THE FUNCTIONAL ARCHITECTURE
OF THE EARLY VISION AND NEUROGEOMETRIC MODELS

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Abstract. The initial sections of the paper give a concise presentation, specially designed for a mathematically oriented audience, of some of the most basic facts on the functional architecture of early vision. Such information is usually scattered in a variety of papers and books, which are not easily accessible by non-specialists. Our goal is thus to offer a handy and short introduction to this topics, which might be helpful for researchers willing to enter the area of the applications of modern Differential Geometry in studies on the visual systems, baptized neurogeometry by J. Petitot. We then offer a survey of three of the most important neurogeometric models: Petitot’s contact model of the primary visual cortex, its extension to A. Sarti, G. Citti and J. Petitot’s symplectic model, and P. C. Bressloff and J. D. Cowan’s spherical model of hypercolumns. We finally discuss the main points of the so-called “conformal model” for hypercolumns (a model that was briefly presented in [D. V. Alekseevsky, Conformal model of hypercolumns in V1 cortex and the Möbius group, in “Geometric science of information”, pp. 65–72, Springer, 2021] and given in detail in [D. V. Alekseevsky and A. Spiro, Conformal models for hypercolumns in the primary visual cortex V1, arXiv 2024]), which can be considered as a synthesis of the symplectic and the spherical models.

Contents

Introduction 2

1. General principles of the organisation of the visual system 6

2. Models of linear visual neurons 10

2.1. Gauss filters on the plane 10

2.2. Kuffler isotropic neurons and Marr filters 11

2.3. Koenderink’s Multiscale Geometry of Image Processing 11

2.4. Derived filters and Hansard and Horaud’s simple cells of order \( k \) 12

2.5. Gabor filters and simple cells of V1 cortex 12

3. The functional architecture of the V1 cortex in statics 13

3.1. Structure of the V1 cortex 13

3.2. The V1 cortex as a fiber bundle: The “engrafted variables” of Hubel and Wiesel and the hypercolumns 14

4. Eye movements and the configuration space of the eye 14

4.1. The eye as a rigid rotating ball 14

2000 Mathematics Subject Classification. 92B99, 68T45.

Key words and phrases. Organisation of the visual system; Neurogeometry of early vision. Columns and hypercolumns of V1 cortex; Donder’s Law; Listing Law; Saccades; Gabor filters; Conformal Geometry of the sphere; Hoffman’s model.
**Introduction**

The human visual system is a highly complicated, hierarchically organised system, consisting of several parts, the eyes, the LGN, the primary visual cortex V1, the cortices V2, V3, V4 etc., all of them related one another with strong feedback. Some of the most fundamental results on the functional structure of the V1 cortex are due to D. Hubel and T. Wiesel, who put forward several crucial ideas, as for instance the distinction between simple and complex visual neurons, the discovery of the columnar structure of the V1 cortex and, in particular, of the singular columns (i.e. the *pinwheels*), etc. They also introduced the notions of *internal parameters* and of *hypercolumns* and promoted the
crucial idea that the V1 cortex might be mathematically represented as a fiber bundle over the retina \( R \). This can be taken as one of the main motivations for the recent activity in applications of differential geometry in the constructions of mathematical models for the early visual system.

In this paper we would like to offer a brief (and, surely not exhaustive) survey of a diverse facts, conjectures and problems, concerning the visual system, with a special attention to the aspects that have been (or that might be in the future) be analysed using differential geometric tools. After such preliminary review, we give a short introduction to neurogeometry, a recent research area in applied mathematics, initiated by J. Petitot and his coworkers (see e.g. [52, 50, 63]), that is meant to produce continuous models for different brain subsystems – in particular to the visual system – using method and results from Differential Geometry, Lie Groups, Differential Equations and Statistics.

In more detail, in the first sections of this paper we begin recalling some basic facts about the functional architecture of the early vision in both the static setting (that is, with still eyes and still stimuli) and in dynamics. We also give a short review of some common mathematical representation of the (linear)oculomotor visual neurons as filters, providing differential geometric interpretations. We then address a few mathematical aspects of the interactions, occurring in the process of the visual perception, between the oculomotor information on the eye position and the information coming from the photoreceptors in the retina. In particular, we use Donders’ and Listing’s laws in order to analyse the configuration space of the eye and consider some of the most basic properties of the saccades and fixational eye movements, which lead to the perception of stable objects. We then discuss the phenomenon of the pre-saccadic shifts of receptive fields and of the remapping process together with the problem of identification between two different retinal images after a remapping. On this regard, we present a conjecture according to which such an identification can be mathematically represented in terms of an appropriate conformal transformation of the eye sphere and we show that such a conjecture is a realisation of the Etcetera Principle of E. Gombrich. Consequences of all this concerning the visual stability problem are also discussed.

As we mentioned above, in the last two sections, our discussion focuses on some important differential geometric models for the primary visual cortex V1 and for the hypercolumns, namely: (a) the pioneer model by W. Hoffman, (b) the contact model introduced by Petitot and Tondut, (c) its symplectic extension by Sarti, Citti and Petitot and (d) Bressloff and Cowan’s spherical model of a hypercolumn.

All these models are basically founded on a general idea by Hubel and Wiesel, namely that the firing of a simple neuron with a receptive field represented by a point \( z \) of the retina \( R \), depends not just on the value at \( z \) of the input density of energy of the incident light, but also on several other data of the local properties of such input function near \( z \) (as, for instance, the orientation and the spatial frequency). The first who transposed this idea into differential geometric terms were W. C. Hoffman and J. Petitot, who mathematically represented the early visual system in terms of a fiber bundle \( \pi : P \to R \) over the retina \( R \). In such representations, each point \( z \) of the retina \( R \) (which is ideally considered as a surface) is a mathematical representation for the receptive field (RF) of a column. Indeed, we recall that the RF of a columns is the union of the RFs of the neurons which are contained in it and that, even if it is slightly larger than each single RF of its neurons, in first approximation it can be considered as a single point.
of the retina. At the same time, the points of each fiber \( \pi^{-1}(z) \subset P \) of a RF \( z \) are mathematical representations of the visual neurons that are in the column with such RF. in the mathematical models of kind, only simple neurons are considered. This is motivated by the fact that the first information coming from the retina is mostly transmitted just to simple neurons.

According to this kind of differential geometric models the coordinates \( \theta_1, \ldots, \theta_k \) of the fibers of a principal bundle correspond to Hubel and Wiesel’s “internal parameters” and are related with the local properties of the input energy function at their base points \( z \in \mathbb{R} \), as, for instance, the orientation, the modulus of the gradient, the coordinate in the color space, etc. As we already mentioned, a fixed simple neuron \( n_{\theta_1^0, \ldots, \theta_k^0} \) of a column with RF \( z \) is mathematically represented by the point \( (\theta_1^0, \ldots, \theta_k^0) \) of a fiber \( \pi^{-1}(z) \) and it is assumed to fire only if the restriction of the input function to its RF \( z \) has the local properties, corresponding to the internal parameters \( (\theta_1^0, \ldots, \theta_k^0) \).

A complete list of the internal parameters, which are relevant for the visual system – and thus the exact number of fiber coordinates for the most appropriate differential geometric model of the form \( \pi : P \to \mathbb{R} \) for the V1 cortex – is not known. The most important internal parameters are surely the orientation and the spatial frequency, but there are many other relevant parameters, as for instance those for the color space, the contrast, the curvature, the temporal frequency, the ocular dominance, the disparity and the direction of the motion. N. V. Swindale [68] estimated the total number of internal parameters as \( 6 \) or \( 7 \) or \( 9 \) to \( 10 \).

Another important and deep idea by Hubel and Wiesel is that the columns are locally grouped into hypercolumns, i.e. sets of columns characterised as follows: A hypercolumn \( H \) is a minimal collection of columns of the V1 cortex with different reactions for each of the possible values for the internal parameters. The basic idea is that a hypercolumn, or, more generally, a system of horizontally connected hypercolumns, is a collection of cells that is responsible for the full perception of the local structure of a retina image. On this regard, we have to mention that, contrary to the columns, the existence of hypercolumns has been debated for a long time, see [70].

The first differential-geometric models of the V1 cortex, proposed in the papers by Hoffman, Petitot and Tondut, and Petitot, can be briefly described as follows. According to Hubel and Wiesel’s results, the simple neurons of the V1 cortex detect the contours, i.e the level sets of the input energy function \( I \) on the retina \( \mathbb{R} \) (that is, the energy density of the light that hits the retina) with large gradient. Starting from this idea, Hoffman was the first who presented a pioneering model (with a few mathematical inaccuracies) of the Visual Cortex in terms of a contact bundle [20]. Inspired by Hubel, Wiesel and Hoffmann’s ideas and motivated by the new experimental discoveries concerning the structures of the orientation maps (results that were made possible by revolutionary Bonhöffer and Grinvald’s techniques of the early nineties), J. Petitot and his collaborator Y. Tondut [50, 51, 52] developed in great detail the so-called contact model for the V1 cortex. In such a model, the retina \( \mathbb{R} \), is identified with the Euclidean plane \( \mathbb{R}^2 \) and the V1 cortex is represented as the projectivised tangent bundle \( \pi : P \mathbb{R}^2 \to \mathbb{R}^2 \). This bundle admits a natural system of coordinates \( (x, y, \theta) \), in which \( (x, y) \) are coordinates for the points of the retina \( \mathbb{R} \) and \( \theta \in [-\pi/2, \pi/2] \) is the orientation of the lines passing through \( (x, y) \), i.e. the angle made by the line and the axis 0x. We remark that \( P \mathbb{R}^2 \) can be also interpreted as the space of the infinitesimal curves (or,
more precisely, the 1-jets of the non-parameterised curves) in $R = \mathbb{R}^2$ and it is equipped with the canonical contact 1-form $\eta = dy - \tan \theta dx$.

Petitot’s contact model was later combined with G. Citti and A. Sarti’s model of perceptual completions of images [20] to determine an extended differential-geometric model of the V1 cortex, which we call Sarti, Citti and Petitot’s symplectic model. In this new model the simple cells of the V1 cortex are described in terms of the points of a bundle with two-dimensional fibers. The two coordinates $(\theta, \sigma)$ of the fibers (= the internal parameters considered in this model) are the previously defined orientation $\theta \in [-\pi/2, \pi/2]$ and a new parameter, the so-called scaling factor $\sigma$, which describes the intensity of response of a neuron to a stimulus. In [63] the authors propose an interpretation of such scaling factor $\sigma$ in terms of the distance between the RF of a neuron (which is assumed to be activated through the so-called maximal selectivity process) and the regular boundary of a retinal figure. Note that such interpretation of $\sigma$ has a non-local character and does not allow to consider it as an internal parameter in the sense of Hubel and Wiesel.

Aiming to determine an alternative (and purely local) interpretation of the scaling factor, in [2] the first author proposed the conformal spherical model for hypercolumns, which is based on ideas of P. Bressloff and J. Cowan’s theory of hypercolumns and leads to an interpretation of $\sigma$ in terms of the normalised spatial frequency, another internal parameter that is equally fundamental as the orientation. The conformal spherical model has been later developed in full detail in [4]. In that paper, it is shown that, in small neighbourhoods of pinwheels, the conformal spherical model reduces to a reduced model, which is mathematically identical to Sarti, Citti and Petitot’s symplectic model. In the last section of this paper, we discuss some important features of such a reduced model and its relation with the symplectic model.

This paper ends with a short discussion of differences between the simple and the complex neurons. It is known that each complex neuron of the V1 cortex collects information from systems of several simple neurons. It is also known that the simple neurons are sensible to the shifts of the contours in their receptive fields, while the complex neurons are not (see e.g. [34, 31, 17]). In our last section, we state the Principle of Invariance and discuss a possible use of this principle to explain such a fundamental difference.

The paper is organised as follows. In §1 we offer an outline of some of the most important known facts on the visual system and the functional architecture of the primary visual cortex V1. Many topics very briefly mentioned in this preliminary section will be discussed in greater detail in the subsequent sections. Models of the visual neurons as filters and some of their geometrical interpretation are discussed in §2. In §3 we provide a description of the functional architecture of the primary visual cortex V1, based on the fundamental ideas of Hubel and Wiesel. Section §4 is devoted to the geometry of the eye movements (i.e. to the fixational eye movements and the saccades) and to a discussion of Donders’ and Listing’s laws. A short introduction to conformal geometry of the sphere is given in §5. The information processing in dynamics is the topic of §6 where we discuss the shift of receptive fields, the remapping phenomenon and the problem of identification of retina images before and after the remapping. In that section, we state the conjecture that the remapping is determined by a conformal transformation. We then show that such a conjecture gives a realisation of the Etcetera Principle by E. Gombrich and we discuss its consequences for the Alhazen Visual Stability Problem. In §7 we provide a short exposition of the contact models of the V1 cortex by Hoffman, Petitot and Tondut.
and Petitot of the symplectic model of Sarti, Citti and Petitot. The concluding section §8 is devoted to models of hypercolumns. More precisely, we describe the geometric structure of Bressloff and Cowan’s spherical model, our modification of such a model in the framework of conformal geometry and a reduced version of such modified model for neighbourhoods of pinwheels. We then discuss the relations between Sarti, Citti and Petitot’s symplectic model, Bressloff and Cowan’s spherical model and our conformal model. In the concluding subsection §8.4, we state the Principle of Invariance and use it for an explanation of the differences between simple and complex cells.

Acknowledgements. We warmly thank J. Petitot for valuable comments and useful advises and suggestions that helped us to improve the overall presentation.

1. General principles of the organisation of the visual system

In this section, we list the main assumptions that we adopt throughout the paper and we outline some well known facts on the visual system, with a particular attention to geometric aspects. Many of the topics, that are just briefly touched here, will be further discussed in the next sections. As for any survey of a very wide area, we are aware that our exposition has little chance to be fully comprehensive. But we need to stress that, as we mentioned above, our goal is essentially to provide a concise and handy overview of the most important facts on the functional architecture of early vision, which can be helpful for mathematician, who are interested in neurogeometry and are not a specialists in the physiology of vision. For additional information on the topics outlined in the following, the reader is referred to the textbooks, reviews and articles on the visual system [34, 15, 40, 36, 38, 41, 45, 50, 51, 21] and the many references therein.

1. Our discussion is limited to the monocular vision given by gray levels (no color).
2. In the first part of this paper, we are going to limit the discussion to the static situation (i.e. when the eye and the stimuli are still). In this setting, it can be assumed that the brain extracts all visual information just from the retinal input function $I_R$, i.e. the density of the energy of the light which is incident to the retina $R$. Such a function is encoded into the excitation of the photoreceptors (rods and cones). Note however that in the natural setting, the eyes are never still, they are continuously moving and it is experimentally proved that, if compensations of the eye movements are made, then a loss of vision occurs within 2-3 seconds [74]. In the dynamics setting, the input energy function $I_R$ is a function not only of the points $z \in R$ of the retina but also of the time $t$, and the vision is the result of an interaction between the stochastic information about the dynamics of the retinal image, encoded in the photoreceptors, and the information about the eye position, given by the oculomotor control system. Copies of the oculomotor commands on the eyes movements (efferent copies or corollary discharges) meet the information coming from the retina in some region of the cerebral cortex, which is probably the medial superior temporal (MST) area [19].
3. We assume that the head is fixed and we consider the eye ball as a rigid body, which may rotate around its center $O$. The retina $R$ is considered as a very large domain of the eye sphere ($= \text{the boundary of the eye ball}$). Sometimes it is convenient to identify the retina with the whole eye sphere. We also assume that the optical center of the eye, i.e. the nodal point $N$, is located on the eye sphere. In reality, $N$ is an inner point of the eye ball, but it is very close to the boundary.
4. The retinal image of an external surface $S \subset \mathbb{R}^3$ is obtained by the central projection with respect to $N$ of the surface $S$ onto the eye sphere. Such a projection is the map $\varphi_N: S \to R$, which sends each point $A$ of $S$ into the point $\overline{A}$ of $R$, which is determined by the intersection between the ray $\ell_{AN}$, originating from $A$ and passing through $N$, and the retina $R$:

$$S \ni A \mapsto \overline{A} := \ell_{AN} \cap R.$$ (1.1)

Under the assumption that each $A \in S$ is the source of an ideal diffused reflected light, the corresponding $\overline{A}$ is the point in the retina that receives the light emitted by $A$ with an intensity that depends on the energy density at the emission point.

5. We assume that the center of the fovea is a point $F$ of the eye sphere, opposite to $N$.

6. We denote by $S^2_{\text{eye}}$ the eye sphere in primary position and by $(x, y)$ the Euclidean coordinates of the tangent plane $T_F S^2_{\text{eye}}$ of $S^2_{\text{eye}}$ at the center of the fovea $F$. The stereographic projection with respect to the pole $N$

$$\text{st}_N: S^2_{\text{eye}} \to T_F S^2_{\text{eye}} = \mathbb{R}^2, \quad p \mapsto \text{st}_N(p) := \ell_{Np} \cap T_F S^2_{\text{eye}}$$

allows to consider $(x, y)$ as standard conformal coordinates for the retina $R \subset S^2_{\text{eye}}$. In these coordinates, the metric of the eye sphere $S^2_{\text{eye}}$, which is given by its embedding into the physical Euclidean space $E^3 = \mathbb{R}^3$, has the form

$$g = f(x, y)(dx^2 + dy^2)$$

for some function $f(x, y)$. In a small neighbourhood of $F$, the function $f(x, y)$ is approximately constant and equal to 1, and $(x, y)$ are approximately Euclidean coordinates for $g$. Under these approximations, the retina $R \subset S^2_{\text{eye}}$ can be (locally) identified with the Euclidean plane $\mathbb{R}^2$.

8. The visual system has a hierarchical structure with a strong feedback. The initial input function $I_R$, which is recorded by the photoreceptors (cones and rods), is very irregular. The purpose of the information processing in the retina is to regularise and contourise the input function $I_R$ and prepare it for decoding. The output of this process is a regularised function $I: R \simeq \mathbb{R}^2 \to \mathbb{R}$, which is the input (energy) function for the visual cortex V1. It is encoded in terms of the excitations of the ganglion cells whose long axons terminate in the LGN (Lateral Geniculate Nucleus). The visual information is first sent from the retina to the LGN through the axons, second it is sent to the primary visual cortex V1, and then to the regions V2, V3, etc., i.e. to all other regions of the visual system. The transformations which correspond to the changes from the input functions $I_R$ on the retina into the corresponding functions $I$ that are the input for the LGN and the V1 cortex, can be mathematically described (in first approximation) as conformal maps with respect to appropriate natural metrics, see [64]. These transformations are called retinotopic (or topographic) mappings.

9. The visual information of the V1 cortex is encoded in the firings of the visual neurons. Each visual neuron works as a filter, i.e. as a functional on the space of all possible input functions. In static, the firing of a visual neuron depends only on the restriction $I|_D$ of the input function $I: R \to \mathbb{R}$ to some small domain $D \subset R$, which is called the receptive field (RF) of the neuron. In dynamics, the situation is much more complicated. We will discuss it in §6.

10. Simple and complex neurons. Hubel and Wiesel divide the neurons into simple and complex. A simple neuron (also called simple cell) works as a linear filter, i.e. as a
linear functional on the space of the input functions, whose output is the average of the restriction \( I_D \) of the input function \( I \) to the receptive field \( D \) of the neuron, in which the mean value is computed weighting each point \( z \in D \) by the value \( W(z) \) of an appropriate weight function \( W : D \to \mathbb{R} \), called receptive profile (RP) of the neuron. The receptive profiles of the simple neurons are well approximated by the so-called Gabor functions, i.e. Gauss functions modulated by a sine or a cosine function (see \( \S 2 \) for details).

The other neurons are the complex neurons (or complex cells). They collect information from systems of several visual neurons and usually work as non-linear functionals. Several models for the complex cells have been proposed – one of the first models was proposed by J. A. Movshon, I. D. Thompson and D. J. Tolhurst \([48]\) (see also \([17, 18]\)). Following an idea by Hubel and Wiesel, they describe a complex cell as a non-linear filter for the information, which is determined by a system of (linear) simple cells with identical orientation but different receptive profiles. According to this model, the processing performed by a complex cell consists of a rectification and a combination of the information, which is collected by the simple cells to which it is connected. A crucial difference between the complex cells and the simple cells is given by the fact that the reaction of a complex neuron to a contour is invariant under shifts of that contour within the receptive field of the neuron. Till now this model is in a good correspondence with experiments (see \([17]\)).

The main limitation of these models of complex and simple cells is that they are static, that is they do not take into account the time evolution of the incoming information. In dynamics the situation becomes much more complicated and the non-linear neurons (filters) play a more important role. In this paper we are mostly concerned with the (linear) simple neurons. Complex neurons will be briefly discussed only in the last section.

11. Processing of the visual information in the retina. Before going from the retina to the visual cortex, a processing of the visual information occurs within the retina. We do not discuss in detail the very complicated system of processing information in retina – for this topic with refer to the excellent survey \([55]\). Here we just mention that, roughly speaking, the retinal processing of the visual retinal information, encoded in the photoreceptors (codes and rodes), consists in regularisations and contourisations of the stimuli. The first physiologist who detected a response on a retinal neuron and proposed a model for such actions was S. W. Kuffer. We will discuss his model in \( \S 2.2 \).

12. As we mentioned above, after the initial retinal processing, most of the retinal information goes to the LGN (the Lateral Geniculate Nucleus), which is a part of the Thalamus. The LGN does not perform a further processing of the information coming from the retina, but it supplies additional instructions or changes for some of the parameters, which are needed for subsequent manipulations, and distributes the updated information among several other subsystems for processing. Most of the information is sent to simple cells of the primary cortex V1. But some is sent directly to the higher visual subsystems V2 and V3. Another very important purpose of the LGN is to provide feed-back from the higher visual systems to the primary information processing system, primarily to the V1 cortex.

13. There are three pathways from the retina to the primary visual cortex V1 through the LGN: The P-pathway, which is mostly responsible for the perception of stable objects, the M-pathway, which is important for the perception of moving objects, and the K-pathway. The function of the K-pathway is not know properly, but it is known that it
is related with the perception of colors. In this paper we consider only the P-pathway. The structure of the other pathways is more involved: For instance the M-neurons (which are responsible for the M-pathway) are non-linear, even those on the retina.

14. The energy function $I : \mathbb{R} \to \mathbb{R}$ on the retina $\mathbb{R}$ is completely determined by its values and the level sets $L_c = \{ z \in \mathbb{R} : I(z) = c \}$ of the assumed values. Only the level sets, not the values, are truly relevant (just think about the fact that when the light in the room is turned on, the illumination of the retina changes dozens of times). This fact is consistent with Hubel and Wiesel’s discovery that the main objects detected in the early vision are the contours, that is the (non-parametrised) level curves $L_c = \{ I = c \}$ of the energy function $I$ with large gradients. Note that, mathematically, a contour is an integral curve of the 1-dimensional distribution, given by the Pfaffian system $dI = 0$, and it depends just on the conformal class $[\omega]$ of the 1-form $\omega = dI$.

15. A contour $L$ though a point of the retina $z \in \mathbb{R}$ is locally approximated by its tangent line $\ell = T_z L \subset T_z \mathbb{R}$ at $z = (x, y)$ or, more precisely, by a small interval $b \subset \ell$ of this line, called bar. The line $\ell$ and the bar $b$ are determined by their orientation $\theta \in [-\pi/2, \pi/2)$, i.e. the angle formed by $\ell$ and the $x$-axis. The space of the infinitesimal contours (also called orientations) is the space of all tangent lines to non-parametrised curves of $\mathbb{R}$, i.e. the projectivised tangent bundle $PTR$ of $\mathbb{R} \simeq \mathbb{R}^2$. We recall that an open dense subset of $PTR$ can be locally identified with the space of 1-jets $J^1(\mathbb{R}, \mathbb{R}) = \{(x, y, \frac{dy}{dx})\}$ of the functions $y = y(x)$ of the real line.

16. The orientation $\theta$ of the tangent line of a contour is a very important (but not unique) internal parameter for the local structure of the input energy function $I$, the main stimulus in the early vision. Another fundamental internal parameter is the spatial frequency \[16, 59, 24]\: Roughly speaking, it is a measure of how often the sinusoidal components of the stimulus (given by its Fourier transform) repeat per unit of length. It is measured by number of cycles per degree, $c/\text{deg}$. It is not an infinitesimal characteristic of a contour $L$, but of the structure of the image in a neighbourhood of the contour. More precisely, it is a datum which is characteristic of the 1-dimensional distribution $D = \ker dI$ near a contour. The Fourier analysis allows to approximate the distribution $D = \ker dI$ by means of a sinusoidal grating. Such a grating is determined by 4 parameters: spatial frequency, contrast, orientation and phase. All these parameters may be considered as internal parameters and they give information on the local properties of the image. In this paper, following Bressloff and Cowan, we focus on the orientation and the spatial frequency. On this topic, we would like to mention that J. G. Robson et al. \[59\] showed that there are many independent channels for the spatial frequency, but only a few of them correlates. For example, the channel with spatial frequency $p = 14 \ c/\text{deg}$ correlates with a channel with a frequency $p'$ if $p/p'$ is $4/5$ or $5/4$.

17. Hyper-specialisation of visual neurons. A visual neuron fires only when, in its receptive field, the local internal parameters of the stimulus (as e.g. its orientation, spatial frequency, contrast, etc.) take (up to small variations) some prescribed values, which are uniquely associated with the neuron. Actually, the firing of many types of visual neurons depend not just on such prescribed values, but also on their rate of change. This is the reason why, in order to perceive a stable object, the eye must constantly move.

\[1\]The degree is the the standard length measure for the eye sphere.
2. Models of linear visual neurons

A fundamental mathematical model for the visual neurons is provided by the following notion. By *linear neuron with receptive field (RF)* $D \subset R \simeq \mathbb{R}^2$ we mean a neuron, which works as a linear filter $T_W$ on the input energy function $I(z)$ of the form

$$I \xrightarrow{T_W} \int_D W(z) I(z) \text{vol} , \quad z = (x, y) ,$$

where we denote by $\text{vol} := dxdy$ and by $W(z)$ a *weight function* (in neurophysiology, it is called *receptive profile (RP)*) which characterises the filter $T_W$. In mathematical language, $T_W$ is a linear functional, determined by the weight function $W$ with support $D$. One may say that it calculates a sort of “mean value” of the restriction $I|_D$ of the input function to the receptive field $D \subset R$, where each point $z$ is counted with the weight $W(z)$.

We recall that a transformation $z \rightarrow z' = \varphi(z)$ with positive Jacobian $J(\varphi) = \det\left|\frac{\partial z'}{\partial z}\right|$, changes the coordinate system $z = (x, y)$ into the new coordinate system

$$z'(z) = (x', y') = (x \circ \varphi^{-1}, y \circ \varphi^{-1}) .$$

Therefore, under such transformation, each receptive profile $W(z)$ changes into

$$\varphi(W)(z') := \left(J(\varphi)|_{\varphi^{-1}(z')}\right)^{-1} W(\varphi^{-1}(z')) , \quad (2.2)$$

i.e. the RPs transform as densities.

In the following subsections, we discuss several types of linear filters that are particular relevant for vision.

2.1. Gauss filters on the plane. The *Gauss filters* are the linear filters with RP given by the Gauss probability distributions of $\mathbb{R}^2$, that is the functions defined as follows (see also §2.5). Let us call *mother Gauss filter* the linear filter $T_{\gamma_0}$ with RP

$$\gamma_0(z) := \frac{1}{\sqrt{2\pi}} e^{-\frac{1}{2}|z|^2} .$$

A *Gauss filter* is the filter with the RP that is obtained from the $\gamma_0$ by means of a transformation of the oriented affine group $\text{Aff}^+(\mathbb{R}^2) = \text{GL}^+(n) \cdot \mathbb{R}^n$, i.e. by a transformation

$$z \xrightarrow{T_{A,\tau}} Az + \tau \quad \text{with} \quad \det A > 0 .$$

The RP $\gamma_{A,\tau}$ of a Gauss filter determined by the transformation $T_{A,\tau}$ is

$$\gamma_{A,\tau}(z) := \frac{1}{\det A} \frac{1}{\sqrt{2\pi}} e^{-\frac{1}{2}|A^{-1}(z-\tau)|^2} .$$

Clearly, the group $\text{Aff}^+(\mathbb{R}^2)$ acts transitively on the space $\mathcal{G}$ of all Gauss filters and its stability subgroup is $\text{SO}(2)$. This action canonically extends to an action of the larger group $\text{SL}(3, \mathbb{R})$, so that $\mathcal{G} = \text{Aff}^+(\mathbb{R}^2)/\text{SO}(2) = \text{SL}(3, \mathbb{R})/\text{SO}(3)$.

The orbit in $\mathcal{G}$ of the mother Gauss filter under the *similarity subgroup*

$$\text{Sim}(\mathbb{R}^2) = \text{CO}(2) \cdot \mathbb{R}^2 \simeq \mathbb{C}^* \cdot \mathbb{C}$$
is an important submanifold $G_0 = \text{Sim}(\mathbb{R}^2)/\text{SO}(2)$ of the manifold of all Gauss filters. If we identify $\mathbb{R}^2$ with the plane of complex numbers $\mathbb{C} = \{z = x + iy\}$, then $\text{Sim}(\mathbb{R}^2)$ is identified with the complex affine group $\mathbb{C}^* \cdot \mathbb{C}$ of the complex transformations 

$$z \mapsto T_{a,b} z = az + b, \quad a \in \mathbb{C}^*, \ b \in \mathbb{C}$$

and the RP of the Gauss filter associated with the transformation $T_{a,b} \in \text{Sim}(\mathbb{R}^2)$ is

$$\gamma_{a,b}(z) = \frac{1}{|a|^2} e^{-\frac{|a-b|^2}{2|a|^2}}.$$

Note that $\gamma_{a,b} = \gamma_{|a|,b}$ for any $a \in \mathbb{C}^*$, meaning that the subgroup $\mathbb{R}_+ \cdot \mathbb{C} \subset \mathbb{C}^* \cdot \mathbb{C}$ acts simply transitively on $G_0$. The parameter $\sigma = |a|$ is called the standard deviation and $b$ is the mean value of $\gamma_{a,b}$. Notice also that, when the standard deviation $\sigma = |a|$ tends to 0, the Gauss functional

$$T_{\gamma_{\sigma,b}}(I(z)) := \int I(z) \gamma_{\sigma,b} \text{vol}(z)$$

tends to the Dirac delta function at $b$, i.e. to the functional $\delta_b(I) := I(b)$. For this reason, the Gauss filters of $G_0$ can be taken as $\sigma$-approximations of the functionals $I \mapsto I(b)$, $b \in \mathbb{C}$.

2.2. Kuffler isotropic neurons and Marr filters. S. W. Kuffler [42, 34] was the first who detected a response to a stimulus of the retinal ganglion cells in mammals. He described the structure of the isotropic (i.e. rotationally invariant) receptive field of an (isotropic) neuron as two concentric discs $D' \subset D$ of the retina and divided the isotropic neurons in two classes: the ON-neurons and the OFF-neurons. The receptive profile $W(x, y)$ of an ON-neuron (respectively, an OFF-neuron) is

- positive (resp. negative) in the inner disc $D'$,
- negative (resp. positive) in the ring $D \setminus D'$

and it is such that $\int_D W(x, y) \text{vol} = 0$. This feature explains why the neurons of this kind give no response when the input function $I$ is constant.

D. Marr [45] showed that a linear filter whose RP is the Laplacian $\Delta \gamma_{a,b}$ of a Gauss density $\gamma_{a,b} \in G_0$ provides a realistic model for a Kuffler neuron. He also explained that a system of such filters produces a regularisation and contourisation of the input function $I$. In other words, it transforms the retina image into a graphics picture. This is the aim of the data processing in retina. We remark that systems of Marr filters (and of their generalisations) are used in computer vision to transform pictures into graphics.

Another realistic model for a Kuffler neuron is a linear filter with RP given by the difference between two Gauss densities, both with same mean value $b$, but with different standard deviations $\sigma, \sigma'$.

2.3. Koenderink’s Multiscale Geometry of Image Processing. J. Koenderink [41, 28] defines the Multiscale Geometry as the geometry which studies the $\sigma$-approximations to Differential Geometry for arbitrary resolution parameters $\sigma$. In his seminal paper [41], he showed that an image can be embedded into a one-parameter family of derived images, parametrised by the resolutions $\sigma$ and governed by the heat equation or other types of diffusion equations, in particular the anisotropic ones (the latter is particularly relevant in computer vision, as they do not diffuse edges).
2.4. Derived filters and Hansard and Horaud’s simple cells of order \( k \). Let \( X \) be a vector field on \( \mathbb{R}^2 \), identified with a derivation of the algebra of real functions. Given a Gauss filter \( T_{\gamma_{a,b}} \), the linear functional \( T_X \cdot \gamma_{a,b} \) with RP \( X \cdot \gamma_{a,b} \) is called derivative of \( T_{\gamma_{a,b}} \) in the direction \( X \). Integration by parts shows that the limit of \( T_X \cdot \gamma_{a,b} \) for \( \sigma = |a| \to 0 \) is the functional which associate to any input function \( I \) its directional derivative \( -(X \cdot I)(b) \) at the point \( b \). In differential geometry, such a functional is identified with the tangent vector \( -X_b \). For this reason, the functional \( T_X \cdot \gamma_{a,b} \) can be considered as a \( \sigma \)-approximation of the tangent vector \( -X_b \). Similarly, the functional \( T_Y \cdot (X \cdot \gamma_{a,b}) \) is a \( \sigma \)-approximation of the second order differential operator at \( b \) given by

\[
I \mapsto Y \cdot (X \cdot I)(b) .
\]

M. Hansard and R. Heraud [31] proposed a definition of a simple visual neuron of order \( k \) as the filter with RP given by a linear combination of directional derivatives of the form

\[
X_1 \cdot X_2 \cdot \ldots \cdot X_k \cdot \gamma_{a,b} .
\]

As we remarked above, such an operator can be considered as a \( \sigma \)-approximation of a linear combination of differential operators of the form \((-1)^k X_1 \circ \cdots \circ X_k|_b\). This means that, geometrically, a simple visual neuron of order less than or equal to \( k \) computes a component of the \( k \)-th order jet of a contour. We recall that the space of all \( k \)-jets of non-parametrised curves of the retina \( R \simeq \mathbb{R}^2 \) are locally parametrised by the space of \( k \)-jets \( J^k(\mathbb{R}, \mathbb{R}^2) \) of the \( \mathbb{R}^2 \) valued functions on the real line, i.e. the space of the Taylor polynomials of functions of one real variable and values in \( \mathbb{R}^2 \) of degree less than or equal to \( k \).

Following an idea by Hubel and Wiesel, Hansard and Horaud also proposed the notion of a complex visual cell as a composition of simple visual neurons of the above kind.

2.5. Gabor filters and simple cells of V1 cortex. Roughly speaking, a Gabor filter is a linear functional with RP given by a Gauss function modulated by \( \cos y \) or \( \sin y \) (see [24, 67] and references therein). More precisely, it is defined as follows. Let us denote by \( \mathcal{G}ab_{\gamma_0} \) and \( \mathcal{G}ab_{\gamma_0}^{-} \) the linear filters with RPs

\[
\gamma_0^+(z) := \gamma_0(z) \cos y = e^{-\frac{1}{2}|z|^2} \cos y , \quad \gamma_0^-(z) := \gamma_0(z) \sin y = e^{-\frac{1}{2}|z|^2} \sin y ,
\]

respectively (here, as usual, \( z = x + iy \)). These RPs conveniently combine into the complex RP

\[
\gamma_0^C(z) := \gamma_0(z) e^{iy} = e^{-\frac{1}{2}|z|^2 + iy} = \gamma_0^+(z) + i\gamma_0^-(z) . \tag{2.3}
\]

The complex filter \( \mathcal{G}ab_{\gamma_0}^C \) with RP \( \gamma_0^C \) is called complex mother Gabor filter, while its real and imaginary parts \( \mathcal{G}ab_{\gamma_0}^+ \) and \( \mathcal{G}ab_{\gamma_0}^- \) are called even and odd mother Gabor filters. In analogy with the definition of the Gauss filters, the Gabor filters are the linear filters \( \mathcal{G}ab_{\gamma_{a,b}} \) that are obtained from the mother filters \( \mathcal{G}ab_{\gamma_0} \) by transformations \( T_{a,b} \in \text{Sim} (\mathbb{R}^2) = \mathbb{C}^* : \mathbb{C} \).

The RP \( \gamma_{a,b} \) of these linear filters can be explicitly given determined from \( \gamma_0^C \) as follows. Let \( a := \sigma e^{i\theta} \), \( b_0 := \text{Re}(b) \), \( b_1 := \text{Im}(b) \). Then, by (2.2), the RP \( \gamma_{a,b}^\pm \) are the real and
imaginary parts of the complex RP
\[ \gamma_{a,b}^C(z) = \gamma_{a,b}^+(z) + i\gamma_{a,b}^-(z) = T_{a,b}(\gamma_0^C(z)) = \frac{1}{\sigma^2}e^{-\frac{1}{2}|z\circ T_{a,b}^{-1}|^2 + iy\circ T_{a,b}^{-1} = \frac{1}{\sigma^2}e^{-\frac{|x-h|^2}{2\sigma^2} + i\frac{(x-h_0)\sin \theta + (y-h_1)\cos \theta}{\sigma}}. \] (2.4)

Since Sim(\(\mathbb{R}^2\)) = \(\mathbb{C}^*\cdot\mathbb{C}\) acts simply transitively on the family of all Gabor filters of the plane, these filters constitute a manifold \(\mathfrak{G}_{ab}\) which we identify with \(\mathfrak{G}_{ab} = \mathbb{C}^*\cdot\mathbb{C}\).

J. D. Daugmann showed in [24] that there exists an uncertainty relation between orientation and spatial frequency of stimuli and that a Gabor filter optimises such uncertainty relation.

Other mathematical models for simple neurons is given by the derived filters of first and second orders of the Gabor filters in the sense of Hansard and Heraud, that is the analogs of the derived filters considered in §2.4. In fact, these types of filters are very close one to the other and, roughly speaking, they are both appropriate for detecting second order jets of contours.

3. The functional architecture of the V1 cortex in statics

3.1. Structure of the V1 cortex. In this section we briefly recall some well known facts on the structure of the V1 cortex. For a more detailed discussion and further information, the reader is referred to the excellent book by D. H. Hubel [34].

The primary visual cortex V1 is a layer which is in average 2.5 mm thick and consists of six sublayers. Hubel and Wiesel discovered that the neurons of the V1 cortex are organised into vertical columns. Each column consists of 80–100 visual neurons (of which approximately 25% are simple cells) and all of them have almost the same receptive field (RF). There are two type of columns. A column is called regular if its simple neurons have almost the same orientation, say \(\theta_0 \in [-\frac{\pi}{2}, \frac{\pi}{2}]\). This means that each of them fires only when a contour crosses their RF with the orientation \(\theta_0\) (up to an error of 15 – 20%). A column is called singular (or pinwheel) if it contains simple cells that can detect contours with any orientation.

According to this, to each regular column one may attribute: (a) the point \(z\) of the retina \(R\), which is the common RF of its simple cells and (b) the common fixed orientation \(\theta_0\) of its neurons. On the other hand, to each pinwheel one may attribute the common RF \(z \in R\) of its neurons and consider the orientations of the simple cells of the column as the values of an internal parameter, which distinguish each neuron from the others. In other words, the correspondence between points of the retina and orientations \(\theta\) is a well defined function if it is restricted to the subset of the points \(z \in R\) that are the RFs of regular columns, but such a function has singularities at the points that are RFs of pinwheels.

The distance between two neighbour pinwheels in the visual cortex is in average equal to 1–2 mm. They serve as a sort of watch towers, which can detect contours of arbitrary orientations. One of the purposes of the fixational eyes movements is to produce shifts of the retina images in such a way that the contours of such images can intersect the RFs of the pinwheels, so that the pinwheels can detect them.
3.2. The V1 cortex as a fiber bundle: The “engrafted variables” of Hubel and Wiesel and the hypercolumns. Hubel and Wiesel remarked that the firing of the simple neurons depends not only on the coordinates \( z = (x, y) \) of their RF in the retina \( R \), but also on many other parameters, called internal, which may be considered as fiber-wise coordinates of a fiber bundle over the retina. In fact, they proposed the first fiber bundle model for the V1 cortex, the so called ice-cube model with two internal parameters: the orientation and the ocular dominance.

In [34] Hubel wrote: "What the cortex does is to map not just two but many variables on its two-dimensional surface. It does so by selecting as the basic parameters the two variables that specify the visual field coordinates (distance out and up or down from the fovea), and on this map it engraves other variables, such as orientation and eye preference, by finer subdivisions."

The complete set of the internal parameters, which are relevant for the visual system, is not known. The most important internal parameters are the orientation and the spatial frequency, but there are many other relevant parameters, as for instance the parameters of the color space, the contrast, the curvature, the temporal frequency, the ocular dominance, the disparity and the direction of the motion.

Another fruitful idea by Hubel and Wiesel is the notion of hypercolumn. They define a hypercolumn as a collection of columns consisting of simple neurons which can measure any possible value for the internal parameters. Unlike the columns, the existence of hypercolumns is not physiologically confirmed and it has been the subject of debate for a long time.

4. Eye movements and the configuration space of the eye

4.1. The eye as a rigid rotating ball. From a mechanical point of view, the eye is a rigid ball \( B_{\text{eye}} \), which can rotate around its center \( O \). The retina approximately occupies two thirds of the eye sphere \( S^2_{\text{eye}} = \partial B_{\text{eye}} \), but, for simplicity, in what follows we identify it with the whole eye sphere. As we mentioned in §1, in this paper we assume that the eye nodal point (or optical center) \( N \) is in the eye sphere and that its opposite point \( F \in S^2_{\text{eye}} \) is the center of the fovea.

There is a primary (standard) position for the eye, which is characterised by the orthonormal frame \( (O, (\mathbf{i}, \mathbf{j}, \mathbf{k})) \) at the center \( O \) of \( S^2_{\text{eye}} \), with \( \mathbf{i} \) giving the frontal direction of the gaze, \( \mathbf{j} \) orthogonal to \( \mathbf{i} \) and giving the horizontal direction oriented from left to right, and \( \mathbf{k} \) giving the vertical direction oriented from bottom to top. This frame determines the primary “fixed head centred coordinates” \((x, y, z)\) for the Euclidean space \( \mathbb{R}^3 \) with origin \( O = (0, 0, 0) \).

Any other position of the eye sphere is determined by an orthogonal transformation \( R \in \text{SO}(3) \) around the point \( O \) (which clearly preserves \( S^2_{\text{eye}} \)) that transforms the orthonormal frame \( (\mathbf{i}, \mathbf{j}, \mathbf{k}) \) into another \( (\mathbf{i}', \mathbf{j}', \mathbf{k}') = R(\mathbf{i}, \mathbf{j}, \mathbf{k}) \) in which \( \mathbf{i}' \) gives a new gaze direction. We recall that any orthogonal transformation \( R \in \text{SO}(3) \) is a rotation around some fixed axis through the origin \( O \). In the following, given a unit vector \( \mathbf{e} \) and an angle \( \alpha \), we denote by \( R_\alpha \mathbf{e} \) the rotation of angle \( \alpha \) around the axis determined by \( \mathbf{e} \).

4.1.1. Helmholtz’s physiological definition of a “straight line”. H. von Helmholtz gave the following physiological definition of a straight line [32] (see also [56] and references
A straight line is a curve $\ell = \{ \gamma(t), t \in \mathbb{R} \}$ of the Euclidean space $\mathbb{R}^3$, which is characterised by the following property: when the gaze moves along the curve $\gamma(t)$, the retinal image of $\ell$ does not change (Fig. 3 & 4).

Indeed, let $\ell = \{ \gamma(t), t \in \mathbb{R} \} \subset \mathbb{R}^3$ be a straight line and $\Pi$ the (unique) plane through $\ell$ and the nodal point $N$. When the eye looks at a point $\gamma(t)$ of the line $\ell$, the corresponding image on the retina is determined by the central projection $\pi_N: \ell \to S^2_{\text{eye}}$ and this is just the intersection between $S^2_{\text{eye}}$ and the plane $\Pi$. Hence such an image is always the same and it does not depend on the point $\gamma(t)$ of the line $\ell$ toward which the gaze is directed.

![Diagram](image)

**Fig. 3 & 4 (from [7]) – Listing’s Law and Helmholtz’s definition of “straight line”**

### 4.2. The configuration space of the eye – Donders’ and Listing’s laws.

**Donders’ law** states that when the head is fixed, the position of the eye is completely determined by the unit vector $i'$ that gives the direction of the gaze. This implies that the set $\Sigma$ of the possible positions of the eye is a surface in the orthogonal group $SO(3)$ (corresponding to the set of all admissible gaze directions $i' \in S^2$). More precisely, we have

**Theorem 4.1** (Donders’ “no twist” law). If the head is fixed, the direction $i'$ of the gaze determines the position of the eye ball and does not depend on the previous eye movements.

This law implies that there is a (local) section

$$s: S^2 \rightarrow \mathcal{OF}(S^2) = SO(3)$$

of the bundle of the oriented orthonormal frames

$$\mathcal{OF}(S^2) = SO(3) \longrightarrow S^2 = SO(3)/SO(2)$$

over the sphere $S^2$ of unit vectors, which transforms any curve of gaze directions

$$t \mapsto \tilde{i}(t) \in S^2$$

into the curve

$$t \mapsto s(\tilde{i}(t)) \in SO(3) = \mathcal{OF}(S^2),$$

given by the rotations $R(t) = s(\tilde{i}(t))$ of the eye ball associated with the gaze curve $\tilde{i}(t)$. The **Listing’s law** determines this surface as follows.

**Theorem 4.2** (Listing’s law – see e.g. [2]). The movement from the standard eye position, associated with the gaze direction $\tilde{i} \in S^2_{\text{eye}}$ to a new position, associated with a gaze $\tilde{i}' \in S^2_{\text{eye}}$, can be always realised by the rotation $R_\omega^\alpha$ by the angle $\alpha = \tilde{i}, \tilde{i}'$ around the axis $R_\omega$, where $\omega$ is the unit vector $\omega := \tilde{i} \times \tilde{i}'$, belonging to the Listing plane $\tilde{i}^\perp$.

More generally, the movement from a gaze direction $\tilde{a} \in S^2_{\text{eye}}$ to a gaze direction $\tilde{b} \in S^2_{\text{eye}}$ is realised by the rotation $R_\omega^\alpha$ by the angle $\alpha = 2(\tilde{i} + \tilde{a}), (\tilde{i} + \tilde{b})$ around the axis
**4.3. Eye movements: the saccades and the fixational eye movements.** The eye movements are very important for vision: Classical experiments by A. Yarbus show that a compensation of all eye movements leads to a loss of vision of stationary objects in $2 - 3$ sec.

One of the possible reasons for this is that the firing of many visual neurons depends on the rate of change of the internal parameters of the stimuli. In this subsection we shortly discuss some special eye movements that occur when the gaze is “fixed”, i.e. concentrated on a stable external point: the saccades and the fixational eye movements (see e.g. [58]).

The saccades are very rapid rotations of the eyes (up to $700^\circ$/sec in humans) of large amplitudes. It is a ballistic movement: After the start, the oculomotor system cannot change its trajectory. For any two admissible (i.e. belonging to the same field of vision) gaze direction $\mathbf{a}, \mathbf{b} \in \mathbb{S}^2_{\text{eye}}$, there exists a unique saccade which change the gaze direction $\mathbf{a}$ to $\mathbf{b}$ and it is realised by the rotation around the axis, which is orthogonal to the plane $\Pi(\mathbf{a}, \mathbf{b}, -\mathbf{i})$, as it describes above in the Listing’s law. The corresponding evolution of the gaze describes a geodesic of $\mathbb{S}^2_{\text{eye}}$ if and only if both $\mathbf{a}, \mathbf{b}$ lie in a meridian of $\mathbb{S}^2_{\text{eye}}$ through the poles $\mathbf{i}$ and $-\mathbf{i}$.

The fixational eye movements include the tremor, the drifts and the microsaccades. The tremor is an aperiodic wave-like motion of the eye of high frequency ($40 - 100$ Hz) but of very small amplitude (in between a few arcsecond and a few arcminutes) [1]. Under the tremor the gaze fills a cone in one tenth of a second. The drifts occur simultaneously with the tremor and are slow motions of the eye, with frequency $1 - 20$ Hz and amplitudes up to $10^\prime$. During a drift, the image of a fixation point stays within the fovea. The microsaccades are fast short jerk-like movements with amplitude $2^\prime - 120^\prime$ (see e.g. [54]).

In 1 second the tremor moves the retinal image of $1 - 1.5$ diameters of the cones of the central part of the fovea, a drift moves along $10 - 15$ diameters of the cones and the microsaccades carry an image across dozen to several hundred diameters of the cones.

**4.3.1. The purposes of the saccades and the fixational eye movements.**

(i) When the eye is fixed, the visual information comes from the light rays passing through the lens of the eye, which can be identified with the rays of the central projection by the nodal point $N$ – see [1] n.3. These rays determine a 2-dimensional submanifold $L(N) \subset L(\mathbb{R}^3)$ of the space $L(\mathbb{R}^3)$ of all lines of $\mathbb{R}^3$. Thanks to the fixational eye
movements, the brain receives information from a neighbourhood of $L(N)$ in the four dimensional manifold $L(\mathbb{R}^3)$.

(ii) The fixational eyes movements produce also shifts of the retinal image, which allow the contours to intersect the receptive fields of the pinwheels, so that they can be detected by the simple cells of those pinwheels. These movements are essential for perceiving immobile objects.

(iii) We conjecture that the main aim of the tremor is to increase the width of the retinal contours, so that they can be detected by several rows of photoreceptors. This allow to estimate the gradient of the input function at the points of the contours.

5. A short introduction to the conformal geometry of the sphere

5.1. The conformal sphere and its group of conformal transformations. In this subsection, we recall some basic notions and results of the conformal geometry of the 2-sphere. For more extended discussions and many additional references for this topic, see e.g. [40, 65, 66].

5.1.1. The conformal sphere. The conformal structure of a Riemannian manifold $(M, g)$ is the class $[g] = \{\lambda g : 0 < \lambda \in C^\infty(M)\}$ of all metrics that are conformally equivalent to $g$. The conformal group of $(M, [g])$ is the group $\text{Conf}(M)$ of the transformations, which preserve the conformal structure $[g]$.

The conformal sphere is the sphere $S^2 = \{x^2 + y^2 + z^2 = 1\} \subset \mathbb{R}^3$ equipped with the conformal structure $[g_o]$, determined by the standard round metric $g_o$. The conformal plane $(\mathbb{R}^2, [g^E])$ is the plane $\mathbb{R}^2$, equipped with the conformal structure $[g^E]$ determined by the standard Euclidean metric $g^E$ of $\mathbb{R}^2$.

Let $N$ and $S$ be the north pole $N = (0, 0, 1)$ and the south pole $S = (0, 0, 1)$ of $S^2$, respectively, and let $\text{st}_N : S^2 \setminus \{N\} \rightarrow \mathbb{R}^2$ be the stereographic projection with respect to $N$ from $S^2 \setminus \{N\}$ onto the tangent plane $T_S S^2 = \mathbb{R}^2$ at the south pole $S$.

It is a conformal diffeomorphism between the conformal sphere minus the north pole $(S^2 \setminus \{N\}, [g_o])$ and the conformal plane $(\mathbb{R}^2, [g^E])$. Such a diffeomorphism has a unique extension to a diffeomorphism $\varphi : S^2 \rightarrow \hat{\mathbb{C}} = \mathbb{C} \cup \{\infty\}$ between $S^2$ and the Riemann sphere $\hat{\mathbb{C}} = \mathbb{C} \cup \{\infty\}$, mapping $N$ to $\infty$. This diffeomorphism can be used to induce a Riemann metric $g'_o := \varphi_* g_o$ and a corresponding conformal structure $[g'_o]$ on $\hat{\mathbb{C}}$. In this way, $\varphi$ is a conformal equivalence between $(S^2, [g_o])$ and $(\hat{\mathbb{C}}, [g'_o])$.

Identifying $S^2 \setminus \{N\}$ with $\mathbb{R}^2$ by means the stereographic projection $\text{st}_N$, the complex coordinate $z = x + iy$ of $\hat{\mathbb{C}}$ can be considered as a complex coordinate on $S^2 \setminus \{N\}$. It is called standard (local) holomorphic coordinate for the 2-sphere.

5.1.2. The conformal group of $S^2$. The group $\text{Conf}(S^2)$ of the conformal transformations of $(S^2, [g_o])$ has two connected components. The universal covering of the connected component of the identity $\text{Conf}^u(S^2)$ of $\text{Conf}(S^2)$ is $\text{SL}(2, \mathbb{C})$ and

$$\text{Conf}^u(S^2) = \text{SL}(2, \mathbb{C})/\{\pm I_2\} \simeq \text{SO}^u(1, 3)$$ (5.5)

(see also §5.3). By means of the conformal equivalence $\varphi : S^2 \rightarrow \hat{\mathbb{C}}$, each $f \in \text{Conf}^u(S^2)$ corresponds to the conformal transformation $\hat{f} := \varphi \circ f \circ \varphi^{-1}$ of the Riemann sphere $\hat{\mathbb{C}}$. 
The transformations \( \hat{f} \) are the \textit{linear fractional transformations}, i.e. the transformations of the Riemann sphere of the form

\[
\hat{f}(z) = \frac{az + b}{cz + d}, \quad A = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \in \text{SL}(2, \mathbb{C}).
\]

The map

\[
A = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \in \text{SL}(2, \mathbb{C}) \mapsto \hat{f}_A(z) := \frac{az + b}{cz + d} \in \text{Conf}(\hat{\mathbb{C}})
\]

is a group homomorphism and its kernel contains exactly two elements, \( \pm I_2 \). It follows that \( \text{Conf}^o(\hat{\mathbb{C}}) \cong \text{SL}(2, \mathbb{C})/\{\pm I_2\} \), as we claimed above.

Consider now the subgroups of \( \text{SL}(2, \mathbb{C}) \) defined by

\[
C^* = \left\{ \begin{pmatrix} a & 0 \\ 0 & a^{-1} \end{pmatrix} \middle| a \in \mathbb{C} \setminus \{0\} \right\},
\]

\[
N^+ = \left\{ A = \begin{pmatrix} 1 & b \\ 0 & 1 \end{pmatrix} \middle| b \in \mathbb{C} \right\} \quad \text{and} \quad N^- = \left\{ A = \begin{pmatrix} 1 & 0 \\ c & 1 \end{pmatrix} \middle| c \in \mathbb{C} \right\},
\]

i.e. the diagonal subgroup and the unipotent subgroups of upper and lower triangular matrices of \( \text{SL}(2, \mathbb{C}) \), respectively. Let also denote by

\[
B^- := N^- \cdot C^*, \quad B^+ := C^* N^+
\]

the Borel subgroups of \( \text{SL}(2, \mathbb{C}) \) given by the lower triangular and the upper triangular matrices, respectively. Notice that each matrix \( A \) of the open and dense subset

\[
\mathcal{U} = \{ A = (a \ b) : a \neq 0 \} \subset \text{SL}(2, \mathbb{C}),
\]

can be decomposed into the product

\[
A = A^{-1}A^0A^+,
\]

with

\[
A^{-1} = \begin{pmatrix} 1 & 0 \\ \frac{c}{a} & 1 \end{pmatrix} \in N^- , \quad A^0 = \begin{pmatrix} a & 0 \\ 0 & \frac{1}{a} \end{pmatrix} \in C^* , \quad A^+ = \begin{pmatrix} 1 & b \\ 0 & 1 \end{pmatrix} \in N^+,
\]

meaning that \( \mathcal{U} \subset \text{SL}(2, \mathbb{C}) \) admits the \textit{Gauss decomposition} \( \mathcal{U} = N^- \cdot C^* \cdot N^+ \).

We conclude this short subsection with a lemma in which we summarize some known facts on the transformations in \( \text{Conf}(S^2) = \text{Conf}(\hat{\mathbb{C}}) \), which are direct consequences of the above descriptions of the conformal transformations in terms of the linear fractional transformations of the Riemann sphere. In the statement, for any given point \( z \in S^2 = \hat{\mathbb{C}} \), we denote by \( (\text{SL}_2(\mathbb{C}))_z \) the stability subgroup \( \text{SL}_2(\mathbb{C}) \) at \( z \) and by \( j_z : (\text{SL}_2(\mathbb{C}))_z \to \text{GL}(T_zS^2) \) the corresponding isotropy representation.

**Lemma 5.1.**

i) \textit{The diagonal subgroup} \( C^* \subset \text{SL}(2, \mathbb{C}) \text{ lies in the intersection} (\text{SL}_2(\mathbb{C}))_0 \cap (\text{SL}_2(\mathbb{C}))_{\infty} \text{ of the stability subgroups at the points} 0, \infty \in \hat{\mathbb{C}} \text{ (points corresponding to} S, N \in S^2) \text{ and the isotropy representations at such points are} \}

\[
j_z(C^*) = \text{CO}(2) = \mathbb{R}^+ \cdot \text{SO}(2), \quad z = 0, \infty.
\]

\textit{Further,} \( C^* \text{ acts on} \mathbb{C} = \hat{\mathbb{C}} \setminus \{\infty\} \text{ as the linear similarity group} \text{CO}(2) = \mathbb{R}^+ \cdot \text{SO}(2). \)
The stability groups \( (\mathrm{SL}(2,\mathbb{C}))_0 \) (\( \mathrm{SL}(2,\mathbb{C}) \)) at the points 0 and \( \infty \) are the Borel subgroups

\[
(\mathrm{SL}(2,\mathbb{C}))_0 = B^- = N^- \cdot \mathbb{C}^*, \quad (\mathrm{SL}(2,\mathbb{C}))_\infty = B^+ = \mathbb{C}^* \cdot N^+
\]

The subgroups \( N^- \) and \( N^+ \) are in the kernels of the two isotropic representations, while the isotropy groups \( j_0(B^-), j_\infty(B^+) \) are both isomorphic to \( \mathrm{CO}(2) = \mathbb{R}^+ \cdot \mathrm{SO}(2) \).

The group \( B^+ = \mathbb{C}^* \cdot N^+ = (\mathrm{SL}(2,\mathbb{C}))_\infty \) (resp. the subgroup \( N^+ \subset (\mathrm{SL}(2,\mathbb{C}))_\infty \)) acts on \( \mathbb{C} = \hat{\mathbb{C}} \setminus \{ \infty \} \cong S^2 \setminus \{ \mathbb{N} \} \) as the group \( \mathrm{Sim}(\mathbb{R}^2) \) of the similarities (resp. the group \( \mathbb{R}^2 \) of translations) of the plane:

\[
z \mapsto az + b \quad (\text{resp. } z \mapsto z + b),
\]

We finally remark that, since \( j_0(N^-) = \{ \text{Id} \} \), on a sufficiently small neighbourhood \( U_\mathbb{S} \subset \hat{\mathbb{C}} \cong S^2 \) of 0, each transformation of \( N^- \) acts almost as the identity map.

5.2. The canonical Cartan connection of the conformal sphere. Let \( \mathcal{F}^o \) be the standard frame of the tangent space \( T_0 \mathbb{R}^2 \cong \mathbb{C} \) of the plane at 0, i.e.

\[
\mathcal{F}^o = (0, (f^o_1 = (1, 0), f^o_2 = (0, 1)))
\]

We call oriented conformal frame at a point \( z \in \mathbb{C} \) an orthogonal frame \( \mathcal{F} = (z, (f_1, f_2)) \) for \( T_z \mathbb{C} \), which has the same orientation of \( \mathcal{F}^o \) and it is given by two vectors \( f_1, f_2 \) of equal length. A conformal frame \( \mathcal{F} \) at \( z \in \mathbb{R}^2 = \mathbb{C} \) can be also identified with the 1-jet \( j^1(h) \) of the unique conformal transformation \( h \in \mathrm{Conf}(\mathbb{R}^2) \) that maps 0 into \( z = h(0) \) and \( \mathcal{F}^o \) into \( \mathcal{F} \).

As the isometry group \( \mathrm{Iso}(\mathbb{R}^2) \) of \( (\mathbb{R}^2, g^E) \) acts simply transitively on total space of the bundle \( \mathcal{O}_C \mathcal{F}_T(\mathbb{R}^2) \to \mathbb{R}^2 \) of the orthonormal frames of \( (\mathbb{R}^2, g^E) \), the similarity group \( \mathrm{Sim}(\mathbb{R}^2) \) acts simply transitively on the total space of the bundle \( \mathcal{C}_T \mathcal{F}(\mathbb{R}^2) \to \mathbb{R}^2 \) of all oriented conformal frames of \( \mathbb{R}^2 \) and there exists a \( \mathrm{Sim}(\mathbb{R}^2) \)-equivariant diffeomorphism

\[
\mathrm{Sim}(\mathbb{R}^2) \ni h \mapsto \mathcal{F}_h := \left( h(0), (h \cdot f^o_1, h \cdot f^o_2) \right) \in \mathcal{C}_T \mathcal{F}(\mathbb{R}^2).
\]

The above definition of conformal frames and of the bundle \( \mathcal{C}_T \mathcal{F}(\mathbb{R}^2) \to \mathbb{R}^2 \) can be generalised to the case of the conformal sphere as follows. A second order conformal frame at a point \( p \in S^2 \) is the 2-jet \( j^2_0(h \circ \varphi^{-1}) \) at 0 of the composition between the conformal equivalence \( \varphi^{-1} : \hat{\mathbb{C}} \to S^2 \) and a conformal transformation \( h \in \mathrm{Conf}^o(S^2) \) mapping \( \mathbb{S} \) to \( p = h(\mathbb{S}) \). The connected conformal group \( G = \mathrm{Conf}^o(S^2) \) acts simply transitively on the manifold \( \mathcal{C}_T \mathcal{F}(S^2)^2 \) of all second order conformal frames at the points of \( S^2 \) and the principal bundle

\[
\pi : \mathcal{C}_T \mathcal{F}(S^2)^2 \to S^2
\]

is identifiable with the homogeneous bundle

\[
\pi : G = \mathrm{Conf}^o(S^2) \to G/G_\mathbb{S} = S^2
\]

where we denote by \( G_\mathbb{S} \cong \mathrm{Sim}(\mathbb{R}^2) \) the stabiliser of the south pole \( \mathbb{S} \). The left action of \( G = \mathrm{Conf}^o(S^2) \) on itself defines a left invariant absolute parallelism (i.e. a flat linear connection) on \( G \), which identifies each tangent space \( T_p G \) of \( G \) with the Lie algebra \( \mathfrak{g} := T_p G = \mathfrak{n}^- + \mathfrak{co}(2) + \mathfrak{n}^+ \). It is called the canonical Cartan connection of the conformal structure of \( S^2 \).
Remark. For any $n$-dimensional manifold $M$ of dimension $n \geq 3$, with a conformal structure $[g]$, E. Cartan introduced a canonical principal bundle of second order conformal frames

$$\pi : P \longrightarrow M = P/ Sim(\mathbb{R}^n)$$

equipped with a Cartan connection (i.e. a flat linear connection on the total space $P$ with certain special invariance properties with respect to the action of the structure group $Sim(\mathbb{R}^n)$). If the dimension is $n = 2$, for a generic 2-dimensional conformal manifold there is no such canonical principal bundle with a Cartan connection (it is a consequence of the fact that the Lie algebra of the conformal vector fields in the generic case is infinite-dimensional). However the conformal sphere $(S^2, [g_0])$ is a special case: the above discussion show that it is possible to construct a natural bundle of second order frames $\pi : \mathcal{CF}^{(2)}(S^2) \longrightarrow S^2$ with a Cartan connection, exactly as it occurs for the conformal manifolds of higher dimension.

5.3. The M"{o}bius projective model of the conformal sphere. Consider an orthonormal frame $(e_0, e_1, e_2, e_3)$ for the Minkowski space-time $\mathbb{R}^{1,3}$, that is the vector space $\mathbb{R}^{1,3} = \mathbb{R}e_0 + \mathbb{R}^3 = \{X = x^0 e_0 + x^1 e_1 + x^2 e_2 + x^3 e_3 = (x^0, \vec{x})\}$ ,
equipped with the Lorentzian scalar product

$$g(X, Y) = -x^0 y^0 + \vec{x} \cdot \vec{y}.$$ (5.8)
The light cone at the origin $0 = (0, \vec{0})$ is the subset of $\mathbb{R}^{1,3}$ defined by $V_0 = \{X \in V, g(X, X) = 0\}$ .

Up to a scaling, the (connected component of the identity of the) Lorentz group $G = SO^0(1, 3)$ has three orbits in $\mathbb{R}^{1,3}$, namely:

- $V_T = G \cdot e_0 = G/ SO(3)$ (the Lobachevsky space),
- $V_S = G \cdot e_1 = G/ SO(1, 2)$ (the De Sitter space),
- $V_0 = G \cdot p = G/ Sim(\mathbb{R}^2)$ with $p = \frac{1}{2}(e_0 + e_1)$ (the light cone).

Consider the projectivisation $\mathbb{R}P^3$ of the 4-dimensional vector space $\mathbb{R}^{1,3}$ and the natural projection

$$\pi : \mathbb{R}^{1,3} \setminus \{0\} \longrightarrow \mathbb{R}P^3 = \mathbb{P}(\mathbb{R}^{1,3}) , \quad \pi(v) = [v] := \mathbb{R}v .$$

Under $\pi$, the three $G$-orbits on $\mathbb{R}^{1,3}$ are projected onto the following three $G$-orbits in $\mathbb{R}P^3$:

- $V_T$ is mapped onto the unit ball $B^3 = \pi(V_T) \simeq V_T$;
- $V_S$ is mapped onto the exterior of the unit ball $\pi(V_S) \simeq V_S/\mathbb{Z}_2$;
- $V_0$ is mapped onto the projective quadric

$$Q = \pi(V_0) \simeq G/(\mathbb{R}^+ \cdot Sim(\mathbb{R}^2)) ,$$

which, as we will shortly see, is identifiable with the conformal sphere.

Any unit time-like vector $e_0$ determines the orthogonal Euclidean hyperplane $e_0^\perp$ and the corresponding translated Euclidean hyperplane $E_{(e_0)} := e_0 + e_0^\perp$. The intersection

$$S^2_{(e_0)} = E_{(e_0)} \cap V_0$$
is the unit sphere of the Euclidean space \( E(e_0) \) and it is diffeomorphic to the quadric \( Q = \pi(V_0) \). Indeed, the map
\[
\psi(e_0) : \mathbb{RP}^3 \setminus \mathbb{P}(e_0^\perp) \to E(e_0), \quad [p] = \mathbb{R}p \mapsto \psi(e_0)(p) := \mathbb{R}p \cap E(e_0)
\]
is a diffeomorphism, which induces a diffeomorphism between \( \varOmega = \pi(V) \subset \mathbb{RP}^3 \) and \( S^2(e_0) \subset E(e_0) \). The pull-back of the round metric \( g_\varOmega \) of \( S^2 = S^2(e_0) \) by such diffeomorphism is a Riemannian metric \( g(e_0) \) of constant curvature 1 on \( \varOmega = \pi(V_0) \). Since replacing the unit time-like vector \( e_0 \) by a different unit time-like vector \( e'_0 \) determines a new diffeomorphism \( \psi(e'_0) \) and a metric \( g(e'_0) \) on \( \varOmega \), which is conformally equivalent to \( g(e_0) \), the conformal structure \( [g(e_0)] \) on \( \varOmega = \pi(V_0) \), determined by the metric \( g(e_0) \) is independent of the choice of \( e_0 \). The group \( G = \text{SO}^o(1, 3) \) acts on \( \varOmega \simeq S^2 \) as the connected Möbius group \( \text{Conf}^o(S^2) \) of the conformal transformations of \( S^2 \).

5.4. The \( \varOmega \)-correlation between projective points and projective planes. The Lorentz metric \( \left\{ E, g \right\} \) determines a one-to-one correspondence between the projective points and the projective planes of \( \mathbb{RP}^3 \) defined by
\[
\mathbb{RP}^3 \ni [v] = \mathbb{R}v \quad \leftrightarrow \quad \Pi_v := \mathbb{P}(v^\perp). \tag{5.10}
\]
It is called correlation with respect to \( \varOmega \). Under this bijection, the three types of projective points \([v] \), determined by the timelike, spacelike and lightlike vectors \( v \in \mathbb{R}^{1,3} \), respectively, correspond to three kinds of projective planes, namely those that are tangent to \( \varOmega \), those that are secant to \( \varOmega \) and those that are not intersecting \( \varOmega \):
\[
[n] = \mathbb{R}n \in \pi(V_T) \quad \leftrightarrow \quad \Pi_n \text{ such that } \Pi_n \cap \varOmega = \emptyset; \tag{5.11}
\]
\[
[m] = \mathbb{R}m \in \pi(V_S) \quad \leftrightarrow \quad \Pi_m \text{ such that } \Pi_m \cap \varOmega = S^1; \tag{5.12}
\]
\[
[p] = \mathbb{R}p \in \pi(V_0) \quad \leftrightarrow \quad \Pi_p \text{ such that } \Pi_p \cap \varOmega = [p]. \tag{5.13}
\]
Note that \( (5.9) \) establishes also a bijection between the affine planes in \( E^3(e_0) \simeq \mathbb{R}^3 \) and the projective planes that are different from \( \pi(e_0^\perp) \). Under this correspondence, the affine planes of \( \mathbb{R}^3 \) which do not intersect \( S^2 \) are in bijection with the projective planes \( \Pi_n \neq \pi(e_0^\perp) \) with \( \Pi_n \cap \varOmega = \emptyset \), i.e. those corresponding to the lines \([n] \in \pi(V_T) \), \([n] \neq [e_0] \).

The following lemma is well known.

**Lemma 5.2.** The stability subgroup \( G[p] = \text{Sim}(\mathbb{R}^3) \) of a point \([p] \in \varOmega = S^2 \) acts transitivity on the orbit \( V_T \) and hence on the set \( \{ \Pi_n, [n] \in \pi(V_T) \} \) of the planes of \( \mathbb{RP}^3 \) not intersecting \( \varOmega \) (corresponding to the affine planes of \( \mathbb{R}^3 \) not intersecting \( S^2 \)).

6. Information processing in dynamics

6.1. Shifts of receptive fields and pre-saccadic remapping. In a seminal paper, J. Duhamel et al. \[25\] showed the existence of anticipated shifts of receptive fields for visual neurons in the lateral intraparietal area (LIP) of a macaque. The same phenomenon was later detected for neurons in many other visual systems, including V1, V2, V3, etc. (see \[46, 71, 22\]).

The shifts of receptive fields (RF) found by Duhamel and collaborators can be shortly described as follows. Assume that, before a saccade, a neuron \( n \) with RF \( z_n \) detects the retinal image \( \vec{A} \) of an external point \( A \) (that is, the image \( \vec{A} \) is in \( z_n \) and that, after
the saccade, the same neuron detects the retinal image $\mathbf{B}$ of another point $B$ (i.e. in $z_n$ there is now $\mathbf{B}$). Experiments give evidences that the neuron $n$ gets information about $B$ approximately 80 ms before the beginning of the saccade, that is when the retinal image $\mathbf{B}$ is not yet at $z_n$, but at some different point $\tilde{z}$, which is the RF of some different neuron $\tilde{n}$. In other words, the neuron $n$ reacts as if before the beginning of the saccade its RF field $z_n$ is changed into the RF $z_{\tilde{n}}$ of some other neuron. Due to this, the phenomenon is named pre-saccadic shift of a RF (see e.g. [46, 71]).

This name is somehow misleading. In fact, each visual neuron has a physiologically fixed RF - it is a domain in the retina which is physiologically connected with the neuron. On the other hand, the eye movement which occurs during a saccade produces a shift of all retinal images of the external points. Due to this, if a neuron $n$ detects a retinal image $\mathbf{A}$ of an external point $A$ at its RF $z_n$ before the beginning of a saccade, after the saccade the same neuron should detects a new retinal image in the RF $z_n$, namely the image $\mathbf{B}$ of a point $B \neq A$. In particular, the detection of $\mathbf{B}$ by the neuron $n$ should occur after (and not before) the saccade. Now the “pre-saccadic shift of the RF of $n$” is the name for the unexpected phenomenon that the neuron $n$ reacts to the stimulus $B$ earlier than when it should be, that is when $\mathbf{B}$ is not yet in $z_n$.

For a long time, it was suggested (see for example [17]) that one of the neurons $\tilde{n}$, having $B$ in its RF, sends information about $\mathbf{B}$ to the neuron $n$ before $\mathbf{B}$ reaches the RF of $n$. However, as it was remarked by M. Zirnsac and T. Moore [75], this explanation looks not very realistic, since it assumes the existence of a huge number of horizontal connections between neurons. Zirnsac and Moore offered a different and more plausible explanation which may be briefly summarised as follows. The global information about the stimulus before the saccade is integrated in some higher order visual subsystem. On the basis of this global information, the visual system chooses a gaze target for a saccade and sends the information about the retinal image $\mathbf{B}$ (detected by a neuron $\tilde{n}$) to the neuron $n$ before the saccade starts. After the saccade, the retinal image $\mathbf{B}$ does come to the RF $z_n$ of $n$ and the preliminary information that was sent to $n$ is corrected.

Following Zirnsac and Moore’s idea, it is sensible to believe that also the microsaccades are not random phenomena, but controlled by higher sections of the visual system, while the drift is just a random process during which the visual cortex and the oculomotor system get stochastic information on the stimulus. We think that a microsaccade $\text{Sac}(A, B)$ from a gaze direction $A$ to a gaze direction $B$ serves to change the retinotopic coordinates associated with the initial direction $A$ to new retinotopic coordinates associated with the final direction $B$. This process is called remapping. The stochastic information about the stimulus during the drift after the saccade $\text{Sac}(A, B)$ is encoded into the coordinates associated with the final gaze $B$, see [3].

6.2. Gombrich’s Etcetera Principle and a conjecture on the remapping. The art historian E. Gombrich formulated the following important idea, called Etcetera Principle, about the mechanism of the saccadic remapping [30, 25]:

“The global pattern in environments such as a forest, beach or street scene enables us to predict more-or-less what we will see, based on the order and redundancy in the scene and on previous experience with that type of environment. Only a few 3 − 4 salient stimuli are contained in the trans-saccadic visual memory and update”.
We now want to state a conjecture about the conformal character of the remapping, which supports the Etcetera Principle. But for this, we first need to recall a few fundamental facts on conformal geometry of the plane and of the sphere and on the Möbius projective model of the conformal sphere.

As in §5.3, let us identify the hyperplane \( E^3_{(\epsilon_0)} = e_0 + e_0^\perp \subset \mathbb{R}^{1,3} \) with the physical 3-dimensional Euclidean space \( E^3 = \mathbb{R}^3 \). Let also identify \( S^2 = S^2_{(\epsilon_0)} \subset E^3_{(\epsilon_0)} = \mathbb{R}^3 \) with the eye sphere \( S^2_{\text{eye}} \). As we pointed out in §5.4, the diffeomorphism (5.9) determines identifications between \( \mathbb{R}P^3 \setminus \pi(e_0^\perp) \) and \( E^3_{(\epsilon_0)} = E_3 \) and between the projective planes \( \Pi_n, [n] \neq [e_0] \), defined in (5.11), and the affine planes \( \Pi \subset E^3_{(\epsilon_0)} = E^3 \) that are external to \( S^2 = S^2_{\text{eye}} \).

Consider now an affine plane \( \Pi \cong \Pi_n \) external to \( S^2_{\text{eye}} \) and the corresponding central projection \( \varphi_N : \Pi \to S^2_{\text{eye}} \), defined in (1.1). By the map (5.10), such central projection corresponds to a map \( \varphi_N : \Pi_n \to \Omega \). A physical rotation \( R^\alpha_v \) of the eye, through the angle \( \alpha \) around the axis \( R^\alpha_n \), determines changes of the images of the external surfaces. In fact, if they are expressed in terms of the retinotopic coordinates (= coordinates that are fixed to the eye sphere \( S^2_{\text{eye}} \)), the images of the external surfaces are transformed under the inverse rotation \( (R^\alpha_v)^{-1} = R^{-\alpha}_v \). In particular, from the point of view of retinotopic coordinates, if the eye rotates by \( R^\alpha_v \), the image of an external plane \( \Pi = \Pi_n \) changes into the image of the rotated plane \( \Pi' = R^{-\alpha}_v(\Pi_n) \). The problem of remapping is the problem of determining a bijection between the points of \( \Pi \) and \( \Pi' \) which induces a simple relation between the points of the retina images \( \varphi_N(\Pi) \) and \( \varphi_N(\Pi') \).

According to Lemma 5.2, there is a Lorentz transformation \( L_{\Pi,\Pi'} \) of the stability subgroup \( G_f \subset G = \text{SO}^0(1,3) \) of the fovea \( \mathcal{F} \in S^2_{\text{eye}} = \mathcal{Q} \), which sends \( \Pi \) to \( \Pi' \). This leads to the following:

**Conjecture.** The brain identifies the points of \( \Pi \) with the points of \( \Pi' \) using the Lorentz transformation \( L = L_{\Pi,\Pi'} \), so that the points of the corresponding retina images \( \varphi_N(\Pi) \), \( \varphi_N(\Pi') \) on \( S^2_{\text{eye}} = \mathcal{Q} \) are related by the associated conformal transformation \( L|_{\mathcal{Q}} \) of \( S^2_{\text{eye}} = \mathcal{Q} \) (see §5.3).

We remark that any conformal transformation of \( \mathcal{Q} = S^2 \) is completely determined by the images of just three points of the sphere under the transformation. This means that the images after remapping of just three retinal points are sufficient to completely reconstruct the global post-saccade retinal image, as the Gombrich Etcetera Principle states.

Note also that if the angle \( \alpha \) of the rotation \( R^\alpha_v \) is small (as it occurs for the microsaccades and other fixational eye movements), then the Lorentz transformation \( L = L_{\Pi,\Pi'} \) is close to the rotation \( R^{-\alpha}_v \).

6.3. **Consequences for the Alhazen Visual Stability Problem.** The visual stability problem consists in finding an explanation of how the brain perceives the stable objects as “stable” in spite of the changes of their retina images, caused by the eye movements. This problem was first formulated in the eleventh century by the Persian scholar Abu ’Ali al-Hasan ibn al-Hasan ibn al-Haytham (latinised, Alhazen) and, since then, it was discussed by several scientists, as R. Descartes, H. von Helmholtz, E. Mach, C. Sherrington and many others (see e.g. [72], [73]).
According to the above conjecture, the pre-saccade remapping acts on the retina images as a conformal transformation. This establishes a relation between the visual stability problem for contours with the classical mathematical problem of Conformal Geometry of characterising the curves of the conformal sphere up to conformal transformations (that is, the conformal version of the Frenet Theory of curves of the Euclidean space). This mathematical problem is completely solved by means of several results by A. Fialkov, R. Sulanke, C. Sharp, A. Shelechov and many others (see e.g. [27] and references therein). V. Lychagin and N. Konovenko recently gave a very general and elegant solution to this problem in terms of differential invariants in [44].

7. Differential geometric models of the V1 cortex

7.1. Geometry of the projectivised tangent and cotangent bundles of 2-dimensional manifolds.

7.1.1. The projectivised tangent and cotangent bundles of an n-manifold. Let $M$ be a manifold of dimension $n \geq 2$ and $\tau : T M \to M$ (resp. $\tau' : T^* M \to M$) its tangent (resp. cotangent) bundle. Changing the fibers $T_x M$ (resp. $T^*_x M$) into their projectivisation $\mathbb{P} T_x M$ (resp. $\mathbb{P} T^*_x M$), one gets the projectivised tangent bundle $\pi : \mathbb{P} T M \to M$ (resp. cotangent bundle $\pi' : \mathbb{P} T^* M \to M$) with fibers isomorphic to the real projective space $\mathbb{R} P^n$.

Let $(x^1, \ldots, x^n)$ be local coordinates on $M$, and denote by $\partial_i = \frac{\partial}{\partial x^i}$ and $dx^i$ the corresponding coordinate vector fields and the dual coordinate 1-forms, respectively. The associated local coordinates for the tangent bundle $T M$ are $(x^1, \ldots, x^n, v^1, \ldots, v^n)$ where we denote by $v^i$ the components of the vectors $v = \sum v^i \partial_i \in T_x M$ in coordinate frames. The coordinates $(v^1, \ldots, v^n)$ may be considered as homogeneous coordinates for the projective spaces $\mathbb{P} T_x M$. In the open subsets of $PTM$ where $v^n \neq 0$, the associated non-homogeneous coordinates are

$$u^1 = \frac{v^1}{v^n}, \quad \ldots \quad u^{n-1} = \frac{v^{n-1}}{v^n}.$$  

This gives local coordinates $(x^1, \ldots, x^n, u^1, \ldots, u^{n-1})$ for $PTM$. The projectivised tangent bundle $PTM$ is naturally identified with the space of the 1-jets of the non-parameterised curves of $M$ and, hence, it may be also considered as the space of the (first order) infinitesimal curves (or contours) in $M$. Any section

$$s : M \to PTM, \quad x \mapsto [v_x] = \mathbb{R} v_x \subseteq PT_x M,$$  

defines a first order ODE in the manifold $M$. The solutions of such equation are the non-parametrised curves $\gamma$ in $M$ whose tangent lines $[\dot{\gamma}_x], x \in \gamma$, coincide with the lines $[v_x]$. In local non-homogeneous coordinates $(x^i, u^j = \frac{v^j}{v^n})$, the ODE associated with a section $s : M \to TM$ reduces to the system

$$\frac{dx^j(x)}{dx^1} = u^j(x^1, x^2, \ldots, x^n), \quad j = 2, \ldots, n.$$  

Similarly, a set of local coordinates $(x^i)$ for $M$ defines an associated system of local coordinates $(x^i, p_j)$ for the cotangent bundle $T^* M$, where the $p_j$ are the components of the 1-forms $p = p_1 dx^1 + \cdots + p_n dx^n \in T^* M$. In the coordinate domains where $p_n \neq 0$,
the projectivised cotangent bundle can be identified with the hypersurface $H = \{p_n = 1\} \subset T^*M$ with coordinates 

$$(x^1, \ldots, x^n, p_1, \ldots, p_{n-1}).$$

The projectivised cotangent bundle $PT^*M$ is equipped with the canonical contact structure $\mathcal{D} \subset T(PT^*M)$, given by the projectivisation of the kernel distribution $\ker \lambda \subset T(T^*M)$ of the Liouville 1-form of the cotangent bundle $\tau^* : T^*(T^*M) \to T^*M$, i.e of the 1-form on $T^*M$ defined by

$$\lambda : T^*M \to T^*(T^*M) \, , \quad p \mapsto \lambda_p := (\tau^*)^p .$$

In terms of the coordinates $(x^i, p_j)$ for $T^*M$, the Liouville 1-form $\lambda$ is the map

$$p = p_idx^i \mapsto \lambda_p = p_idx^i .$$

We remark that the restriction $\lambda_H = p_1dx^1 + \cdots + p_{n-1}dx^{n-1} + dx^n$ of the Liouville form to the hypersurface $H = \{p_n = 1\} \subset T^*M$ is a contact 1-form on $H$ and defines the contact distribution $\mathcal{D}_H = \ker \lambda_H \subset TH$, spanned by the vector fields

$$\partial_{p_1}, \quad \partial_{x_j} - p_j\partial_{x_{n}}, \quad j = 1, \ldots, n-1 . \quad (7.15)$$

### 7.1.2. Special properties of $PTM$ and $PT^*M$ when $\dim M = 2$. Let us now assume that $M$ is a surface, i.e. $\dim M = 2$. In this case, the projectivised tangent and cotangent bundles have a canonical identification $PTM = PT^*M$

determined as follows: any line $[v] = \mathbb{R}v \in PTM$, generated by a vector $0 \neq v \in T_xM$, can be naturally identified with the line $[p_v] \in PT^*_xM$, given by the annihilator $0 \neq p_v \in T^*_xM$ of $\mathbb{R}v$. Vice versa, any line $[p] \in PT^*_xM$ can be identified with the line $[v_p] \in T_xM$ if the vectors $0 \neq v_p \in \ker p$.

Let $(x, y)$ be local coordinates on $M$ and $(x, y, p_1, p_2)$ the associated coordinates for covectors $p = p_1dx + p_2dy$. As we observed above, the open subset $\{p_2 \neq 0\} \subset PT^*M$ can be naturally identified with the hypersurface $H := \{p_2 = 1\}$ of $T^*M$. This hypersurface has coordinates $(x, y, p = -p_1)$ and consists of the covectors of the form $\eta = dy - pdx \in T^*_x(x,y)$. The naturally corresponding elements of $PTM$ are the lines of (annihilating) vectors $[v_y] = [\partial_x + p\partial_y] \in PTM$. Reducing (7.15) and (7.14) to the case $n = 2$, we get that the contact distribution $\mathcal{D}_H = \ker \lambda|_H$ is spanned at each point by the pair of vector fields $\partial_p$ and $\partial_x + p\partial_{y}$, and that a section

$$s : M \to PT^*M = PTM, \quad (x, y) \mapsto [v_{(x,y)}] = [v^1\partial_{x} + v^2\partial_{y}], \quad (7.16)$$

is associated with a first order ODE, which, in a domain where $v^i \neq 0$, has the form

$$\frac{dy}{dx}_x = p(x, y) , \quad \text{where} \quad p(x, y) := \frac{v^2(x, y)}{v^1(x, y)} = \tan\theta_{(x,y)} , \quad (7.17)$$

where $\theta_{(x,y)} \in [-\frac{\pi}{2}, \frac{\pi}{2})$ is the orientation of the covector $p(x, y)$: It is the angle between the coordinate direction $\partial_{x}$ and the line $\mathbb{R}v(x,y)$, determined by any conformally flat

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2We recall that a contact structure on a manifold is maximally non integrable field of hyperplanes in the tangent spaces of the manifold.
metric \( g = \lambda(x,y)(dx^2 + dy^2) \). Due to this, the sections \((\partial, \lambda)^*\) are called fields of orientations.

We now recall that any (smooth) function \( F \) on \( M \) determines the section \( dF : M \to T^*M \) defined by
\[
dF(x,y) := \left( \frac{\partial F}{\partial x} dx + \frac{\partial F}{\partial y} dy \right) \bigg|_{(x,y)}.
\]
The complement \( M' \subset M \setminus \{(x,y) : dF(x,y) = 0\} \) of the critical point set is an open subset, on which the section \( dF : M' \to T^*M' \) determines a section
\[
[dF] : M' \to PT^*M' = PTM'
\]
of the projectivised cotangent bundle. Under the above described identification between \( PT^*M' \) and the hypersurface \( H = \{p_2 = 1\} \subset T^*M' \), such a section \([dF]\) has the form
\[
dF = dy - p(x,y)dx \quad \text{with} \quad p(x,y) = -\frac{\partial F}{\partial y}.
\]
The associated field of orientations \((\partial_x + p(x,y)\partial_y)^*\) in the projectivised tangent bundle \( PTM' \) defines the ODE
\[
\frac{dy}{dx} = p(x,y), \quad p(x,y) = -\frac{\partial F}{\partial y} \quad (7.18)
\]
Since the vector field \( Z = \partial_x + p(x,y)\partial_y \) is such that \( Z(F(x,y)) \equiv 0 \), the images of the integral curves of the ODE \([7.18]\) are the level sets of the function \( F(x,y) \), i.e. they are the contours determined by \( F \).

7.1.3. The relation between the projectivize bundle and the circle bundle of a surface. Let \( g \) be a Riemannian metric on a surface \( M \) and denote by \( S(M) = S(M,g) \to M \) the corresponding \( S^1 \)-bundle, given by the unit vectors
\[
S(M) = \{ v \in TM \, : \, g(v,v) = 1 \} \subset TM,
\]
or, equivalently, by the \( S^1 \)-bundle of the unit covectors \( \xi = g(v,\cdot) \)
\[
S(M) = \{ \xi \in T^*M \, : \, g^{-1}(\xi,\xi) = 1 \} \subset T^*M.
\]
The total space \( S(M) \) of this bundle can be identified with the space of the infinitesimal oriented contours and, as the projectivised tangent bundle \( PTM \), is naturally equipped with a contact structure, i.e. by the kernel distribution of the restriction \( \lambda|_{S(M)} \) to \( S(M) \) of the Liouville form \( \lambda \) of \( T^*M \).

The total space of the \( S^1 \)-bundle \( S(M) \to M \) is a \( \mathbb{Z}_2 \)-covering of the total space of \( PT^*M \to M \), with projection \( \tilde{\pi} : S(M) \to PTM^* \) given by the map that identifies opposite (co)vectors. Local coordinates \((x,y)\) of \( M \) define local coordinates \((x,y,\tilde{\theta})\) for \( S(M) \), where for any vector \( v \in S_x(M) \subset T_xM \) we denote by \( \tilde{\theta} \in [-\pi, \pi) \) the angle between \( v \) and the positive coordinate axis \( Ox \).

Note that any simple smooth curve \( \gamma \) in \( M \) has two natural orientations, i.e two different ways of moving along the curve. Each orientation determines a canonical natural parametrisation \( \gamma(t) \) by the arc length \( t \) and a corresponding canonical lift to \( S(M) \)
\[
\gamma(t) \mapsto \hat{\gamma}(t) = (\gamma(t), \tilde{\theta}(t)).
\]
7.1.4. On the notion of “orientation”. The standard fiber of both bundles $S(M) \to M$ and $PTM \to M$ is $S^1 \simeq \mathbb{P}R^1$ and the two bundles are each other locally isomorphic by means of the local diffeomorphism

$$(x, y, \hat{\theta}) \to \left(x, y, \theta = \frac{\hat{\theta}}{2} \right).$$

In many papers (see e.g. [13, 63]), the angle coordinate $\hat{\theta} \in [-\pi, \pi)$ of $S(M)$ is called “orientation”, but it is of course different from the above defined orientation $\theta \in \left[-\frac{\pi}{2}, \frac{\pi}{2}\right)$ of the covectors in $PTM$. We do not follow this habit and, through the rest of the paper, we will use the name “orientation” just for the above defined coordinate $\theta$ of $PTM$.

7.2. Hoffman’s pioneering model of the V1 cortex. The first attempt to develop a differential geometric model for the primary visual cortex V1 appeared in a pioneering and very stimulating paper by W. Hoffman [33]. In particular, among other important ideas, for the first time Hoffmann pointed out the crucial role of the Möbius conformal group $SO(1, 3)$ in descriptions of the functional structure of the primary visual cortex.

Hoffman proposed a model, in which the V1 cortex is mathematically represented as the 3-dimensional total space $V = CR$ of a fiber bundle

$$\pi : V = CR \to R$$

over the retina $R$, whose fibers correspond to the columns of the V1 cortex. According to this model, the simple neurons of a column form an orientation response field (ORF) and the collection of all such ORFs determine lifts of retinal contours to curves in $V$. The tangent vectors to these lifts define a contact structure on $V$. In Hoffman’s words,

“the thing one first thinks of is that the visual contours are integral curves of the cortical vector field embodied in the ORFs. In other words, the visual map is a tangent bundle $TCR = V \to R$, where $R$ denotes the retinal manifold and $V$ the cortical “manifold of perceptual consciousness.” But the ORFs unfortunately do line up head to tail as in an Euler line approximation to an integral curve. Furthermore, the ORFs have an areal character as well as a line-element one.”

Unfortunately, in [34] diverse mathematical errors and inaccuracies occurred. For instance, it was stated that the V1 cortex should be identified with the tangent bundle $TR$ or cotangent bundle $T^*R$ of the retina, while on the contrary it is now known that it should be identified with the projectivisations of these bundles. It is also claimed that the conformal group $SO(1, 3)$ acts transitively on the contact bundle, but this is not true. Other faults of this kind appeared.

However, despite of these problems, there is no doubt that Hoffmann’s ideas promoted and strongly influenced all subsequent developments of differential geometric models for the visual system. Following a suggestion of J. Petitot, the area of applied geometry which originated from Hoffman’s work is nowadays called neurogeometry.
7.3. Petitot’s contact models. After Hoffman’s pioneering model, in a paper by J. Petitot and Y. Tondut and in several subsequent works of J. Petitot a new precise contact model for the V1 cortex and laid the foundations of neurogeometry was developed systematically and in great detail.

More precisely, in [52, 50] (see also [52, 62, 20, 69, 10]) it was introduced a model for the V1 cortex, in which the retina $R$ is identified the Euclidean plane $R = \mathbb{R}^2$ and the V1 cortex is identified with the projectivised cotangent bundle

$$\pi : PT^*\mathbb{R}^2 = \mathbb{P}R^1 \times \mathbb{R}^2 \simeq S^1 \times \mathbb{R}^2 \longrightarrow R = \mathbb{R}^2.$$ 

According to Petitot’s model, each fiber $\pi^{-1}(z), z \in \mathbb{R}^2$, of the bundle $PT^*\mathbb{R}^2$ corresponds to a pinwheel with RF $z \in R = \mathbb{R}^2$, while each point $(z, \theta)$ of a fiber $\pi^{-1}(z)$ corresponds to a single simple neuron of a pinwheel. In this way, the simple neurons of the pinwheels of the V1 cortex are parameterised by their receptive fields $z \in R = \mathbb{R}^2$ and their orientations $\theta$. In such a model, given a (regularised) input function $I(x, y)$ on retina, a simple neuron with receptive field $z_o$ and orientation $\theta_o$ fires when there is a retinal contour $C = \{I(x, y) = \text{const.}\}$ that passes through $z_o = (x_o, y_o)$ and with tangent line at $z_o$ with orientation $\theta_o$.

We recall that a retinal contour $C = \{I(x, y) = \text{const.}\}$ is a non-parametrised curve. For such a curve we may always choose a parametrisation, say $\gamma(t) = (x(t), y(t)), t \in (a, b)$. If we assume that $\dot{x}(t) \neq 0$, we may also change the parameter from $t$ to $x$ and represent the contour $C$ as the image of a parameterised curve of the form $z(x) = (x, y(x))$. Denoting by $x \mapsto \theta_x \in [-\pi/2, \pi/2]$ the map which gives the orientations of the tangent line of the curve for any $x$, as we pointed in (7.17), the function $y(x)$ is a solution to the ODE

$$\frac{dy(x)}{dx} = \tan \theta_x. \quad (7.19)$$

Therefore, given a contour $C$, the curve $c(x) = (x, y(x), \theta_x)$, given by the fired neurons, is a curve in $PT^*\mathbb{R}^2 (= \text{the V1 cortex})$, which is a lift of the curve $(x, y(x))$ and with tangent vectors

$$\dot{c}(x) = \partial_x + \frac{dy(x)}{dx} \partial_y + \dot{\theta}_x \partial_\theta = \partial_x + \tan \theta_x \partial_y + \dot{\theta}_x \partial_\theta.$$ 

The curve $c(x) = (x, y(x), \theta_x)$ is horizontal in the sense that it is tangent to the contact distribution $\mathcal{D}_H$ of $PT^*\mathbb{R}^2 \simeq H = \{v^1 = 1\} \subset T^*\mathbb{R}^2$ at each point: Indeed,

$$\lambda_H(\dot{c}(x)) = (dy - \tan \theta_x dx)(\dot{c}(x)) = \tan \theta_x - \tan \theta_x = 0$$

for any $x$. The curves in the cotangent bundles that are lifts of this kind of curves on the base manifold are called Legendrian lifts. We may therefore say that in Petitot’s model the firing of the simple neurons in the pinwheels of the V1 cortex carry out the Legendrian lifts of the contours.

One of the main aims of the processing of the visual system is to integrate the information, which is encoded in the firing of the neurons, and obtain in this way a global description of the contours, that is of the curves that are solutions to the differential equation (7.19).

Note that the most important retinal contours are the closed contours, which constitute the boundaries of retinal images of three dimensional objects (see [37, 39]). Any closed contour divides the retina into two parts: one of them is the “image of an object”, the
other is the background on which the object is located. The determination of which the two parts is the “image of an object” is mathematically equivalent to fixing an orientation of the contour, that is to choosing one of the two possible directions for a movement along the contour: Once a region is considered as “image of an object”, there is a unique orientation for the contour such that the “image” is on its left with respect to the orientation and, conversely, once an orientation is fixed, there is only one region that lies on the left of the contour with respect to the orientation and thus only one region which is considerable as the “image of an object”.

It would be interesting to understand where and how the visual system determines the orientations of the contours, that is how it lifts curves of the non-oriented infinitesimal contours of $PT^\ast \mathbb{R}^2$ into curves of oriented infinitesimal contours in $S(\mathbb{R}^2)$. Optical illusions show that when both sides of a closed contour admit meaningful interpretations, the visual system involuntarily and periodically changes the orientation of the contour. This indicates that the orientations of contours are determined by the high levels of the visual system.

7.4. Sarti, Citti and Petitot’s symplectic model. In [63], the authors proposed a symplectisation of Petitot’s contact model, the so called symplectic model. According to such a model, each simple cell of the V1 cortex is characterised not only by its RF $z$ in the retina (which, as in previous Petitot’s contact model, is identified with $\mathbb{R}^2$) and its orientation $\theta$, but also by a new parameter $\sigma$, which is called scaling and corresponds to the intensity of the reply of the neuron to a stimulus. In more detail, for the symplectic model, the V1 cortex is represented by the total space of a principal bundle over $\mathbb{R}^2 = \mathbb{R}^2 = \mathbb{R}^2 = C^\ast \times R^+$:

$$\pi : P = C^\ast \times R \longrightarrow R,$$

with fiber given by the group of the non zero complex numbers $C^\ast = S^1 \times \mathbb{R}^+ = \{\sigma e^{i\theta}\}$. Such a $C^\ast$-bundle $P$ can be also identified with either of the following manifolds:

- the group $G = \text{Sim}(\mathbb{R}^2)$ of similarities of $\mathbb{R}^2$

  $$G := \text{Sim}(\mathbb{R}^2) = (\mathbb{R}^+ \cdot \text{SO}(2)) \times T_{\mathbb{R}^2} = C^\ast \ltimes \mathbb{R}^2,$$

  where $T_{\mathbb{R}^2} = T_C$ denotes the group of the parallel translations of $\mathbb{R}^2$

- the cotangent bundle with the zero section removed $T^\ast_\mathbb{R} R$ of the retina $R = \mathbb{R}^2$.

By the identification $P = T^\ast_\mathbb{R} R$, the bundle $P$ is naturally equipped with a symplectic structure, namely the non-degenerate closed 2-form $\omega = d\lambda$ determined by the Liouville form $\lambda$ of $T^\ast_\mathbb{R} R$. In what follows, we call the symplectic bundle $\pi : P = G = T^\ast_\mathbb{R} R \rightarrow R$ the Sarti-Citti-Petitot (SCP) bundle.

The identification between the V1 cortex and the bundle $P = \text{Sim}(\mathbb{R}^2) \rightarrow R = \mathbb{R}^2$, given in Sarti, Citti and Petitot’s symplectic model, is based on the one-to-one correspondence between neurons and points of $P = \text{Sim}(\mathbb{R}^2)$ defined as follows. Consider the complex mother Gabor filters $G_{ab \gamma_{C0}}$, with the RP (2.3) and let $(G_{ab \gamma_{+ \gamma_{C0}}}, G_{ab \gamma_{- \gamma_{C0}}})$ be the real mother Gabor filters, whose RPs are by the real and imaginary parts of $\gamma_{C0}$. Let also $(n^\alpha_{\gamma_{C0}}, n^-_{\gamma_{C0}})$ be a pair of simple neurons of the V1 cortex that work as the pair of mother Gabor filters $G_{ab \gamma_{+ \gamma_{C0}}}, G_{ab \gamma_{- \gamma_{C0}}}$. As we explained in §2.5, any element $a \cdot T_b \in C^\ast \cdot C$, transforms the pair of $(\gamma_{C0}^+, \gamma_{C0}^-)$ into the pair $(\gamma_{a,b}^+, \gamma_{a,b}^-)$ defined in (2.4). The symplectic model
of Sarti, Citti and Petitot is based on the following fundamental assumption:

The V1 cortex consists of pairs of simple neurons \((n_{a,b}^+, n_{a,b}^-)\), in which the neurons \(n_{a,b}^\pm\) work as the Gabor filters \((G_{ab}^+, G_{ab}^-)\) and are therefore parameterised by the elements the similarity group \(P = \text{Sim}(\mathbb{R}^2) = \mathbb{C}^* \times \mathbb{C}\).

7.5. A physiological interpretation for the coordinates \((z, \theta, \sigma)\) in Sarti, Citti and Petitot’s model: the Principle of Maximal Selectivity. In [63] (see also [20], p. 312), Sarti, Citti and Petitot consider the following Principle of Maximal Selectivity:

“The intracortical circuitry is able to filter out all the spurious directions and to strictly keep the direction of maximum response of the simple cells”.

According to this principle, for any input function \(I : \mathbb{R} \to \mathbb{R}\), at each point \(z = (x, y) \in \mathbb{R}\), there is a neuron with RF \(z\) which provides the maximal output for the stimulus. According to the symplectic model, such a neuron corresponds to a point of the fiber \(P|_z = \pi^{-1}(z) \simeq \mathbb{C}^*\) and it therefore corresponds to special values \((\theta_z, \sigma_z)\) for the coordinates of the fiber \(\mathbb{C}^* = S^1 \times \mathbb{R}^+\). As a consequence of the Principle of Maximal Selectivity, a stimulus determines a section of the SCP bundle \(\pi : P \to \mathbb{R}\):\[
\rho : \mathbb{R} \to P, \quad \rho(z) := (z, \theta_z, \sigma_z)
\]
given by the neurons with maximal responses. Since \(P\) is identified with the cotangent bundle \(P = T^*_z \mathbb{R}\), this section can be considered as a 1-form \(\rho\) on \(\mathbb{R}\). Sarti, Citti and Petitot proved that \(\rho\) is closed and hence that the surface \(\rho(\mathbb{R}) \subset T^*_z \mathbb{R}\) is Lagrangian.

By the results in [63], given a point \(z\) and an input function \(I\), the above defined 1-form \(\rho(z) := (z, \theta_z, \sigma_z)\) is such that the real number \(\frac{1}{\sqrt{2}} e^{\sigma_z}\) is essentially equal to the distance of \(z\) from the nearest point of a nearby boundary of a figure (that is a contour on which the gradient \(dI\) is very large) and \(\theta_z\) is equal to the orientation of the tangent line of this boundary at such nearest point in the boundary. This immediately leads to the following physiological interpretation for the parameters that distinguish simple neurons with the same RF:

*a neuron with RF \(z\) and corresponding to the pair of parameters \((\theta, \sigma)\) fires when \(\frac{1}{\sqrt{2}} e^{\sigma_z}\) is equal to the distance of \(z\) from the nearest point of the boundary of a figure and \(\theta\) is the orientation of the tangent line of this boundary at such nearest point*

This is a physiological interpretation for the coordinates \(\theta\) and \(\sigma\) of the SCP bundle, which is however based on purely non-local properties of the input function \(I : \mathbb{R} \to \mathbb{R}\). In fact, according to the such an interpretation, the firing of a simple neuron does not depends on the infinitesimal behaviour of \(I\) at a RF \(z\), but on its behaviour at finite distances from \(z\). This means that, following Sarti, Citti and Petitot’s discussion, the scaling \(\sigma\) cannot be considered as an “internal parameter” in the sense of Hubel and Wiesel.

8. Models of hypercolumns

8.1. Bressloff and Cowan’s spherical model of a hypercolumn. As we mentioned in the Introduction and in [3.2] according to Hubel and Wiesel a hypercolumn is a collection of columns of the V1 cortex, in which the internal parameters may take all
possible values. P. Bressloff and J. Cowan proposed a Riemannian spherical model for the hypercolumns, based on the assumption that the internal parameters are just two: the orientation $\theta$ and the spatial frequency $p$.\cite{Bressloff2012, Cowan2013, Bressloff2014}

They assumed that a hypercolumn $H$ is a domain in the V1 cortex, associated with two pinwheels $S, N$, corresponding to the minimal and maximal values $p_-, p_+$ of the spatial frequency. According to the model, the simple neurons of the hypercolumn $H$ are parametrised by the orientation $\theta$ and the normalised spatial frequency $\phi$, defined by

$$\phi := \pi \frac{\log(p/p_-)}{\log(p_+/p_-)}.$$ 

The normalisation is chosen in such a way that $\phi$ may assume only values in the interval $[0, \pi]$. For any choice of $\theta$ and $\phi$, there is a corresponding simple neuron $n = n(\theta, \phi)$ in $H$, which fires only if a stimulus occurs in its RF and with orientation normalised spatial frequency $\theta$ and $\phi$.

Bressloff and Cowan proposed a mathematical interpretation of these parameters as spherical coordinates of the 2-sphere $S^2$, with $\theta \in [0, 2\pi)$ corresponding to the longitude and $\phi = \phi' + \pi/2 \in [0, \pi]$ to the polar angle or shifted latitude (with $\phi' = \phi - \pi/2$ latitude in the usual sense). The shifted latitudes of the pinwheels $S, N$ are 0, $\pi$, but the longitude (=orientation) is not defined for them – in fact, the pinwheels are able to detect contours of any orientation. Following this mathematical interpretation of $\theta$ and $\phi$, Bressloff and Cowan identified an hypercolumn $H$ with the sphere $H_{BC} = S^2$ and the pinwheels $S, N$ of $H$ with the south and the north pole of $H_{BC} = S^2$. Then they used such a clever model to describe the evolution of the excitation of visual neurons according to the Wilson-Cowan equation and got many interesting results.

We now recall that the RF of a simple neuron $n$ is very small, so that it can be considered as a single point $z(n)$ of the retina. In Bressloff and Cowan’s spherical model, the map that sends each simple neuron $n$ of a hypercolumn $H$ to its RF $z(n)$ is considered as a smooth map between the surfaces

$$z : H_{BC} = S^2 \rightarrow R_H := z(H_{BC}), \quad n \mapsto z(n)$$

where we denote by $R_H$ the the region of the retina, which is the receptive field of the whole hypercolumn (i.e. the union of the RF of all its neurons). This map (or, more precisely, its restriction to some appropriate open set) is assumed to be a diffeomorphism. This implies that, in Bressloff and Cowan’s model, the spherical coordinates $(\theta, \varphi)$ of $H_{BC}$ may be considered also as coordinates for (an open subset of) the receptive field $R_H$ of the hypercolumn $H$ and cannot be considered as internal parameters in the sense of Hubel and Wiesel. Only for the neurons in the pinwheels $S, N$ of the hypercolumn (i.e. those on which the “latitude” $\varphi$ takes extremal values) the parameter $\theta$ can be considered as an “internal parameter”.

8.2. The need of improvements for Sarti, Citti and Petitot’s symplectic model and Bresloff and Cowan’s spherical model. In this short section, we would like to point out a couple problems for Sarti, Citti and Petitot’s symplectic model and for Bresloff and Cowan’s spherical model, which indicate the need of some improvements for those two models. A development in this direction is given by the conformal spherical
model of a hypercolumn and the corresponding reduced model, discussed in the next subsection.

In their symplectic model, Sarti, Citti and Petitot describe the simple neurons of the V1 cortex in terms of the bundle of conformal frames

$$\pi : \text{Sim}(\mathbb{R}^2) \longrightarrow \mathbb{R}^2 = \text{Sim}(\mathbb{R}^2)/\text{CO}(2)$$

over the retina $R = \mathbb{R}^2$. In this model, the simple neurons of the V1 cortex appear in pairs $(n^+, n^-)$ and the neurons $n^\pm$ of any such pair work as the Gabor filter $G_{ab}^\pm$ defined in §2.5. They are therefore parameterised by the elements $(a, b)$ of the similarity group $\text{Sim}(\mathbb{R}^2) = \mathbb{C}^\ast \times \mathbb{C}$. Each fiber $\pi^{-1}(z) \simeq \mathbb{C}^\ast$ represents a column with the RF $z$ and the (pairs of) simple neurons in such a column are parameterised by the two coordinates of $\mathbb{C}^\ast = S^1 \times \mathbb{R}^+$, the orientation $\theta$ and the scaling $\sigma$. In particular, according to this model, the columns of the V1 cortex represented by the fibers $\pi^{-1}(z)$, $z \in R$, of the SCP bundle are just the pinwheels: In fact, they contain simple neurons that are able to detect any possible orientation $\theta$ for the contours that pass through their receptive fields $z$.

This remark shows that, in the symplectic model, the V1 cortex behaves as a collection of pinwheels with no regular column among them. Since it is known that most of the columns of the V1 cortex are regular, we think that this represents a somehow weak point of the symplectic model.

Let us now focus on Bressloff and Cowan’s spherical model. In this model the simple neurons of a hypercolumn $H$ are mathematically represented as points of a sphere $H_{BC} = S^2$ and are distinguished each other by the two spherical coordinates of $S^2$, identified with the orientation $\theta$ and the normalised spatial frequency $\phi$ of the neurons. But, as we pointed out at the end of §8.1 in Bressloff and Cowan’s model, the spherical coordinates $\theta$, $\phi$ cannot be considered as internal parameters for the hypercolumn (with the exceptions of the neurons in the two pinwheels $S$, $N$ of the hypercolumn). In other words, according to the spherical model, most of the simple neurons of a hypercolumn are not associated to any value of an internal parameter in the sense of Hubel and Wiesel. We think that also this aspect of the spherical model is a weak point.

As we will see in the next two subsections, the conformal spherical model offers an improvements of Bressloff and Cowan’s model, in which new internal parameters occur and yields a simplified version, which can be considered a refined version of Sarti, Citti and Petitot’s model of the V1 cortex and suggests an alternative physiological interpretation of the scaling parameter $\sigma$, based on purely local properties of the input function.

8.3. The conformal spherical model of a hypercolumn and the associated reduced model. We now discuss the conformal spherical model, shortly announced in [3] and presented in detail in [4].

We recall that in Bressloff and Cowan’s Riemannian spherical model, a hypercolumn $H$ is mathematically represented as a sphere $H_{BC} = S^2$ equipped with the standard round metric $g_o$. The basic new idea introduced in [2] was to construct an improvement of such spherical model replacing the standard Riemannian sphere $(S^2, g_o)$ by the conformal sphere $(S^2, [g_o])$, i.e. by the 2-sphere equipped with the conformal structure $[g_o]$ (see §5 for main definitions and fundamental results).
Inspired by the method of the construction of Citti, Sarti and Petitot’s symplectic model, the fundamental assumption of the conformal spherical model is that the simple neurons of a hypercolumn appear in pairs \((n_g^+, n_g^-)\), in which the neurons \(n_g^\pm\) work as the Gabor filters with RPs \(\gamma_g^\pm\) given by the real and imaginary parts of the RP

\[
\gamma_g^C(x, y) = \frac{1}{J(g)(x, y)} \gamma_0^C(g^{-1}(x, y))
\]

where

- \(\gamma_0^C(x, y)\) is the RP of the “mother” Gabor filter defined in (2.3);
- \(g\) is an element of the connected group \(\text{Conf}^o(S^2) \simeq \text{SO}^o(1, 3)\) of conformal transformations of \((S^2, [g_0])\) (see (5.5)).

In other words, the neurons \(n_g^\pm\) behave as the Gabor fields, whose RPs are the real and imaginary parts of the complex Gabor filter, which is obtained from the “mother” complex Gabor filter \(\text{Gab}_0^C\) by changing the coordinates \((x, y)\) by the conformal transformation \(g\) and using the fact that, under changes of coordinates, the RP profiles transform as densities – see (2.2).

In this way, according to the conformal spherical model, the (pairs of) simple neurons of a hypercolumn are parametrized by the elements of \(\text{Conf}^o(S^2) \simeq \text{SO}^o(1, 3)\).

On the other hand, as we pointed out in §5.2, the group \(\text{Conf}^o(S^2)\) is the total space of the homogeneous bundle

\[
\pi : \text{Conf}^o(S^2) \longrightarrow S^2 = \text{Conf}^o(S^2)/\text{Sim}(\mathbb{R}^2),
\]

which is in turn identifiable with the total space of the bundle \(\pi : \mathcal{F}(2)(S^2) \longrightarrow S^2\) of the second order conformal frames of \(S^2\). This means that, according to the conformal spherical model, a hypercolumn \(H\) is identified with the total space of the bundle (8.20) with fiber given by the 4-dimensional group \(\text{Sim}(\mathbb{R}^2)\).

In this model, the coordinates of the fiber \(\text{Sim}(\mathbb{R}^2)\) are internal parameters for the simple neurons of the hypercolumn \(H\). If such fiber coordinates are ignored, one gets that the neurons of the hypercolumn are parameterised just by the two spherical coordinates of \(S^2\) and Bressloff and Cowan’s spherical model is recovered.

On the other hand, the conformal spherical model and Riemannian spherical model crucially differ in the following aspects:

- According to the Riemannian spherical model, any point, which is different from the north pole \(N\) and south pole \(S\) of Bressloff and Cowan’s sphere \(H_{BC} = S^2\) (or, more precisely, each point of an open and dense subset \(U \subset H_{BC} \setminus \{N, S\}\)), is assumed to be the RF of exactly one simple neuron, while the north pole \(N\) and the south pole \(S\) are assumed to be the RFs of two pinwheels, the only two columns that Bressloff and Cowan assume to be contained in a hypercolumn;
- According to the conformal spherical model, any point \(z \in S^2\) – with no distinction – is assumed to be the common RF (or the union of several RFs, but all of them very close each other) of a system of simple neurons, each of them distinguished from the other by 4 internal parameters. Assuming that one of the internal parameters is the orientation \(\theta\), the system of simple neurons with a given RF \(z\) is organised into a collection of several sub-systems, one per each value of
the internal parameter $\theta$, and containing simple cells that are parameterised by the remaining 3 internal parameters.

In the conformal spherical model, the north and south poles $N, S \in S^2$ are still the common RFs of many neurons, possibly organised in regular columns or pinwheels (as it occurs in the Riemannian spherical model), but – in contrast with the Riemannian spherical model – the poles $N$ and $S$ are no longer the only points of the sphere with such a property. In fact, according to the conformal spherical model all points of $S^2$ are assumed to the common RFs of a large family of simple neurons.

As we mentioned above, the conformal spherical model naturally leads to a second model for small neighbourhoods of the poles of $S^2$, called reduced model, which can be considered as a local version of Sarti, Citti and Petitot’s symplectic model. Such a reduced model offers a physiological interpretation for the scaling parameter $\sigma$ in terms of the normalised logarithm of the spatial frequency, which is a purely local property of the input function.

As we showed in §5.1.2, there is an open and dense subset $U \subset \text{SL}(2, \mathbb{C})$ which admits a Gauss decomposition of the form $U = N^- \cdot \mathbb{C}^+ \cdot N^+$, where $N^\pm$ and $\mathbb{C}^+$ are the subgroups of $\text{SL}(2\mathbb{C})$ defined in (5.7). On the other hand, according to Lemma 5.1 and the subsequent remark, the 1-dimensional complex subgroup $N^+$ acts on the tangent space $T_S S^2$ as the group of parallel translations while the local actions of the elements in $N^-$ are very close to the identity map near $S$.

Let us now pick a small neighbourhood $V \subset T_S S^2$ of the origin of the tangent space $T_S S^2$ and denote by $V_S \subset S^2$ the neighbourhood of the south pole $S$ in $S^2$, which corresponds to $V$ via the stereographic projection $s_N : S^2 \setminus \{N\} \to T_S S^2$. Since the map $s_N$ is $N^+$ equivariant, the open subset $U^{(N^+)} \subset N^+$ of the elements in $N^+$ that transform the origin $0 \in T_S S^2$ into the other points of $V \subset T_S S^2$, is such that

$$U^{(N^+)} \cdot S = V_S.$$

Ignoring the closed to identity local action of the transformations in $N^-$ (i.e. focusing just on the group $\mathbb{C}^+ \cdot N^+$ and neglecting the contribution of $N^- \cdot \mathbb{C}^+ \cdot N^+$ of $\text{SL}(2\mathbb{C})$), we get that the simple neurons corresponding to the fibers over $V_S \subset S^2$ are represented just by the elements of $\mathbb{C}^+ \times U^{(N_+)} \subset \mathbb{C}^+ \cdot N^+$. Such simple neurons occur in pairs $(n^+(g), n^-(g))$, associated with the element $g \in \mathbb{C}^+ \cdot U^{(N^+)}$, and work as pairs of Gabor filters with RPs, which are the real and imaginary parts of the complex Gabor filters, with RP are obtained from the mother complex RP $\gamma_0^C$ by the transformations $g \in \mathbb{C}^+ \times U^{(N_+)}$.

This remark lead to the reduced model which consists precisely of the following assumption: the simple neurons of a hypercolumn corresponding to the points of a (sufficiently small) neighbourhood $V_S \subset S^2$ of the south pole $S$ of $H_{BC} = S^2$ are parameterised by an open subset of the form $\mathbb{C}^+ \cdot U^{(N^+)} \subset \mathbb{C}^+ \cdot N^+$ of the group $\text{SL}(2, \mathbb{C})$.

Notice that the reduced model can be considered as a localisation of the Sarti, Citti and Petitot’s symplectic model, in which the translation group $\mathbb{R}^2 \subset \text{Sim}(\mathbb{R}^2)$ is replaced by a sufficiently small open subset $V_S \subset N^+$ of $N^+ \subset \text{SL}(2, \mathbb{C})$. The replacement of the non-compact manifold $\mathbb{R}^2$ with a small subset $U^{(N_+)}$ of $N^+ \simeq \mathbb{R}^2$ make the symplectic model more realistic, even if there is still an unrealistic assumption that the neurons
corresponding to a fiber $\pi^{-1}(z) \simeq \mathbb{C}^*$ are parametrised by the points of the non-compact group $\mathbb{C}^*$. In order to reach an even more realistic model, it would be natural to “localise” not only the base manifold but also the fibers of the bundle (i.e. to replace the standard fiber $\mathbb{C}^*$ by a compact neighbourhood of the identity). An improvement in this direction is discussed in [4], to which we refer for the details.

According to the reduced model, the neurons associated with the points an appropriate portion $V_S$ of the Bresloff and Cowan’s sphere $H_{BC} = S^2$ are parameterised by the coordinates for the 4-dimensional space $\mathbb{C}^* \cdot U^{(N+)} \subset \mathbb{C}^* \cdot N^+$: two real parameters, given by modulus and the argument of a complex coordinate of the open subset $U^{(N+)}$ of the group $N^+(\simeq \mathbb{C})$ and two real parameters, given by the modulus and the argument of a complex coordinate for the group $\mathbb{C}^*$. In [4] it is pointed out that the two real parameters for the subset $U^{(N+)} \subset N^+$, say $\tilde{\theta}$ and $\tilde{\varphi}$, can be used in two different ways:

(a) to parameterise the projections of the points onto the base of the bundle $\pi : \mathbb{C}^* \cdot U^{(N+)} \to V_S \subset S^2$ or

(b) to parameterise the points of the fiber of the bundle $\pi : \mathbb{C}^* \cdot U^{(N+)} \to V_S \subset S^2$.

If $\tilde{\theta}$ and $\tilde{\varphi}$ are used as in (a), they are “external parameters” for the considered collection of simple neurons, i.e. they parameterise the RFs in the sphere $H_{BC} = S^2$ and they can be identified with the orientation and the normalised logarithm of the spatial frequency of the neuron, as in Bressloff and Cowan’s Riemannian spherical model. On the other hand, if $\theta$ and $\varphi$ are used as in (b), they are “internal parameters” for the fiber bundle and they can be identified with the internal parameters $\theta$ and $\sigma$ of Sarti, Citti and Petitot’s symplectic model. A comparison between these two interpretations for the parameters $\tilde{\theta}$ and $\tilde{\varphi}$ immediately yields to a physically interpretation of the scaling parameter $\sigma$ as the Bressloff and Cowan’s normalised logarithm of the spatial frequency of the neurons.

In [4] it is also remarked that an analog of the above reduced model may be constructed also for the neurons corresponding to the points of a neighbourhood $V_N$ of the north pole or of any other point $z \in H_{BC} = S^2$. It is also noticed that the neurons with RF given by the north pole $N$ (resp. south pole $S$) are characterised by having the maximal (resp. minimal) value for the spatial frequency. It is known that the processing of high-frequency and low-frequency information differs from each other [26].

These observations suggest the possibility of the following new speculative model for a hypercolumn. As in Bressloff and Cowan’s model, assume that the RF of the neurons of a hypercolumn $H$ constitute a retinal domain $R_H \subset R$, which is diffeomorphic to (an open and dense region of) Bressloff and Cowan’s sphere $H_{BC} = S^2$ and are therefore parameterised by the spherical coordinates $\theta, \phi$ with the above described interpretations in terms of orientation and spatial frequency. Let us now split the retinal domain $R_H$ into two subdomain $R_H = V_S \cup V_N$, corresponding to the southern hemisphere (centred at the south pole $S$) and the northern hemisphere (centred at the north pole $N$). Then let us consider two copies of the reduces conformal model, one for the system of neurons associated with $V_S$ and another for the system of neurons associated with $V_N$. We conjecture that the first (which identifies an appropriate system of neurons with a bundle of the form $\pi_S : P_S = \mathbb{C}^* \cdot U^{(N+)} \to V_S$ for some $U^{(N+)} \subset N^+$) can be used as model for a system of neurons that processes low spatial frequency visual information, while the second (concerning a bundle $\pi_N : P_N = \mathbb{C}^* \cdot U^{(N-)} \to V_N$ for some $U^{(N-)} \subset N^-$) can
be associated with a system of neurons that processes high spatial frequency visual information.

8.4. **The Principle of Invariance and an application of the reduced model.** Let $K$ be a group of transformations of a space $V$ and denote by $O = Kx$ an orbit of one point $x$ of $V$. The following obvious $K$-invariance principle holds.

**Principle of invariance.** If $K$ is a group of transformations of a space $V$, the information, which a system of uniformly distributed observers on an orbit $O = Kx \subset V$ sends to a common center, is invariant with respect to the transformations of the group $K$.

This principle can be used to explain the main difference between the firing of simple and complex neurons [34, 31, 17]. As we recalled in § n. 7, the firing of a complex cell is invariant with respect to the shifts of stimuli inside of its receptive field, in contrast with a simple cell. This can be explained by assuming that the RP of all the simple cells connected to the complex cell are derived from a mother RP via transformations of the group $K = \mathbb{R}^2$ of translations. By the above Principle of Invariance, the information, which is obtained by the complex cell, must be shift invariant. We recall that, according to the reduced model, the simple neurons of a small neighbourhood of a pinwheel are assumed to work as Gabor filters, which are obtained from the mother Gabor filter by transformations of the similarity group $\text{Sim}(\mathbb{R}^2) = CO(2) \cdot \mathbb{R}^2$. This group contains the normal subgroup $\mathbb{R}^2$ of translation. By the above Principle of Invariance, the information, which a complex cell receives from such a system of simple cells, will be translation invariant.

**Declarations**

D.A. was supported by the Grant Basis-Foundation Leader n 22-7-1-34-1. Besides this, no other funds, grants, or support was received.

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