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A neural model of decision-making by the superior colicullus in an antisaccade task

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Abstract

In the antisaccade paradigm subjects are instructed to perform eye movements in the opposite direction from the location of a visually appearing stimulus while they are fixating on a central stimulus. A recent study investigated saccade reaction times (SRTs) and percentages of erroneous prosaccades (towards the peripheral stimulus) of 2006 young men performing visually guided antisaccades. A unimodal distribution of SRTs (ranging from 80 to 600 ms) as well as an overall 25% of erroneous prosaccade responses was reported in that large sample. In this article, we present a neural model of saccade initiation based on competitive integration of planned and reactive saccade decision signals in the intermediate layer of the superior colliculus. In the model the decision processes grow nonlinearly towards a preset criterion level and when they cross it, a movement is initiated. The resultant model reproduced the unimodal distributions of SRTs for correct antisaccades and erroneous prosaccades as well as the variability of SRTs and the percentage of erroneous prosaccade responses.

Keywords: Eye movements; Antisaccades; Buildup neurons; Burst neurons; Nonlinear accumulator model; Decision making; Saccade reaction times; Superior colliculus

1. Introduction

A paradigm often used to investigate decision processes is the antisaccade paradigm (Hallett, 1978), a reaction time task in which the subjects are instructed to perform eye movements in the opposite direction from the location of a stimulus that appears in their right or left peripheral visual field while they are fixating on a central stimulus. Antisaccade reaction times (aSRTs) are longer than would be expected by considering synaptic delays and nerve conduction (Hanes & Schall, 1996) and vary randomly from trial to trial (Everling & Fischer, 1998). The distribution of aSRTs is unimodal and the percentage of erroneous prosaccades towards the peripheral stimulus has been observed to be 25% (Evdokimidis et al., 2002; Smyrnis, Evdokimidis, Stefanis, Constantinidis, & Avramopoulos, 2002).

The slowness and variability of response time (RT) observed in visuomotor tasks has been explained by decision processes involving stochastic accumulation of information (Carpenter & Williams, 1995; Hanes & Schall, 1996; Luce, 1986; McClelland, 1979; Ratcliff, van Zandt, & McKoon, 1999; Reddi & Carpenter, 2000; Usher & McClelland, 2001). In the LATER model (Carpenter & Williams, 1995; Reddi & Carpenter, 2000), a decision signal rises linearly from an initial level in response to incoming information about a stimulus, with its rate varying randomly from trial to trial, until it reaches a fixed criterion or threshold level, at which point a response is initiated (Reddi, Asrress, & Carpenter, 2003). Although the model accurately predicts the latencies of saccades in various simple reaction experimental paradigms (step and countermanding paradigms) as well as the shapes of the distributions (Asrress & Carpenter, 2001; Carpenter & Williams, 1995; Leach & Carpenter, 2001; Reddi et al., 2003;

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Reddi & Carpenter, 2000), it is unable to predict the error rate in these paradigms. Moreover, the predicting power of the LATER model fails when the model is applied to choice reaction paradigms (e.g. antisaccade task) (see discussion section for details).

The present modelling work addresses some of the limitations of the previous models. It extends an already established leaky competitive neural model of visually guided eye movements in the presence/absence of distractors (Trappenberg, Dorris, Munoz, & Klein, 2001) the inputs of which are modelled as decision signals with linearly rising and randomly varying from trial to trial rates as in the LATER model (Carpenter & Williams, 1995; Reddi & Carpenter, 2000) to explain the variability of response times and the percentage of erroneous responses in the antisaccade task (Smyrnis et al., 2002). The model explains how reactive (erroneous prosaccades) and planned saccades (antisaccades) compete against each other in the intermediate layers of the superior colliculus (SC) and how a decision is formed and executed. The neural circuitry that supports this process simulates successfully responses of buildup neurons (Moschovakis & Karabelas, 1985; Munoz & Wurtz, 1995a, 1995b) and burst neurons of the intermediate layers of the SC (Moschovakis, Karabelas, & Highstein, 1988; Munoz & Wurtz, 1995a, 1995b; Waitzman, Ma, Optican, & Wurtz, 1991) in the antisaccade task (Everling, Dorris, & Munoz, 1998). Also, the model provides a functional rationale of how buildup cells in these SC layers process decision signals from converging unimodal pathways and how these converging decision signals compete against each other to yield an error and/or a correct eye movement in the form of a phasic response from the burst neurons. Finally, the model suggests why the response times in the antisaccade task are so long and variable and predicts accurately the shapes of correct and error RT distributions as well as their response probabilities.

2. Materials and methods

2.1. General description

An earlier version of the neural model that will be presented in this section was first reported in Cutsuridis, Evdokimidis, Kahramanoglou, Perantonis, and Smyrnis (2003). In the current and more comprehensive model, the preparation of an antisaccadic eye movement consists of two independent and spatially separated decision signals representing the reactive and planned saccade plans. A movement is initiated when these decision signals, represented by the neuronal activity of SC buildup neurons with nonlinear growth rates varying randomly from a normal distribution, gradually build up their activity until reaching a preset criterion level. The crossing of the preset criterion level (Durstewitz, 2003, 2004; Grammont & Riehle, 1999; Matell, Mech, & Nicolelis, 2003; McEchron, Tsend, & Disterhoft, 2003; Roux, Coulmance, & Riehle, 2003; Schultz, Dayan, & Montague, 1997) in turn releases the "brake" from the SC burst neurons and allows them to discharge resulting in the initiation of an eye movement. One of the key assumptions of the model is that in the superior colliculus, the two decision processes are integrated at opposite colliculi locations and they compete with each other via lateral excitation and remote inhibition (Behan & Kime, 1996; Meredith & Ramoa, 1998; Moschovakis et al., 1988; Munoz & Istvan, 1998; Olivier, Dorris, & Munoz, 1999). The growth rate in one decision process slows down when the other decision process is active at the same time.

The neural model proposes that (1) the competition between the SC buildup neurons encoding the decision signals and the randomly varying nonlinear growth rates of the decision processes are the underlying neural mechanisms needed to explain why the aSRTs are so long, (2) the randomly varying nonlinear growth rates of the decision processes generate accurately the correct and error latencies as well as the shape of the distributions seen in the antisaccade task (Evdokimidis et al., 2002; Smyrnis et al., 2002), and (3) the interplay between the criterion level and the randomly varying growth rates of the decision processes can successfully simulate the error rates in the antisaccade task.

2.2. Mathematical formalism

The neural model is a leaky competitive integrator (Amari, 1997; Arai, Keller & Edelman, 1994; Grossberg, 1973; Kopecz, 1995; Kopecz & Schoner, 1995; Taylor, 1999; Trappenberg et al., 2001) of the intermediate layer of the superior colliculus. The neural architecture of the model is described in Fig. 1. Self-excitation and lateral inhibition is assumed between all neurons in both superior colliculi (see Eq. (1)).

Neurons in the model are represented as simple nodes. The central node represents a fixation neuron (black), whereas the peripheral nodes alternatively represent buildup (grey) and burst (white filled) neurons of the right and left superior colliculus. For the sake of simplicity, all three types of neurons lie in the same layer, although experimental (Munoz & Wurtz, 1993, 1995a, 1995b) and computational (Arai et al., 1994; Grossberg, Roberts, Aguilar, & Bullock, 1997) studies have shown that fixation and buildup neurons lie in the same layer of the rostral and caudal pole of the SC respectively, whereas burst neurons lie in a separate layer from the previous two.

Although some of the equations (Eqs. (1)–(3)) presented in this section have been developed before (Trappenberg et al., 2001), new equations are also introduced (Eqs. (4)–(6)). In order to improve the readability of this section, we list in this section all the equations (new and old) of the model.

The internal state $x_i(t)$ of the node with index i is governed by

$$\tau \frac{\mathrm{d}x_i(t)}{\mathrm{d}t} = -x_i(t) + \sum_j w_{ij} A_j(t) + I_p(t) + I_r(t) - u_o + I_n \tag{1}$$

where τ is a time constant, w_{ij} is the synaptic efficacy from node i to node j, A_j is the activity function of node j, I_r and I_p are the reactive and planned inputs that the SC receives from other cortical areas, u_o is a global inhibition term, and I_n is the background noise. The value of u_o is set to zero for the buildup