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Superior Colliculus geometry for spatio-temporal transformation

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N.T. and B.G. performed the research and wrote the paper. D.B. contributed in formalizing and generalizing the mathematical results. A.B. designed the research and related the theoretical aspects to neurophysiology. J.J.S. designed research and participated in writing the paper.

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Abbreviations: BN, burst neurons; BUN, build-up neurons; SC, superior colliculus; SG, brainstem saccade generator.

abstract

The superior colliculus maps encode the position of targets in retinotopic space using a linear or a logarithmic mapping, depending on the species considered. In turn, the motor map projects to the saccade generators where this spatial code is transformed into a temporal one.

We use a set of five hypotheses in accordance with current neurobiological knowledge concerning the spatio-temporal transformation to show that the logarithmic and linear mappings are the only possible ones. Finally, given these mappings, we analytically determine the weights of the projections from the superior colliculus to the saccade generators, and prove that, surprisingly, they depend linearly on the target coordinates in the visual space.

1 Introduction

The superior colliculus (SC) –corresponding to the tectum in non-mammalian vertebrates– is a layered structure located in the midbrain, which receives multisensory input and accordingly generates changes in gaze orientation. It drives, in particular, the brainstem nuclei in charge of eye saccade generation (brainstem saccade generators, SG). The sensory inputs and the corresponding output commands are coded on retinotopic neuronal maps whose mapping codes target position in polar coordinates. A specific logarithmic deformation on the amplitude axis of this mapping was found in cats (1; 2) as well as in monkeys (3; 4) (see Fig. 1), whereas in some other species, the mapping seems to simply be linear (rats (5), goldfish(6), for instance).

The generation of a saccade is driven by the activation of a large population of cells in the motor map, centred around the position corresponding to the metrics of this saccade (see upper part of Fig 2). This distributed spatial code is transformed into a Cartesian temporal code (the so-called *spatio-temporal transformation*), as the saccade generators drive horizontal and vertical movements using a frequency code (see lower part of Fig 2). The hypothesis that the command sent to the saccade generators is the result of a weighted vector summation of all the movements represented by the activated motor cells has received support from both experimental (7; 8) and modelling studies (9; 10). The specific weights of this sum have to take into account the coordinate system change, as first noted by (8), and were found using optimisation algorithms in previous modelling studies (11; 12; 13).

In this work, we show that a set of five hypotheses concerning the neural implementation of the spatio-temporal transformation, in accordance with current neurobiological knowledge, generates a mapping that is necessarily linear or complex logarithmic. Finally, given these mappings, we analytically determine the weights of the projections from the SC to the saccade generators, and surprisingly prove that for they linearly depend on the target coordinates in the visual space.

Coordinates on the SC layers. The question of the nature of the coordinate system that should be used to describe the mapping on the collicular layers has to be raised. Indeed, the colliculus, and especially its superficial visual layers, are convex. The

maps proposed in biological studies are obtained with various methods: projections on the Horsley-Clarke plane (like in 5; 14; 3; 15), empirical flattening of the surface by cutting (16), or locally cylindrical coordinates (17). None of these methods respects the curvature of the surface. Only Siminoff *et al.* (5) propose a correction –on two axes only rather than for the whole surface– that takes the curvature into account.

Solving this question is beyond the scope of this paper, we however stress that our results concern the activity of the intermediate motor layers of the colliculus, which seems to be much more planar, or at least unfoldable. We will therefore use a Cartesian coordinate system (X, Y) to localize points on the surface of these intermediate or deep layers.

Mapping formulation. Two-dimensional saccades result from the conjunction of the activity of horizontal and vertical brainstem generators. So the final motor coordinate system is *a priori* a Cartesian one. However, Robinson (3) has shown that for the monkey, the sensorimotor maps of the SC are more adequately described by a deformed polar coordinate system.

The equations mapping retinotopic polar coordinates (R,θ) onto the collicular surface (Cartesian coordinate (X,Y) in millimetre), first introduced by (4), are:

$$X = B_x \ \ln(\frac{\sqrt{R^2 + 2ARcos(\theta) + A^2}}{A}) \quad (1)$$

$$Y = B_y \ atan(\frac{Rsin(\theta)}{Rcos(\theta) + A}) \quad (2)$$

With the following parameter settings: $A = 3.0 \ deg$, $B_x = 1.4 \ mm$ and $B_y = 1.8 \ mm$. The corresponding mapping is depicted in Figure 1. Even if a precise evaluation of these parameters for the cat was not provided, the cat's mapping depicted in (1) seems to be in accordance with such a description, with a B_y/B_x ratio close to 2.

As noted in (4), this mapping can however be reformulated it as complex logarithm of a linear function of eccentricity, as proposed by (18) in its modelling of the striate cortex mapping. Using z, the complex variable defined as:

$$z = \alpha + i\beta \quad (3)$$

where α and β represent the horizontal and vertical amplitude of the saccade, eqns. 1 and 2 can be rewritten:

$$\frac{X}{B_x} + i\frac{Y}{B_y} = \ln(\frac{z+A}{A}) \tag{4}$$

Five properties of the spatio-temporal transformation. We state below five independent biological properties concerning the spatio-temporal transformation from the SC to the SG and formulate them mathematically so as to use them as the basis of the proof that linear or logarithmic (as defined by eqns. 4) mappings are the only possible ones.

Notations. Note that some of the numbers below are in $\mathbb{C}$

- $S = X + iY$ is the complex formulation of coordinates on the SC map,
- $z = \phi(S)$: bijection from the plane of the right (resp. left) colliculus motor layer to the left (resp. right) visual hemifield,
- The metrics $z_0 = \alpha_0 + i\beta_0$ of a given saccade in visual coordinates can be expressed in collicular coordinates as a specific $S_0 = \phi^{-1}(z_0)$. We will refer to a given saccade using this S_0 vector.
- $Out_{S_0}(t) = Out^H_{S_0}(t) + iOut^V_{S_0}(t)$: command sent to the saccade generators (H: horizontal, V: vertical) in order to generate a given S_0 saccade,
- $w_S \in \mathbb{C}$: weights of the connections from the neuron located in S to the saccade generators,
- $\mathcal{A}_{S_0}(S,t) \in \mathbb{R}$: activity on the map at location S and time t for a S_0 saccade. By activation, we strictly mean measure distribution and able to integrate exponential functions.

We now state the five properties.

Weighted sum. The output of the SC fed to the saccade generators is generated by weighted sums of the activity of the SC motor cells, ie.

$$Out_{S_0}(t) = \sum_S w_S \mathcal{A}_{S_0}(S,t) \tag{5}$$

Stereotyped integral. The global activity of each cell S during a whole saccade depends on its location with respect to S_0 only, ie.

$$\int_t \mathcal{A}_{S_0}(S,t) = K_{\mathcal{A}}(S - S_0) \tag{6}$$

Linearity. The saccade generators react linearly to the command coming from the SC,

$$\int_t Out_S(t) = Cz \quad (C \in \mathbb{R}) \tag{7}$$

Similitude. For any activity $\mathcal{A}$ respecting the stereotyped integral hypothesis, the projection weights from the SC to the SG is a similitude in z,

$$\forall \mathcal{A} \; \exists \; a, b \in \mathbb{C} \qquad w_S = a.(z + b) \tag{8}$$

Smooth mapping. The mapping $z = \phi(S)$ is $\mathcal{C}^1$, satisfies $\phi(0) = 0$, and is aligned with the X and Y axes in 0 ($\frac{\partial}{\partial X}\phi(0) \in \mathbb{R}^+$ and $\frac{\partial}{\partial Y}\phi(0) \in i\mathbb{R}^+$).

2 Results

The need for an exponential. Let us now look for the condition such a mapping must satisfy.

From equations 5 and 7, it can be derived:

$$C\phi(S_0) = \int_t Out_{S_0}(t) = \sum_S w_S \int_t \mathcal{A}_{S_0}(S,t)$$

Applying this for $\int_t \mathcal{A}_{S_0}(S,t) = \delta_{S,S_0+u}$ (where δ is the Kronecker symbol) and using 8 leads to

$$C\phi(S_0) = a(u)\,(\phi(u + S_0) + b(u))$$

When differentiating this equation with respect to X and Y, we get easily

$$\begin{cases} \frac{\partial}{\partial X}\phi(0)\frac{\partial}{\partial X}\phi(u+S_0) = \frac{\partial}{\partial X}\phi(u)\ \frac{\partial}{\partial X}\phi(S_0) \\ \\ \frac{\partial}{\partial Y}\phi(0)\frac{\partial}{\partial Y}\phi(u+S_0) = \frac{\partial}{\partial Y}\phi(u)\ \frac{\partial}{\partial Y}\phi(S_0) \end{cases}$$

Let us introduce the change of coordinates $S \mapsto Z$ that makes the Jacobian of $\widetilde{\phi}$ (ie. the funtion ϕ in the new coordinates) equal to I at 0. By the hypothesis of smooth mapping, we know that

$$Z = \frac{X}{B_X} + i\frac{Y}{B_Y}$$

for some $B_X, B_Y \in \mathbb{R}^+$.

Then, a standard theorem in analysis states that,

$$\exists\, C_1, C_2, \lambda, \mu \text{ in } \mathbb{C} \quad \begin{cases} \frac{\partial}{\partial X}\widetilde{\phi}(Z) = C_1 \exp(\lambda\widetilde{X} + \mu\widetilde{Y}) \\ \\ \frac{\partial}{\partial Y}\widetilde{\phi}(Z) = C_2 \exp(\lambda\widetilde{X} + \mu\widetilde{Y}) \end{cases}$$

Remark we could have assumed condition (8) for continuous densities only and would have obtained the same result (19). We choose to present this proof for simplicity.

The Schwarz's theorem tells us that $\mu = i\lambda$

At this point, we must consider two cases.

- $\lambda \neq 0$ and so $\mu \neq 0$

  in that case,

  $$\widetilde{\phi}(Z) = \frac{1}{\lambda}\,(\exp(\lambda\, Z) - 1) \qquad \lambda \in \mathbb{C}$$

  which can be rewritten if $\lambda \in \mathbb{R}^+$

  $$\frac{X}{B_X} + i\frac{Y}{B_Y} = \ln(\frac{z+A}{A})$$

- $\lambda = 0 \Leftrightarrow \mu = 0$

  in that case,

  $$\widetilde{\phi}(Z) = Z$$

which can be rewritten

$$\frac{X}{B_x} + i\frac{Y}{B_y} = z$$

Remark that this case is simply the limit case of the exponential mapping when $\lambda \to 0$.

Let us now verify that the necessary conditions find above are also sufficient by explicitely computing a and b.

$$\begin{cases} a &= C(\sum_u \exp(\lambda\, \widetilde{u}).K_{\mathcal{A}}(u))^{-1} \\ \\ b &= \frac{C}{a\lambda}((\sum_u \exp(\lambda\, \widetilde{u}).K_{\mathcal{A}}(u))^{-1} - (\sum_u K_{\mathcal{A}}(u))^{-1}) \end{cases}$$

About the limited extend of the colliculus The weighted sum hypothesis is formulated as a summation on $\mathbb{R}^2$. We can however take into account the limited extend of the colliculus by modifying our hypotheses on three points. First, we restrict this summation to a finite area domain D of S, corresponding to the actual surface of the colliculus. Second, we consider only S_0 saccades in a subdomain $D_0 \in D$, corresponding to the part of this surface coding for saccades. Third, we suppose that $\mathcal{A}_{S_0}(S,t) = 0$ for S outside D and S_0 in D_0, which means that the activations generating saccades shall not extend outside the collicular surface.

Then the same proof, using only small u, gives exactly the same formulas as above, but only for $(X,Y) \in D_0$.

From affine to linear projection. If we additionally suppose that the integrated activity on the map $K_{\mathcal{A}}(u)$ depends only on the distance to Z_0 in the dilated coordinate (ie. that it depends on the norm of $\widetilde{u}$), the constant b disappears (proof to be found in the supporting information).

This dependence on the norm $\widetilde{u}$ could be implemented by a circular symmetry of $\mathcal{A}$ deformed by the dilation $u \to \widetilde{u}$.

Projection of the Superior Colliculus to the Brainstem. Using the equation of the logarithmic mapping, in the case of $\lambda \in \mathbb{R}$ (which is the case for the monkey), the projections from the superior colliculus to the brainstem in this specific case are analytically expressed as:

$$w_\alpha = a(A\,\frac{1}{\lambda}(\exp(\lambda\frac{X}{B_x})\,cos(\lambda\frac{Y}{B_y})-1)+b) \quad (9)$$

$$w_\beta = aA\,\frac{1}{\lambda}\exp(\lambda\frac{X}{B_x})\,sin(\lambda\frac{Y}{B_y}) \quad (10)$$

Using the parameters $A = 3°$, $B_x = 1.4mm$ and $B_y = 1.8mm$ (specific to the monkey) and $a = 1$, $b = 0$, $\lambda = 1$ the projections have the shapes represented in Fig. 3.

About the singularity of the mapping In the linear case, there is no problem with these formulas, but in the logarithmic case, a singularity appears for $z = -A$. For example, if $\lambda > 0$, the weights cannot work for too negative values of X. Here comes the fact that there are two colliculi, the first one computes the saccades to the right (with $\lambda > 0$) and the other one (with $\lambda < 0$) the saccades to the left. Vertical saccades are computed by a combination of both.

Coming back to the stereotyped integral property. The property that the total activation of one neuron on the superior colliculus during the saccade depends only on its distance to the saccade is the really new property introduced by this work. We have shown that this property induces a logarithmic mapping. But from another point of view, the existence of a logarithmic mapping implies that the activity on the colliculus satisfies $\exists K, K' \,\forall\, Z_0$:

$$\sum_Z \exp(\lambda(Z-Z_0)) \int_t \mathcal{A}_{Z_0}(Z,t) = K \quad (11)$$

$$\sum_Z \int_t \mathcal{A}_{Z_0}(Z,t) = K' \quad (12)$$

This is of course different from our *stereotyped integral* property but we can see that the obvious way of satisfying those two constraint is to suppose the stereotyped integral property. Moreover, if we suppose that λ can have various values, the stereotyped integral becomes the only possibility.

Coming back to the similitude property. Requiring that the projection weights are described by a similitude in z (*i.e.* in visual coordinates) is the less intuitive of our five hypotheses as it does not seem to have any functional justification. However, we

can keep the four other hypotheses, suppose that ϕ^{-1} is either linear or logarithmic (mappings probably evolved under perception constraints). Then, it can be proved that the only possible system of weights which works for any $K_{\mathcal{A}}$ is a similitude in z (a proof is presented in supporting information).

3 Discussion

In this paper, we showed that collicular mapping has to be either linear or logarithmic in order to control the SG correctly, assuming five basic properties concerning the spatio-temporal transformation. This result also shows that a continuous transition from the linear to the logarithmic mapping can be made, affecting neither the neural substrate nor the underlying computations generating saccadic movements. In an evolutionary perspective, it suggests that the appearance of a fovea and the corresponding modification of the mapping of the visual areas could have happened in a progressive manner without requiring any modification of the final stages of the saccadic circuitry. Finally, we analytically expressed the weighting of the projections from the SC to the SG.

The five basic properties. We first want to discuss the neurobiological relevance of the five properties on which we based our demonstration, for the monkey and the cat.

The *weighted sum* property corresponds to the simplest way to transmit the activity of a population of SC neurons to the SG, as no additional circuitry is needed between SC motor cells and SG bursters in order to, for example, select the most active neuron only. Moreover, relying on such a population coding is more resilient to noise in neurons'activity. As previously stated in introduction, this hypothesis has received support from both experimental and modelling studies.

The *stereotyped integral* property states that the shape of the activity on the SC map $\mathcal{A}_{Z_0}$ does not have to be perfectly stereotyped in space and time for any saccade Z_0, as long as the activity of each cell integrated over saccadic signal duration depends only on its location with regards to Z_0. This hypothesis is weaker than the stereotyped Gaussian used in numerous models (20, for instance), it avoids putting too much constraint on the precise tuning of the activity profiles of the SC neurons. The advantage of not

demanding temporal stereotypy is that our scheme complies with models considering that the SC is or not in the saccade control feedback loop: the duration of a saccade of a given metric can vary from one execution to another as long as the integrated activity is constant.

This *stereotyped integral* property is the most speculative one, as we are not aware of any direct neurobiological evidence of it. It has however the advantage to be compliant with the results obtained by (21) concerning population activity in the SC of monkeys, contrarily to the models based on spatial and temporal stereotypy. This electrophysiological study shows that for saccades of various amplitudes:

1. the number of active burst neurons (BN) and build-up neurons (BUN) is constant, a result compatible with a stereotyped activation,

2. that the peak activity of BN and BUN tends to decrease with larger amplitudes, a result incompatible with a strict stereotypy,

3. that the cumulative activity (over the whole SC population, during a whole saccade) is approximately constant with respect to saccade amplitude for the BN, while it is linearly increasing for the BUN.

This last result shows that our *stereotyped integral* hypothesis is compatible with the activity of the BN only. The consequence of assuming it, is that we predict that the BN only are implied in the computation of the motor output of the SC, at least in monkeys. This does not exclude BUN projections to the saccade generators, but suggests that their role is different; they might, for example, be part of the triggering system controlling the omnipause neurons.

We are not aware of similar results at the scale of SC populations of neurons in cats that could shed a complementary light on our *stereotyped integral* hypothesis. As the feline morphology and physiology of SC neurons seems to be quite different from the primate one (22), such a study is necessary to state its validity in cats.

The *linearity* property states that the saccade amplitude has to linearly depend on the SG input. The burst neurons of the SG, which receive the SC output and generate the phasic part of the motoneuron activity responsible for saccadic eye movement,

exhibit an affine relationship between the number of spike they emit during a saccade and the amplitude of the saccade, in monkeys (23; 24) as well as in cats (25; 26). If the summed offsets of the burst neurons coding for two opposite directions are equal, then the linearity hypothesis holds true.

The *similitude* property states that the projection weights from the SC to the SG are a similitude of the saccade metric *in visual space coordinates*. This unintuitive property was indeed derived from the evidence that in cats this projection is affine on the horizontal axis (27). Neither the fact that the vertical projection is affine nor the fact that the whole projection function is a similitude, a subset of the affine functions, were however proved. The supporting information of this paper contains a generalization of our results, showing that if we relax the *similitude* hypothesis by assuming affine projection only, three additional types of mappings become acceptable and all the resulting five mappings can be nonlinearly twisted. Finding animals whose mapping corresponds to one of these three mappings would favor the affine hypothesis.

Note that this hypothesis is formulated so that *similitude* has to be true for any $\mathcal{A}$. Thus our result states that with a complex logarithmic mapping, we can consider any $\mathcal{A}$ function verifying the property of *stereotyped integral*, and always be able to find the parameters a and b so that a weighted sum of the activity of the SC neurons will generate accurate saccades. This means that the precise shape of $\mathcal{A}$ can change during lifetime and be different from one individual to another, as long as an adaptive mechanism exists to tune a and b, without changing the mapping of the SC maps.

The hypothesis, that the *similitude* must be true for any $\mathcal{A}$ function verifying the property of *stereotyped integral*, is quite strong. However, our proof holds true even with restricted families of activations. For example, if the *similitude* has to be true for Gaussian functions with small perturbations of covariance and mean, we still obtain the two mappings.

Concerning the *smooth mapping* property, stating that the mapping function ϕ is continuous comes directly from the well known retinotopy of SC maps. Stating that its first derivative is also continuous means that the variation of the magnification factors on the maps are smooth, which is verified in all studied species. Finally, axes X and Y used to describe the maps are chosen so as to be aligned with the horizontal and

vertical directions in 0, which is exactly what the condition on the partial derivatives of ϕ mean.

The fact that these neurobiological properties and the known SC mappings can be combined together in a mathematical proof strengthens their coherence and reduces the concern of their individual uncertainties. Experimentally exploring the validity of these five properties in other species than cat and monkey, especially those having a linear mapping, could reveal whether our results can be generalized among vertebrates.

SC to SG projection weights. As regards the projection from the superior colliculus to the saccade generator, we must say that to our delight similar profiles have been obtained by (11) using a training procedure based on their model of the SC (see figure 4). It shows both that these weights can be obtained by learning and that our theoretical approach is corroborated by a more experimental one. Nevertheless, in another paper, (13) obtained different profiles as they used a mixed velocity and position feedback to control SC activity, which transgresses our *stereotyped integral* hypothesis.

A few neurobiological studies tried to evaluate the weights of the connections from the SC to the SG. The density of SC neurons projecting to the horizontal SG in monkeys estimated by (28) have variation tendencies compatible with our results, at least for a range of saccades for which head movement are negligible. The technology available to estimate projection weights is however too limited yet to provide a full account of or to reject our result.

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Supporting information

Proof of the "From affine to linear projection" remark

When expanding the exponential as a series, we get

$$\sum_u \exp(\lambda\, \widetilde{u}).K_{\mathcal{A}}(u) = \sum_{\rho,\phi} \sum_n \frac{(\lambda\rho)^n e^{in\phi}}{n!}\, .K_{\mathcal{A}}(\rho)$$

Now, using that

$$\sum_\phi e^{in\phi} = \delta_{n,0}$$

We get

$$b = 0$$

Proof of the "Coming back to similitude property" remark

We showed that

$$\exists C_{K_{\mathcal{A}}} \in \mathbb{R} - \{0\}, C_{K_{\mathcal{A}}}\phi(S_0) = \sum_S w_S K(S - S_0)$$

is satisfied by weights being a similitude function of z. We define $\Delta = (1/C_{K_{\mathcal{A}}})w_S - (1/C^{sim}_{K_{\mathcal{A}}})w^{sim}_S$, where $C^{sim}_{K_{\mathcal{A}}}$ and w^{sim}_S correspond to the similitude solution. The equation above enables to say that $K * \Delta = 0$. If we consider the case $K_{\mathcal{A}} = \delta_u$, for $u \in \mathbb{R}^2$, then we see that $\Delta(u) = 0$.

Note that this proof is identical considering the more general case of affine projection (see the following paragraph).

A generalization of the similitude hypothesis. If we relax the hypothesis of similitude by just asking for an affine projection, ie. $w_S = \mathbf{a}(z + b)$, where $\mathbf{a}$ is a 2×2 invertible matrix representation we then get five types of solutions.

Indeed, noting $J(S)$ the Jacobian of ϕ at point S leads to

$$J(u)J(0)^{-1}J(S_0) = J(u + S_0)$$

As above, we perform the change of coordinates $S \mapsto Z$ to make $J(0) = I$. Then, using a theorem of Cartan and Von Neumann (Bourbaki, 1972, Groupes et Algèbres de

Lie, Chapitres 2 et 3, Dunod, Paris, France) guarantees the existence of two commuting matrices M_1 and M_2 such that

$$\widetilde{J}(Z) = \exp(M_1\ X + M_2\ Y)$$

By distinguishing between the different kind of sub-vector spaces $\mathbb{R}(M_1, M_2)$, we obtain five solutions, where P is a 2×2 invertible matrix (allowing a twist in the mapping) and $W = P^{-1}(Z)$ is seen as a complex number $U + iV$.

1. $\widetilde{\phi}(Z) = P\ \frac{1}{\lambda}(\exp(\lambda W) - 1) \quad \lambda \in \mathbb{C}$
2. $\widetilde{\phi}(Z) = P \begin{pmatrix} \frac{1}{\lambda}(exp(\lambda U) - 1) \\ \frac{1}{\mu}(exp(\mu V) - 1) \end{pmatrix} \quad \lambda, \mu \in \mathbb{R}$
3. $\widetilde{\phi}(Z) = P \begin{pmatrix} \frac{1}{\lambda}(\exp(\lambda U) - 1) \\ \exp(\lambda U)(V + \frac{\nu}{\lambda}(\frac{1}{\lambda} - U)) - \frac{\nu}{\lambda^2} \end{pmatrix}$
   $\lambda, \nu \in \mathbb{R}$
4. $\widetilde{\phi}(Z) = P \begin{pmatrix} \frac{1}{\lambda}(\exp(\lambda U) - 1) \\ V \end{pmatrix} \quad \lambda \in \mathbb{R}$
5. $\widetilde{\phi}(Z) = Z$

Figures captions

Fig. 1: Conformal mapping from the polar coordinates (R, θ in degrees) in visual space to the monkey superior colliculus maps (X, Y in mm). Isoradial lines are represented by plain curves and isodirectional lines by dashed curves.

Fig. 2: Spatio-temporal transformation from the superior colliculus motor layers to the saccade generators. BN: burst neurons; BUN: build-up neurons; EBN: excitatory burst neurons; MN: motoneurons; TN: tonic neurons. Gray shading: activity of the population of neurons coding for a $(R = 10°, \theta = 45°)$ saccade. SG are simplified: circuitry devoted to the triggering of saccades is omitted. Insets: temporal activity of the EBNs during the execution of the saccade. The transformation from spatial to temporal coding results from selective weighted projections from SC neurons to the SGs (strength is represented by line width): neurons N1 and N2 project to the leftward SG only, as they code for horizontal saccades, and the N2 projection is stronger as it codes for a saccade of larger amplitude; neuron N3 projects to both upward and leftward SGs as it codes for a $(R = 5°, \theta = 67.5°)$ saccade.

Fig. 3: Plots of the weight from all the motor cells of the superior colliculus to the brainstem horizontal burst generator (upper section) and to the vertical burst generator (lower section) in monkeys. The values of these weights were obtained by the *exact equations* described in text (eqns. 9 and 10).

Fig. 4: Plots of the weights obtained by (11) with a learning algorithm for a map covering from 0 to 20 degree in amplitude and from -65 to 65 degree in direction.

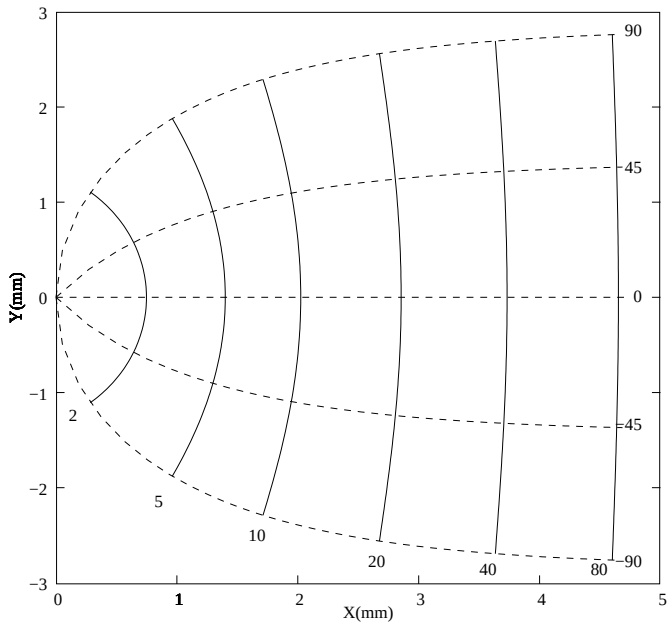

Figure 1:

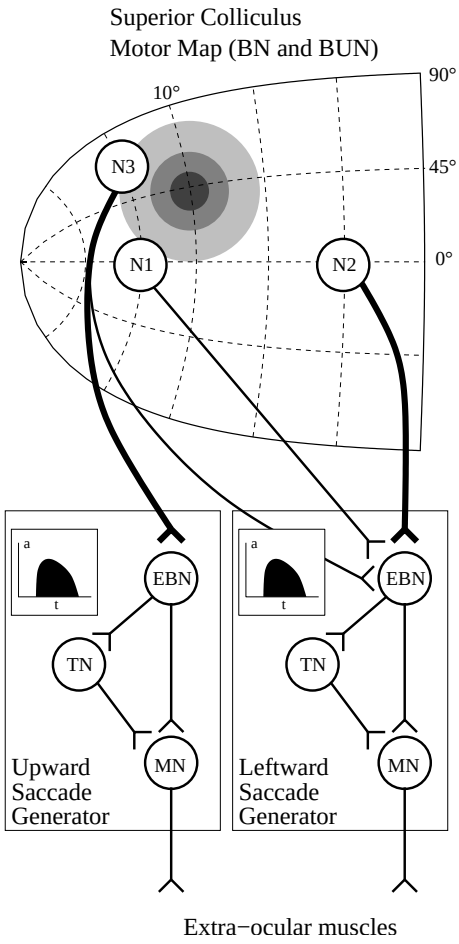
Superior Colliculus
Motor Map (BN and BUN)
90°
10°
45°
0°
N3
N1
N2
a
t
EBN
TN
MN
Upward
Saccade
Generator
a
t
EBN
TN
MN
Leftward
Saccade
Generator
Extra−ocular muscles

Figure 2:

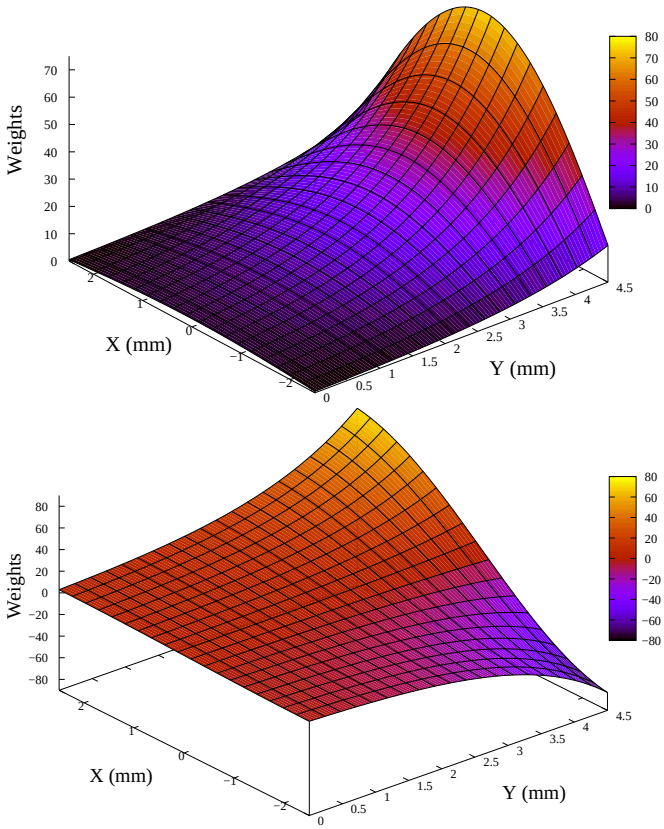

Figure 3:

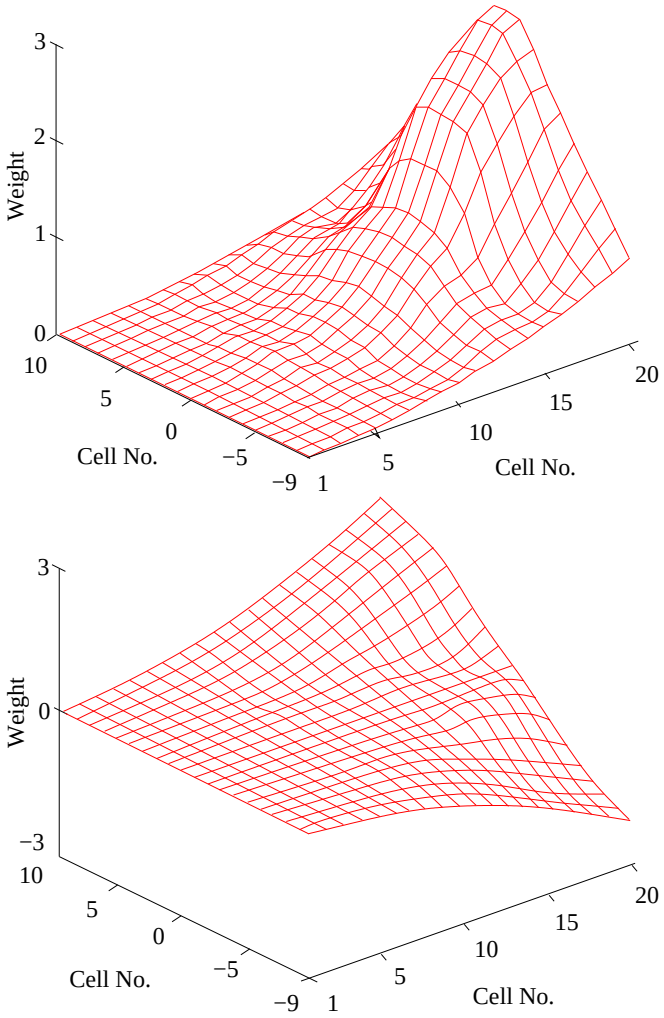
3
2
1
0
Weight
10
5
0
−5
−9
Cell No.
1
5
10
15
20
Cell No.
3
0
−3
Weight
10
5
0
−5
−9
Cell No.
1
5
10
15
20
Cell No.

Figure 4: