Saccade control through the collicular motor map: Two-dimensional neural field model

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Abstract. In this paper, principles of neural computing underlying saccadic eye movement control are applied to formulate a *mapped neural field model* of the spatio-temporal dynamics in the motor map of the superior colliculus. A key feature of this model is the assumption that dynamic error coding in the motor map might be realized without efference copy feedback but only through the nonlinear, spatio-temporal dynamics of neural populations organized in mapped neural fields. The observed activity pattern suggests a particular, space-variant scheme of lateral interconnections within the motor map.

1 Introduction

A major role in gaze control plays the superior colliculus (SC), a sensorimotor transformation center in the mammalian brain stem. Whereas the upper SC layers contain a retinotopic map of the visual hemisphere, the deeper layers host a motor map of rapid eye movements (saccades) [Sparks and Mays, 1990]. That is, the location of active neurons in the deep layers represents the vector of motor errror, i.e. the amplitude and direction of the saccade to reach the target. The range of possible saccades prior to which a given neuron discharges defines its movement field (MF) while the neuron is firing for a specific but large range of movements. The topography of the motor map is such that horizontal motor error is encoded mainly along the rostro-caudal axis, and vertical motor error along the medio-lateral axis. The visual and the motor map seems to be in spatial register [Grantyn, 1988; Hilbig and Schierwagen, 1994]. Activity in the visual map then could be conveyed to corresponding areas in the motor map, thus moving the eye from its current fixation point to the target that activates the visual cells.

Experimental studies [Munoz *et al.*, 1991] showed that in the cat's SC during a saccade the activity hill travels through the motor map from its initial location towards the fixation zone (a hill-shift effect). The instantaneous hill location on the map specifies the remaining motor error (dynamic error coding). The saccade is terminated when the travelling activity hill reaches the fixation zone where it ceases. Recent investigations demonstrated that in the monkeys' SC the hill-shift effect is also present although the situation seems to be more complex [Munoz and Wurtz, 1995].

These studies suggest how the spatial representation of activity on the motor map is transformed into the temporal code (frequency and duration of discharge)

required by motoneurons: by continuous, dynamic collicular control of the eye movement. Thus, the trajectory of activity on the SC motor map seems to spatially encode the instantaneous eye movement motor error signal.

The neural mechanisms by which the collicular motor map might realize this dynamic motor error coding are currently under debate. Most distributed models of saccade generation used fast efference copy feedback for continuously updating the dynamic motor error (for review, see [Wurtz and Optican, 1994]). In this paper we employ an alternative assumption which is both structurally and computationally simpler to show that collicular dynamic error coding might be realized without feedback but only through the nonlinear, spatio-temporal population dynamics of the collicular neurons. It turns out that a particular type of lateral interconnections within the motor map is favored by the observed activity pattern.

2 Neural Field Model of SC

The neurobiological findings suggest to consider the SC as a neural system the layers of which may be characterized by anatomical and physiological parameters remaining more or less constant within the layer but varying between layers. A particular useful approach for studying the dynamic behavior of neural populations in layers is represented by continuous neural field models [Milton *et al.*, 1995]. Thus, we modeled the motor map as a 2-dimensional neural field.

Let $u(\mathbf{x}, t)$ be the average membrane potential of neurons located at position $\mathbf{x} = (x, y)$ at time t. The average activity (pulse emission rate) of neurons at $\mathbf{x}$ at t is given by the sigmoid-shaped nonlinearity $f[u(\mathbf{x}, t)]$, and the average strength of synaptic connections from neurons at position $\mathbf{x}'$ to those at position $\mathbf{x}$ by $w(\mathbf{x}, \mathbf{x}')$. For homogeneous fields $w(\mathbf{x}, \mathbf{x}') = w(|\mathbf{x} - \mathbf{x}'|)$ holds. With u_0 the global threshold of the field and $s(\mathbf{x}, t)$ the intensity of applied stimulus from the outside of the field to the neurons at position $\mathbf{x}$, the neural field equation reads

$$\tau \frac{\partial u(\mathbf{x}, t)}{\partial t} = -u(\mathbf{x}, t) + \iint_{\mathcal{R}^2} w(\mathbf{x}, \mathbf{x}') f[u(\mathbf{x}', t)] d\mathbf{x}' - u_0 + s(\mathbf{x}, t), \qquad (1)$$

which is the 2-dimensional generalization of Amari's equation [Amari, 1977].

For fields of lateral-inhibition type, excitatory connections dominate for proximate neurons and inhibitory connections dominate at greater distances, described e.g. by a radially symmetrical weighting function of on-center off-surround type modelled by a difference of Gaussians,

$$w(\mathbf{x} - \mathbf{x}') = g_e \cdot \exp\left(-\left(\frac{\mathbf{x} - \mathbf{x}'}{\sigma_e}\right)^2\right) - g_i \cdot exp\left(-\left(\frac{\mathbf{x} - \mathbf{x}'}{\sigma_i}\right)^2\right) \qquad (2)$$

where g_e and σ_e are the height and width of the excitatory center and g_i and σ_i are the corresponding values for the inhibitory surround.

A categorization of the dynamics of 1-dimensional fields has been provided (see [Amari, 1977] for details). In the case of 2-dimensional neural fields, a similar categorization of the dynamics can be given but the results are more complex. Neural wave patterns include standing, traveling and rotating activity waves, depending on the relative spatial extent of excitatory and inhibitory connectivity. We note that 1-dimensional trajectories of activity hills as observed in the motor map of SC are not found in *continuous* 2-dimensional neural fields.

3   Model Structure and Simulations

In Amari's theory of neural fields, space-invariance or homogeneity of the weighting function is essential. However, there is evidence that, e.g. in the internal cortical processing, space-variance occurs [Mallot *et al.*, 1990]. Likewise, it has been shown that MFs of collicular neurons typically have a skewed (asymmetrical) sensitivity profile [Ottes *et al.*, 1986] which suggests that the strengths of the lateral connections are depending on both input and output site rather than on their mere difference.

Space-variant couplings are also suggested in the present context by the analyses of specific *active media* (AM), i.e. fields of FitzHugh-Nagumo (FHN) neurons. The FHN model holds a prominent position in studies of AM because of its simplicity and qualitative corresponence with more complicated models [Schierwagen, 1989]. A particularly important result from investigations of 2-dimensional FHN fields is the following: a *discrete* field model with space-variant, asymmetrical weighting functions exhibits dynamic behavior which corresponds to 1-dimensional trajectories of activity hills. This means, these hills fail to spread laterally to excite the adjacent field regions, if the asymmetry of the weighting function is strong enough [Keener, 1988].

Based on these theoretical results we modeled the collicular motor map by a discrete version of a *mapped neural field* of the Amari type. That is, the field model, Eqn. (1), was endowed with rotationally asymmetric, space-variant weighting functions $w(\mathbf{x}, \mathbf{x}')$ described as a difference of 2-dimensional Gaussian functions. The weighting function $w(\mathbf{x}, \mathbf{x}')$ is given in normal form by

$$
\begin{aligned}
w(\mathbf{x}, \mathbf{0}) = \quad & g_e \cdot \exp\left(-\left(\frac{x}{\sigma_{e_x}}\right)^2 - \left(\frac{y}{\sigma_{e_y}}\right)^2\right) \\
& - g_i \cdot \exp\left(-\left(\frac{x}{\sigma_{i_x}}\right)^2 - \left(\frac{y}{\sigma_{i_y}}\right)^2\right)
\end{aligned}
\tag{3}
$$

where $\mathbf{x} = (x, y)$. g_e, σ_{e_x} and σ_{e_y} are the height, x-axis width and y-axis width of the excitatory center, and g_i, σ_{i_x} and σ_{i_y} are the corresponding values for the inhibitory surround. In addition, the major semi-axes of the elliptical isoefficacy contours, described by σ_{e_x} and σ_{i_x}, differed for the half-planes $x < 0$ and $x > 0$ which was characterized by the compression factor, κ .
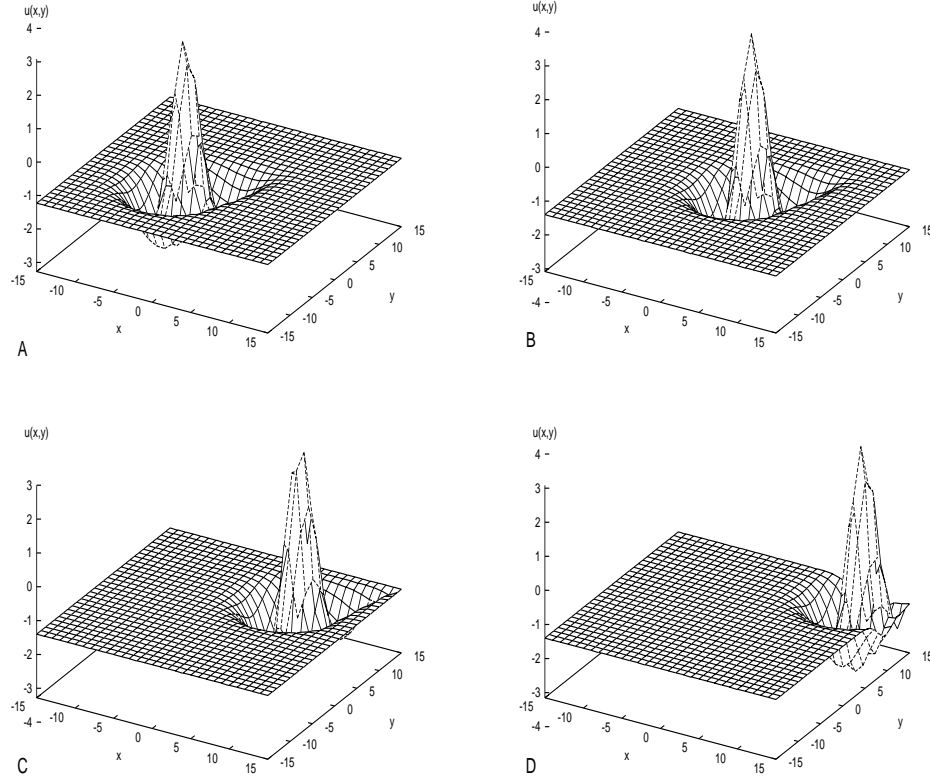
Fig. 1. Simulation of the hill-shift effect with the mapped neural field model. The SC motor map was spatially represented by a 30×30 grid. Eqn. (1) was integrated employing the Euler scheme with a time step of $\Delta t = 0.1$. The 2-dimensional, spatial integral in Eqn. (1) was computed by repeated 1-dimensional integration, using the extended trapezoidal rule with stepsize $\Delta x = \Delta y = 1.0$. **(A)-(D)** Example of simulated activity pattern in the neural field model. Starting from initial location $(-5, -5)$, the activity hill moves over the field which is shown at different, consecutive times $t = 2$ **(A)**, $t = 9$ **(B)**, $t = 16$ **(C)**, $t = 23$ **(D)**. Parameters used in the simulations are $\tau = 1$, $u_0 = 1.4$, $s(\mathbf{x}, t) = 0$, $g_e = 3.6$, $g_i = 4.0$, $\sigma_{e_x} = 2.8$, $\sigma_{e_y} = 1.4$, $\sigma_{i_x} = 5.7$, $\sigma_{i_y} = 2.8$, $\kappa = 0.5$.

The 2-dimensional motor map was modelled by a 30×30 grid. All the neurons of the grid had a step transfer function f. The map origin corresponding to the fovea region was fixed at point $(15, 15)$ (Fig. 1). Space-variant processing in the model has been realized through the asymmetrical center and surround structure of the weighting function described by Eqn.(3) and through the radial organization of the weighting functions, in accordance with the radially organized asymmetry found in collicular neurons [Ottes *et al.*, 1986].

As the initial state we chose a localized excitation on the grid that should eventually develop into a hill of activity on the mapped field. The localized excitation

had cubical shape and covered a 2×2 area within which the field potential was set to $u = 1.0$. We run 30 simulations, placing the activity hill in randomly selected locations of the field.

The simulated pattern of activity in the neural field model showed a clear anisotropy, resulting from the space-variant coupling of the neurons. The direction of movement was determined by the orientation of the steeper decaying flank of the weighting function defined by κ. In the example shown in Fig. 1, the initial location of the activity hill was at $(-5, -5)$. The asymmetrical, radially oriented weighting functions caused the hill to move towards the origin $(15, 15)$ of the map coordinate system where it stopped and finally decayed (Fig. 1A-D).

4   Conclusions

In this paper we proposed a model of the spatio-temporal dynamics in the motor map of the SC. In particular, we studied which qualitative behaviors of the collicular neurons can be obtained if the model is based on some high-level computing principles governing saccadic eye movement control, i.e. neural mapping, population coding and space-variant processing in layered systems. A model type that is especially appropriate to incorporate these principles is provided by neural fields.
In generalizing Amari's concept of homogeneous, space-invariant fields, we modelled the collicular motor map as a 2-dimensional neural field endowed with space-variant weighting functions.
In simulations with the mapped neural field model, we could reproduce the hill-shift effect observed experimentally in the collicular motor map, i.e. our model exhibited 1-dimensional trajectories of activity hills. Thus, our study has presented evidence for the assumption that collicular dynamic error coding can be realized without efference copy feedback. A recent model study on the hill-flattening effect found in burst neurons of the monkey's SC arrived at similar conclusions [Massone and Khoshaba, 1995].

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