the model by reproducing a simulated version of a task used by (McPeek & Keller, 2004). In this task, a Rhesus monkey is asked to perform selection between one target and three distractors, before and after local injection of either Lidocaine or Muscimol (both producing similar results) in the area of the intermediate-depth SC maps coding for the position of the target. Inactivation of these sites led to random selection of one of the distractors and the target. Since the initial target remains selected in the drug condition, the neurons coding for its position are clearly not totally inhibited, but must maintain a reduced level of activity. Since the random selection performed by the animal in this condition offers roughly equal chances of selection for the "reduced" target and distractors, we make the hypothesis that the effect of the injection was to broadly decrease the salience of the target down to that of the distractors, leading the SC to choose between signals

with equal saliences, thus choosing stochastically between all of them.

In our simulation setup, we modelled this hypothesis by submitting as input a target of salience 1 among three distractors of salience 0.5 for the control condition, and four inputs of salience 0.5 in the drug condition.

3 Results

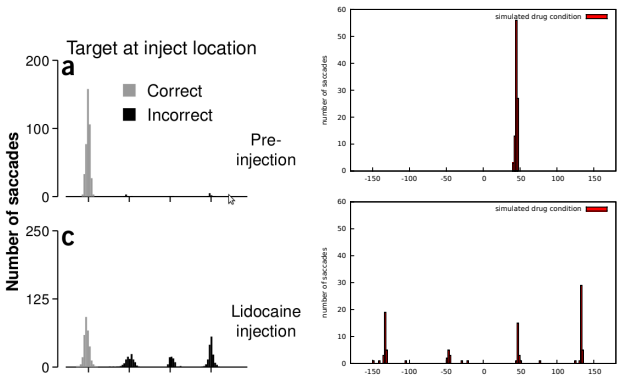

Figure 2: Distribution of saccade directions in-vivo (left) and in simulations (right) during normal selection (top) and after drug injection (bottom)..

Fig. 2, top-right shows accurate selection of the target in the control setup. Furthermore, our model selects only one target with a stochastic distribution between all potential targets when all signals have equal saliences. These results concur with those of (McPeek & Keller, 2004), cf. Fig. 2 left.

Fig. 3 left shows the activity of a neuron in the integration map coding for the center of a potential target when selected or not. In both cases we first observe a noisy race-like integration component after presentation of the target, and then either a sharp burst as the target is selected and the corresponding activity in the integration map is enhanced by the BG, or no burst but a decrease of activity due to the hyper-inhibitory effect of the BG. This activity profile is akin to that recorded by (McPeek & Keller, 2002) for Visuo-Motor prelude neurons in the middle layers of the SC, shown in Fig. 3 Right, and lead us to believe that these VM-prelude neurons could perhaps act as the biological race-like integrator of our model.

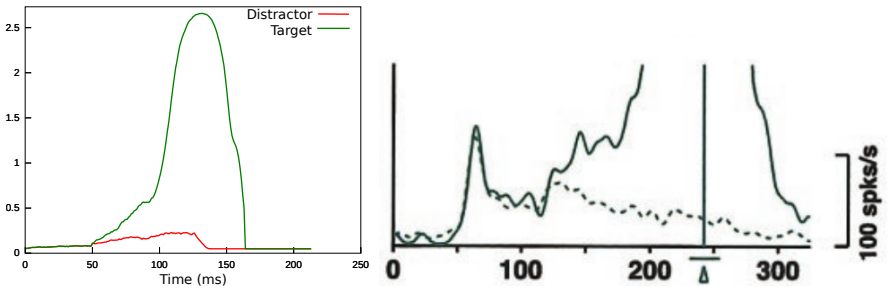

Figure 3: Left: single-neuron activity in the integration map when coding for either a selected or unselected target; Right: activity of Visuo-Motor Prelude neurons recorded in the macaque SC in the same conditions.

4 Discussion

We propose a neuromimetic model of the purely subcortical loop linking the SC and the BG, whose main feature is a race-like accumulator map of the visual signal in the intermediate layers of the SC that feeds the BG, and a dual set of reciproqual connexions from the BG to the SC, one with shunting inhibition of the connexion between the visual and integration maps of the model, and the other with direct inhibition of the activity of the layer below the integration map. These two features manage to produce accurate selection in conditions with no clear target/distractor distinction, and to reproduce the stochastic selection feature observed in-vivo by (McPeek & Keller, 2004). This model propose a role for the loop between the SC and BG, but we do not exclude a complementary participation of collicular lateral inhibitions in the selection process.

Further work will have to be done in order to properly characterize all the components of the model with regards to their biological counterparts, and also on the modelling of the Lidocaine/Muscimol experiment: we modelled the effets of the drugs by bluntly capping the peak value of the target's salience, which could be changed to an increase of the time-constants of the neurons in the affected area. We could also pry into the implication of the cortex in the preparation and execution of saliences with longer latency, especially when processing signals more complex than those transmitted by the direct pathway between the retina and SC, and when involving cognitive functions that the SC-BG loop cannot account for (as the planification for a sequence of saccades).

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