Division of labor between M and P visual pathways: different visual pathways minimize joint entropy differently

Luiz Carlos de Lima Silveira, Cézar Akiyoshi Saito, Harold Dias de Mello Jr., Vladímir de Aquino Silveira, Givago da Silva Souza, Anderson Raiol Rodrigues and Manoel da Silva Filho

Universidade Federal do Pará, Brazil

Abstract

Visual perception and action are strongly linked with parallel processing channels connecting the retina, the lateral geniculate nucleus, and the input layers of the primary visual cortex. Achromatic vision is provided by at least two of such channels formed by the M and P neurons. These cell pathways are similarly organized in primates having different lifestyles, including species that are diurnal, nocturnal, and which exhibit a variety of color vision phenotypes. We describe the M and P cell properties by 3D Gábor functions and their 3D Fourier transform. The M and P cells occupy different loci in the Gábor information diagram or Fourier Space. This separation allows the M and P pathways to transmit visual signals with distinct 6D joint entropy for space, spatial frequency, time, and temporal frequency. By combining the M and P impacts on the cortical neurons beyond V1 input layers, the cortical pathways are able to process aspects of visual stimuli with a better precision than it would be possible using the M or P pathway alone. This performance fulfils the requirements of different behavioral tasks. **Keywords:** vision, M and P pathways, visual parallel processing, fourier space, joint entropy, information theory.

Introduction

In this paper we will review the organization of the primate visual system in multiple pathways from the point of view that the M and P visual pathways separation is advantageous for information transmission, allows optimization of the spatial, time, spatial frequency, and temporal frequency trade-offs, and enables the transmission of more accurate information. The basic idea presented in this manuscript is that estimation of the information content of the visual pathways is important to understanding of the functioning mechanisms of the neural circuits and perception.

Parallel visual pathways

At daylight, the image of the external world formed on the retinal surface is sampled by the cone mosaic and the cone output is transferred by specialized neural circuits to bipolar cells and ganglion cells. The latter are the last elements of the retinal circuitry, responsible for sending the results of retinal processing to high level visual centers and can be regarded as specialized devices with specific spatiotemporal properties to represent visual image contrast. The ganglion cell response to visual stimulation is the key element to understanding how the visual system works, how it samples the environment, and how efficiently it performs this task.

The visual system of humans and other primates is organized in several parallel pathways that perform information transfer from photoreceptors to the thalamus, pretectum, superior colliculus, and other centers located in the diencephalon and mesencephalon. The pathways connecting the retina to the lateral geniculate nucleus (LGN) and primary visual cortex (V1) are considered particularly important for conscious perception of visual stimuli as well as to provide key visual information for the programming of actions (Milner & Goodale, 1995). Among them, the magnocellular (M) and parvocellular (P) pathways play important roles, coding visual information available at the retinal image and then transferring this information to the V1 entrance layers (Silveira, Grünert, Kremers, Lee, & Martin, 2005).

The visual system continuously samples the domains of space and time, measuring contrast at several spatiotemporal coordinates. This operation is constrained within limits imposed by fundamental physics which are common to all sorts of devices, whenever they sample a given domain to perform any kind of measurement. The first of such constraints are the conflicting requirements to attain

Luiz Carlos de Lima Silveira is a professor in the Departamento de Fisiologia, Instituto de Ciências Biológicas and Núcleo de Medicina Tropical at Universidade Federal do Pará. Manoel da Silva Filho and Cézar Akiyoshi Saito are professors in the Departamento de Fisiologia, Instituto de Ciências Biológicas at Universidade Federal do Pará. Harold Dias de Mello Jr., Givago da Silva Souza and Anderson Raiol Rodrigues are graduate students of the Universidade Federal do Pará. Vladímir de Aquino Silveira is an undergraduate student of the Universidade Federal do Pará. Correspondence regarding this article should be directed to Dr. Luiz Carlos de Lima Silveira, Universidade Federal do Pará, Instituto de Ciências Biológicas, Departamento de Fisiologia, 66075-900 Belém, Pará, Brazil. Telephone and fax: + 55-91-3241-0032. E-mail: luiz@ufpa.br

simultaneous precision in the domains of space and time, a problem that becomes particularly difficult when the visual system has to do its job at low levels of illumination.

There is however an even more fundamental constraint. Natural visual stimuli exhibit simultaneous spatial or temporal singularities and periodicities, and the visual system has to evaluate not only the stimulus' spatiotemporal coordinates, but simultaneously its spatiotemporal frequency spectrum. It is a general, basic problem in the design of measuring devices, strictly governed by the principles of information theory, to achieve accurate sampling in all domains of interest (i.e. time, temporal frequency, space, and spatial frequency). Infinitely precise time or spatial sampling can be performed by devices provided with infinitesimal temporal or spatial windows, but no discrimination of spatial or temporal frequencies would be possible with such devices. Conversely, infinite precision in the spatial or temporal frequency domains can be attained by filters, each one perfectly tuned for a single spatial or temporal frequency, sampling through infinitely extended spatial or temporal windows, but these filters would be unable to precisely mark the spatial localization or occurrence in time of any event.

However, these extremes of spatial or temporal accuracy as well as spatial and temporal spectral accuracy do not exist in the physical world. They are mathematical idealizations. All physical devices, either natural or manmade, built to store, transmit or analyze visual information, represent different degrees of compromise between precision in space-time domain and precision in spatiotemporal frequency domain (Gábor, 1946).

The evidence so far indicates that the M and P neurons respond differently in all domains of the space-time, though displaying a considerable degree of overlap in every domain. Each pathway, M or P, represents a particular tradeoff for precision in space, time, spatial frequency, and temporal frequency, providing higher order visual neurons, similar to those found in the dorsal and ventral streams of the visual cortex, with the possibility to retrieve visual information with the particular combination of precision in all these domains that suits the demands of the behavioral task to be performed (Silveira, 2004).

The information theory of Dénes Gábor

In a fundamental paper on theory of communication, the Hungarian scientist Dénes Gábor (1900-1979), who won the 1971 Nobel Prize in Physics for his invention and development of the holographic method (Gábor, 1992), investigated the problem of simultaneous description of a phenomenon in terms of its energy distribution in the domains of time and temporal frequency. His observations can be extended to any pair of related domains, and generalized to complex situations such as the sampling and coding of a retinal image, in which time, two dimensions of space and their three Fourier-transformed spectral dimensions are equally relevant.

Gábor (1946) developed a quantitative description, in which the amount of information that can be transmitted by a limited frequency band in a limited time interval can be analyzed in terms of elementary quanta of information belonging to a plane where time and temporal frequency are orthogonal coordinates. In this plane, Gábor's Diagram of Information (also called Fourier Space), the shapes and sizes of the elementary quanta of information depend on the time response and frequency band-pass of the device that is performing the time-frequency analysis. The shorter the time response, the higher the precision in the time domain; the more limited the frequency band-pass, the higher the precision in the temporal frequency domain. In addition, one of Gábor's demonstrations was that the precision in the two related domains are inversely related, in such a way that whenever it increases in one domain, it simultaneously decreases in the other Fourier related domain. This is most commonly expressed by the uncertainty or entropy (the inverse of precision) in the two related domains by mathematical identities of this kind:

$$\Delta t \times \Delta f \geq \frac{1}{2}$$

In this identity, Δt and Δf are the entropy in the time domain and temporal frequency domain, respectively, and their product is the joint entropy. This identity is a fundamental formulation in Information Theory, explicitly establishing that the joint entropy cannot go below a certain minimum of the order one, due to the impossibility of simultaneous increase of time and temporal frequency accuracies. This relation was first inductively formulated by Hartley (1928) and then put in a mathematical basis by Gábor (1946) using the Schwarz inequality. The minimum value depends on the metrics being employed, in this case 1/2 due to the use of variance as an entropy measurement.

Efficient image sampling

Ganglion cells code the information content of the retinal image with a certain degree of joint entropy in a 6D Fourier Space: time, temporal frequency, 2D space, and 2D spatial frequency. The exact joint entropy value depends on the mathematical function that best describes cell response function in all domains of interest. Some functions result in large joint entropy, while others return small values for this parameter.

If all ganglion cells located in a given retinal region were of a single class, having similar response functions, they would have approximately the same joint entropy. Moreover, all cells would operate with the same trade-off between entropy in different domains. Conversely, ganglion cells that analyze every region of the visual field belong to several different classes. Visual information coding in multiple, different channels, seems to be a general principle of visual system organization for all mammals and possibly for vertebrates in general. This is the case for the domestic cat, a very popular animal model for visual studies, in which α, β, and other less studied ganglion cell classes, each of them projecting to specific LGN layers,

are involved in achromatic vision and exhibit different sensitivities in space, time, spatial frequency, and temporal frequency domains. In primates, there is evidence that M, P, and some K cells are involved in achromatic vision, and that each cell class codes contrast with a particular combination of spatial, temporal, spatial frequency, and temporal frequency sensitivity (Silveira, Saito, Lee, Kremers, da Silva Filho, Kilavik, Yamada, & Perry, 2004; Silveira et al., 2005).

Also, the response properties of the major ganglion cell classes have been quantified with enough detail that it is feasible to find a general mathematical function applicable to them. Thus, it is possible to estimate the exact value for their 6D joint entropy and to test how far from the theoretical minimum ganglion cells operate.

Gábor functions

Gábor (1946) demonstrated that a group of functions offers the smallest joint entropy in the domains of time and temporal frequency, having the smallest possible area in the Fourier Space. These elementary functions - $\Psi(t)$ -, nowadays called Gábor functions, have the form of a harmonic oscillation modulated by a probability function:

$$\Psi(t) = e^{\left[-\alpha^2 (t-t_0)^2\right]} \times e^{i\left[2\pi f_0 (t-t_0)+\theta\right]}$$

where α and to t_0 represent the probability function sharpness and peak, while f_0 and θ represent oscillation frequency and phase. $\Psi(t)$ is represented by points of the complex plane associated with real values of time as the third coordinate. As time elapses, $\Psi(t)$ spirals around the time axis in the surface of a solid of revolution that has the shape of a probability function.

The Fourier Transform of the Gábor function gives its spectrum - $\Phi(f)$ - , which has the same analytical form of the original time function:

$$\int \Psi(t) \times e^{-i2\pi ft} dt = \Phi(f)$$

$$\Phi(f) = e^{\left[-\left(\frac{\pi}{\alpha}\right)^2 (f-f_0)^2\right]} \times e^{i\left[-2\pi t_0 (f-f_0)+\theta\right]}$$

The entropy in time and temporal frequency is the product of a constant by the root mean square of the deviation of the signal from the mean in each domain:

$$(\Delta t)^2 = 2\pi \left[\left[\frac{\left[\int \Psi * t^2 \Psi dt\right]}{\left[\int \Psi * \Psi dt\right]}\right] - \left[\frac{\left[\int \Psi * t\Psi dt\right]}{\left[\int \Psi * \Psi dt\right]}\right]^2\right]$$

$$(\Delta f)^2 = 2\pi \left[\left[\frac{\left[\int \Phi * f^2 \Phi df\right]}{\left[\int \Phi * \Phi df\right]}\right] - \left[\frac{\left[\int \Phi * f\Phi df\right]}{\left[\int \Phi * \Phi df\right]}\right]^2\right]$$

Gábor (1946) also showed that any function can be expanded in terms of elementary functions, $\Psi(t)$. As time and temporal frequency entropies are related to the probability function sharpness by

$$\Delta t = \frac{1}{\alpha} \sqrt{\frac{\pi}{2}}$$

$$\Delta f = \alpha \frac{1}{\sqrt{2\pi}}$$

changing the value of α, changes the trade-off between time and temporal frequency precision, and results in a range of different Gábor functions. When $\alpha \to 0$ and $\alpha \to \infty$, the Gábor function becomes a sine-wave or an impulse function, respectively. Then, the expansion of a function in these conditions becomes the usual Fourier expansion and time analyses, respectively, which can be regarded as two extremes of the Gábor expansion.

Originally, the work of Gábor (1946) dealt with hearing and time devices in general, being restricted to the domains of time and temporal frequency, but later it was largely used to model the receptive fields of visual neurons in space, spatial frequency, time, and temporal frequency (Marcelja, 1980; Daugman, 1980, 1983, 1984, 1985, 1989; Kulikowski & Bishop, 1981; Kulikowski, Marcelja, & Bishop, 1982; Wang, Qi, Jing, & Yu, 1988; Wang, Qi, Yao, & Wang, 1993).

Spatial response

The presence of M and P ganglion cells seems to be a general feature of the primate retina (Kremers, Silveira, Yamada, & Lee, 1999; Silveira et al., 2004, 2005). They were first described in diurnal, trichromatic anthropoids, such as humans and macaque monkeys, but more recently their presence has been confirmed in all diurnal and nocturnal, mono, di, and trichromatic anthropoids so far studied, and even nocturnal prosimians. In particular, the presence of both M and P cells in color blind primates at approximately the same numbers as in other primates with a variety of color vision phenotypes is a clear indication that these cells play a fundamental role in achromatic vision (Silveira, Yamada, Perry, & Picanço-Diniz, 1994; de Lima, Silveira, & Perry, 1996; Yamada, Silveira, & Perry, 1996; Yamada, Silveira, Perry, & Franco, 2001). The involvement of P cells with red-green color-opponency seems to be a later addition to primate vision (Mollon & Jordan, 1988).

The M and P cell responses in the domain of space are represented by their 2D spatial impulse responses, which bear a direct relationship with their receptive field response profiles. M and P cells have elliptical or approximately circular receptive fields with a center-surround organization: a central region that responds with one polarity surrounded by a peripheral region responding with opposite polarity to light (de Monasterio & Gouras, 1975; Croner & Kaplan, 1995; Lee, Kremers, & Yeh, 1998).

Anatomically, there is a very consistent difference between M and P dendritic field sizes: the dendritic field diameters of M cells are about three times larger than P-cell dendritic-field diameters, dendritic fields of cells of both classes dramatically increase diameters from the fovea towards retinal periphery. For other mammalian ganglion cell classes, there is a certain ratio between receptive-field center sizes and dendritic field sizes (Peichl & Wässle, 1979) and it is expected that this rule also holds for M and P cells. Some authors have found a consistent difference between M and P receptive-field center sizes while others have found a considerable degree of scatter and overlap between the two (Silveira et al., 2005).

A similar disagreement between different studies is observed in published measurements for receptive field sizes of thalamic M and P neurons. A possible cause for this discrepancy is the difficulty to conduct accurate spatial measurements near to the fovea, once in this region the receptive fields are too small, especially for P cells. In this region of the macaque retina, the receptive field diameter amounts to about 0.15° and 0.06° for M and P cells, respectively. These values increase towards retinal periphery, M cells becoming consistently three times larger than P cells. These issues were recently reviewed elsewhere (Silveira et al., 2005).

Ganglion cell receptive-field spatial profile has been modeled using a number of circularly symmetrical functions such as Difference of Gaussians (Rodieck & Stone, 1965), Marr-Hildreth (Marr & Hildreth, 1980), and Gábor functions (Wang, et al., 1988; Wang, et al., 1993; Silveira, 1996; Silveira & de Mello Jr., 1998). In spite of their similarities, these functions occupy areas of very different size in the Fourier Space, in such a way that it would be of great advantage for the visual system if cell response adopts the form of a Gábor function. To date, there is no unambiguous demonstration of which functional form ganglion cell response mostly conforms to. Testing which function is the best descriptor of M and P cell receptive field profiles demands precise measurements of their response, especially when probing receptive field surrounds (Silveira & de Mello Jr., 1998).

A special feature of several retinal ganglion cell classes, including M and P cells, is that they come in two subclasses, the "on" and "off" cells, those that increase their firing rate when light is increased or decreased, respectively (Kuffler, 1953). The usual explanation for the existence of "on" and "off" cells is that this arrangement provides an extension of the dynamic range for contrast coding. Silveira and de

Mello Jr. (1998) proposed an alternative explanation. Their underlying assumption is that retinal mosaics perform a sort of mathematical expansion of visual stimuli. A Gábor expansion needs paired quadrature-phase receptive fields centered in the same visual field location (Marcelja, 1980; Kulikowski & Bishop, 1981). Function expansions of this sort, such as the Gábor expansion or the Fourier expansion, should be done using sine and cosine terms (phase quadrature pairs), or amplitude and phase terms, or in complex form. The simplest way to implement it in the visual system is to have pairs of receptive fields in phase quadrature such as sine and cosine for each spatial location. This kind of phase-quadrature receptive fields have been proven to exist in the neurons of the primary visual cortex (Pollen & Ronner, 1981). In the retina, there is an 180° phase difference between "on" and "off" pairs of M or P ganglion cells, which correspond to cosine and minus cosine Gábor functions. However, there is a certain offset between "on" and "off" mosaics in such a way that the resulting phase difference is much less than 180°. Silveira and de Mello Jr. (1998) estimated from M cell peripheral mosaics stained with the neurofibrillar method of Gros-Schultze that the mean distance between neighbor cells of opposite polarity corresponds to a spatial phase difference of 106°. Thus, higher level interaction between "on" and "off" subclasses of M cells may account for an approximate form of phase quadrature which is necessary for a full encoding of information presenting in the retinal image. Inspection of well labeled patches of P cells with Biocytin retrograde transport supports a similar conclusion for this cell class as well (Yamada et al., 1996).

Assuming that M and P cells are linear operators, their performance in the 2D spatial frequency domain will be inversely proportional to their performance in the 2D spatial domain. Thus, as P cells have receptive fields more restricted in space than M cells (see Figure 1A-B), they perform less precisely in the spatial frequency domain, responding to a larger spatial frequency band than M cells do (see Figure 1C-D). As a consequence of their symmetrical behavior in the domains of space and spatial frequency, and assuming that they are well described by similar functions such as Gábor functions, M and P cells have approximately the same joint entropy, occupying similar areas in the Fourier Space, however with very different trade-off between precision of spatial and spatial frequency (Silveira, 1996; Silveira & de Mello Jr., 1998).

Temporal response

M and P cells respond differently to the stimulus' temporal features. In fact, one of the first electrophysiological attempts to classify primate retinal ganglion cells was based on their response to temporal luminance steps (Gouras, 1968). Both M and P cells respond to luminance contrast, but they differ in their response time course. M cells discharge transiently to luminance step changes or luminance pulses and are called phasic or transient, while P cells exhibit more sustained discharges and are called tonic
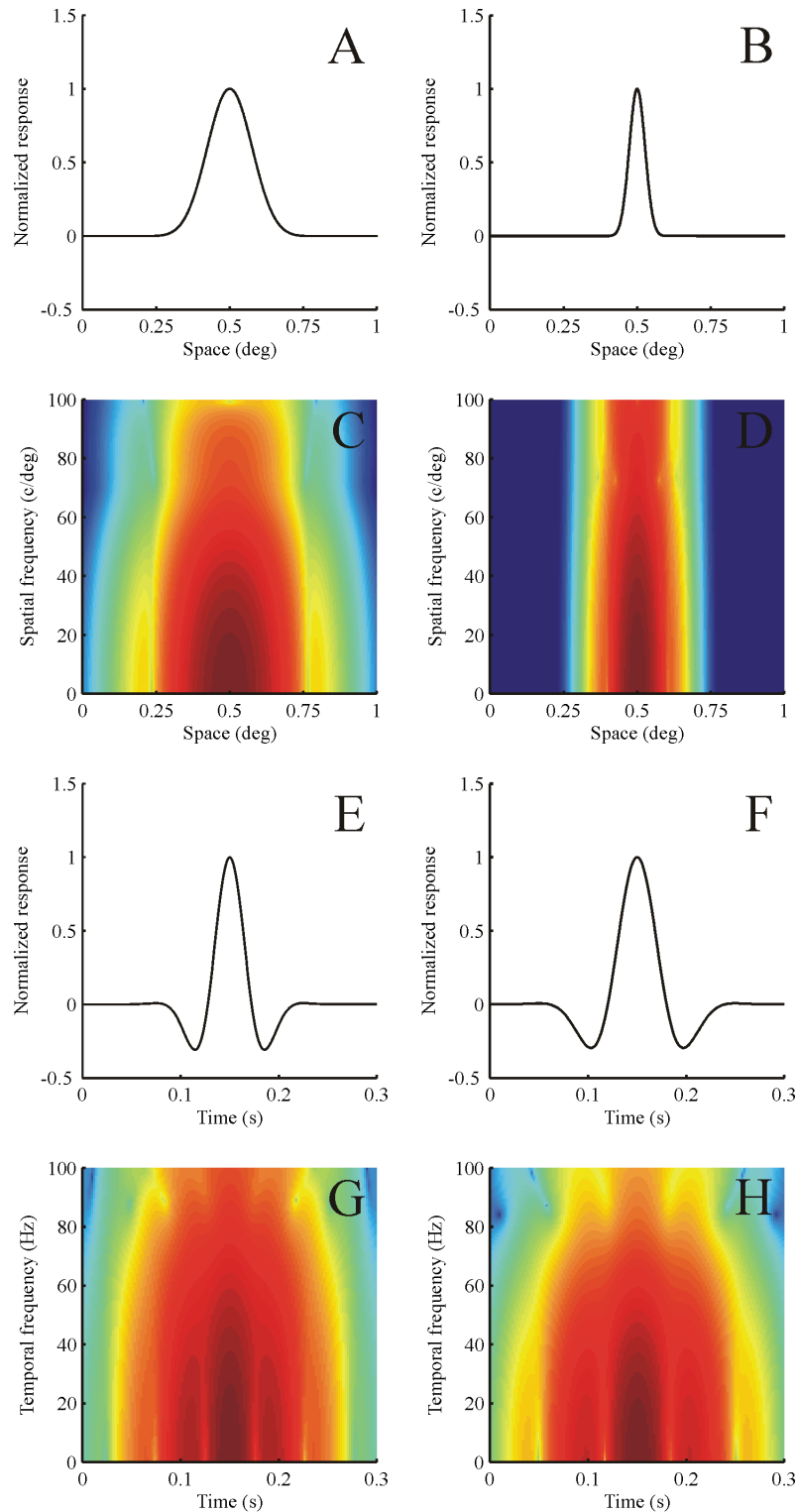
Figure 1. Visual response in the space, spatial frequency, time, and temporal frequency domains for an M cell located at 4° (left column) and a P cell located at 5° from the fovea centralis (right column). (A-B) Cell spatial impulse function. It can be represented by the receptive field profile, in this case modelled by a Gábor Function. (C-D) Cell spatial response in Fourier Space. (E-F) Cell temporal impulse function. (G-H) Cell temporal response in Fourier Space. In the spectrograms, cell's response energy ranged from low (bluish) to high (reddish) levels. M cells respond with higher precision than P cells in the spatial frequency and time domains, while P cells are more precise than M cells in the space and temporal frequency domains. The plots are normalized representations of cell responses calculated from published data on ganglion cell's temporal properties (Purpura et al., 1990) and spatial properties (de Monasterio & Gouras, 1975; Croner & Kaplan, 1995; for details, see Silveira & de Mello Jr., 1998). For the plots of Figures 1-3, the Levenberg-Marquardt method (Press, Teukolsky, Vetterling, & Flannery, 1992) was used to find Gabor functions that best matched spatial (Croner & Kaplan, 1995) and temporal (Purpura et al., 1990) data.
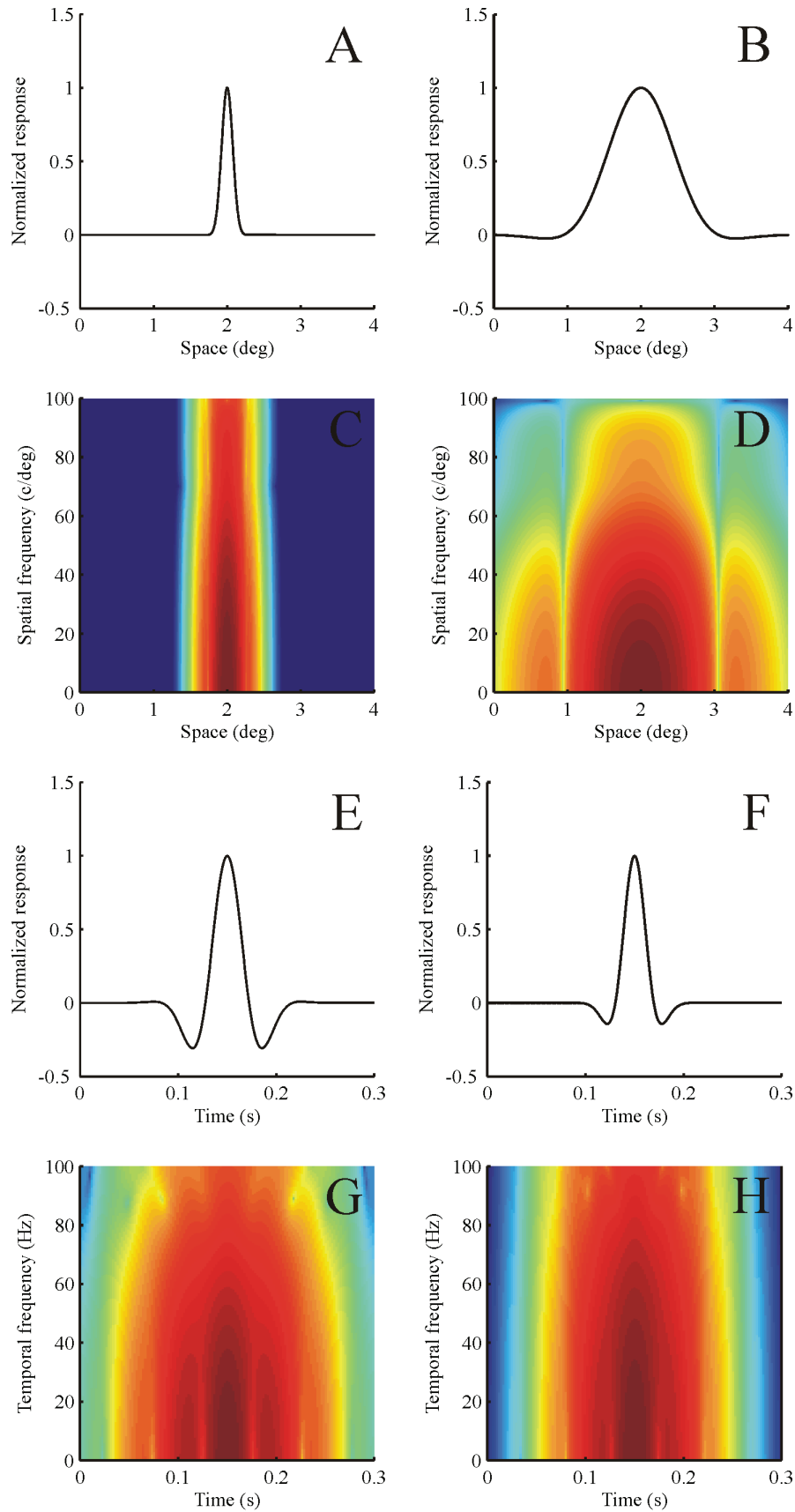
Figure 2. Visual response in the space, spatial frequency, time, and temporal frequency domains for an M cell located at 4° (left column) and another M cell located at 38° from the fovea centralis (right column) to illustrate the effect of retinal eccentricity. Central cells respond with higher precision than peripheral cells in the space and temporal frequency domains, while peripheral cells are more precise than central cells in the spatial frequency and time domains. Plots, conventions, and sources as in Figure 1.
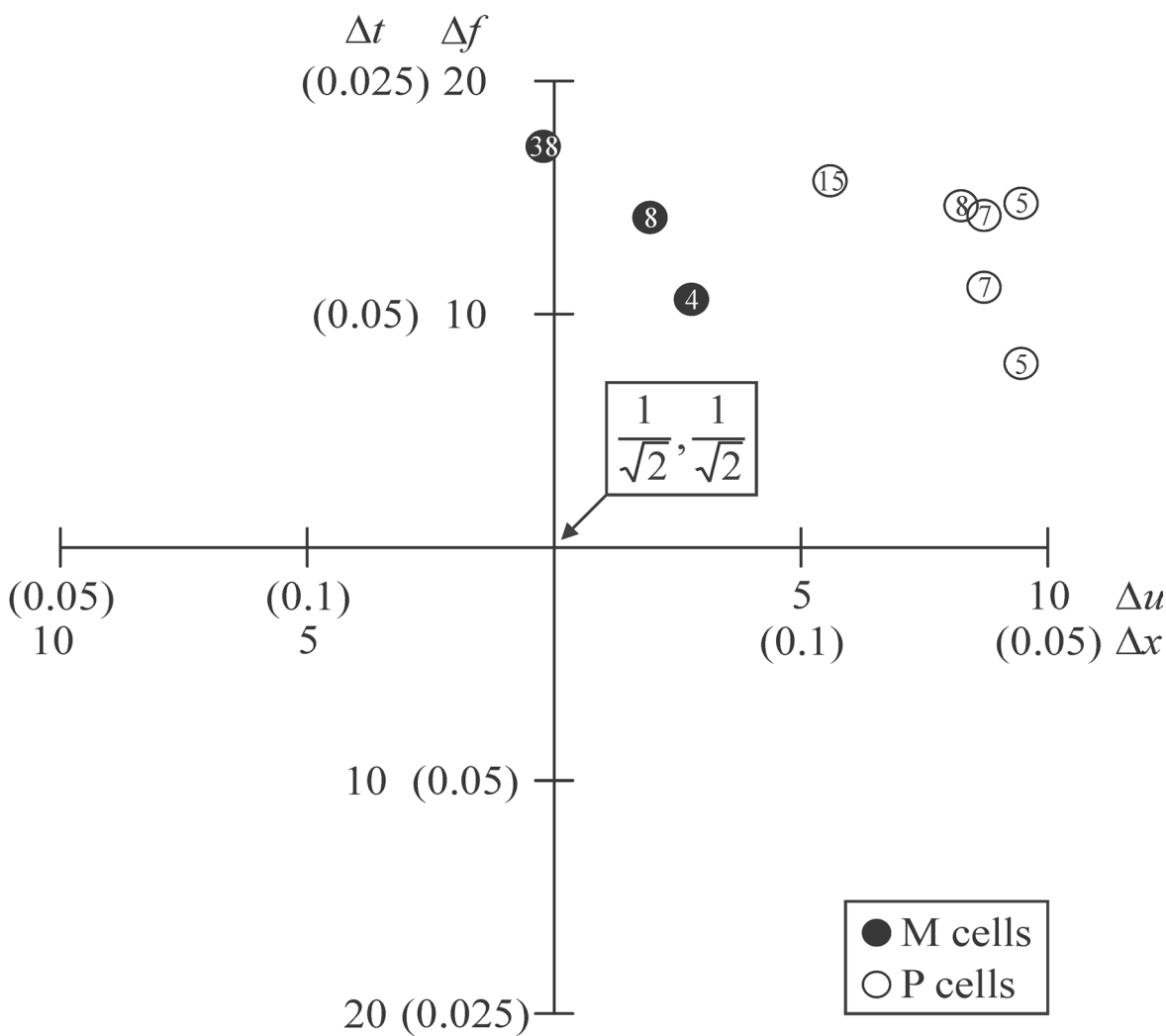
Figure 3. Spatiotemporal trade-off for M and P ganglion cells located at different retinal eccentricities. The entropy values for space (Δx), spatial frequency (Δu), time (Δt), and temporal frequency (Δf) for six P cells (empty circles) and three M cells (filled circles) were calculated from published data on ganglion cell's temporal properties (Gielen et al.; 1982; Purpura et al., 1990) and spatial properties (de Monasterio and Gouras, 1975; Croner and Kaplan, 1995; for details, see Silveira & de Mello Jr., 1998). With increasing eccentricity (in degrees, indicated for each data point) M and P cells increase their precision in the time and spatial frequency domains at expenses of precision in temporal frequency and space. Modified from Silveira and de Mello Jr. (1998).

or sustained (Gouras, 1968; Purpura, Kaplan, Tranchina, & Shapley, 1990; Lee, Pokorny, Smith, & Kremers, 1994).

To analyze the M and P cell temporal properties in a comparable way to the analysis of their spatial properties, it is necessary to measure their temporal impulse functions. The superposition principle allows one to obtain cell impulse functions in the time domain from their response to steps or pulses. M and P cell impulse functions in the time domain can also be obtained by a Fourier transform of M and P responses to sinusoidal luminance temporal modulation.

Data comparing M and P cells located in the same visual field regions are limited, but they suggest that M cells have more localized temporal impulse functions than P cells for achromatic stimuli (Gouras, 1968; Purpura, Kaplan, Tranchina, & Shapley, 1990; Lee,

Pokorny, Smith, & Kremers, 1994; Kremers, 1999; Kremers, Weiss, & Silveira, 2004). Thus, M cells seem to have the necessary machinery to signal with a higher degree of precision an event occurrence when compared with P cells (see Figure 1E-F). Sinusoidal temporal modulations have been used to measure the frequency response of M and P cells to luminance contrast at both retinal and thalamic levels. M cell response is more restricted than P cell response in the time domain. Consequently, an inverse relation in the temporal frequency domain is expected, assuming that these two cell classes respond linearly in the input range considered. In general terms, this is what has been found: M cell response covers a larger temporal frequency range than P cell response, having a higher

frequency peak and a higher cut-off frequency than P cells (see Figure 1G-H). The temporal properties of M and P cells have recently been elsewhere reviewed (Silveira et al., 2004, 2005).

Effects of eccentricity and retinal illuminance

In primates, several aspects of retinal organization change dramatically with distance from the fovea, following the steep cone density decrease. Thus, the study of several morphological and physiological aspects of neurons of the visual system only makes sense when performed as a function of retinal eccentricity. Until recently there was no systematic account of how visual field eccentricity affects M and P temporal properties, both in the time domain and the temporal frequency domain. However, as the spatial

properties of such cells change dramatically with eccentricity, and taking in consideration the trade-off between spatial and temporal precision as well as time and temporal frequency precision that the visual system must accomplish to perform different behavioral tasks, it has been predicted that M and P cell temporal properties should similarly change with eccentricity (Silveira, 1996; Silveira & de Mello Jr., 1998). Quite recently, a growing amount of evidence has been accumulated supporting such prediction (Kremers, Silveira, & Kilavik, 2001; Solomon, Martin, White, Rüttiger, & Lee, 2002; Solomon, Lee, White, Rüttiger, & Martin, 2005; Kilavik, Silveira, & Kremers, 2003). In general, as eccentricity increases, both M and P cell responses become less localized in space and temporal frequency, and more localized in spatial frequency and time (see Figures 2 & 3) (Silveira, 1996; Silveira & de Mello Jr., 1998).
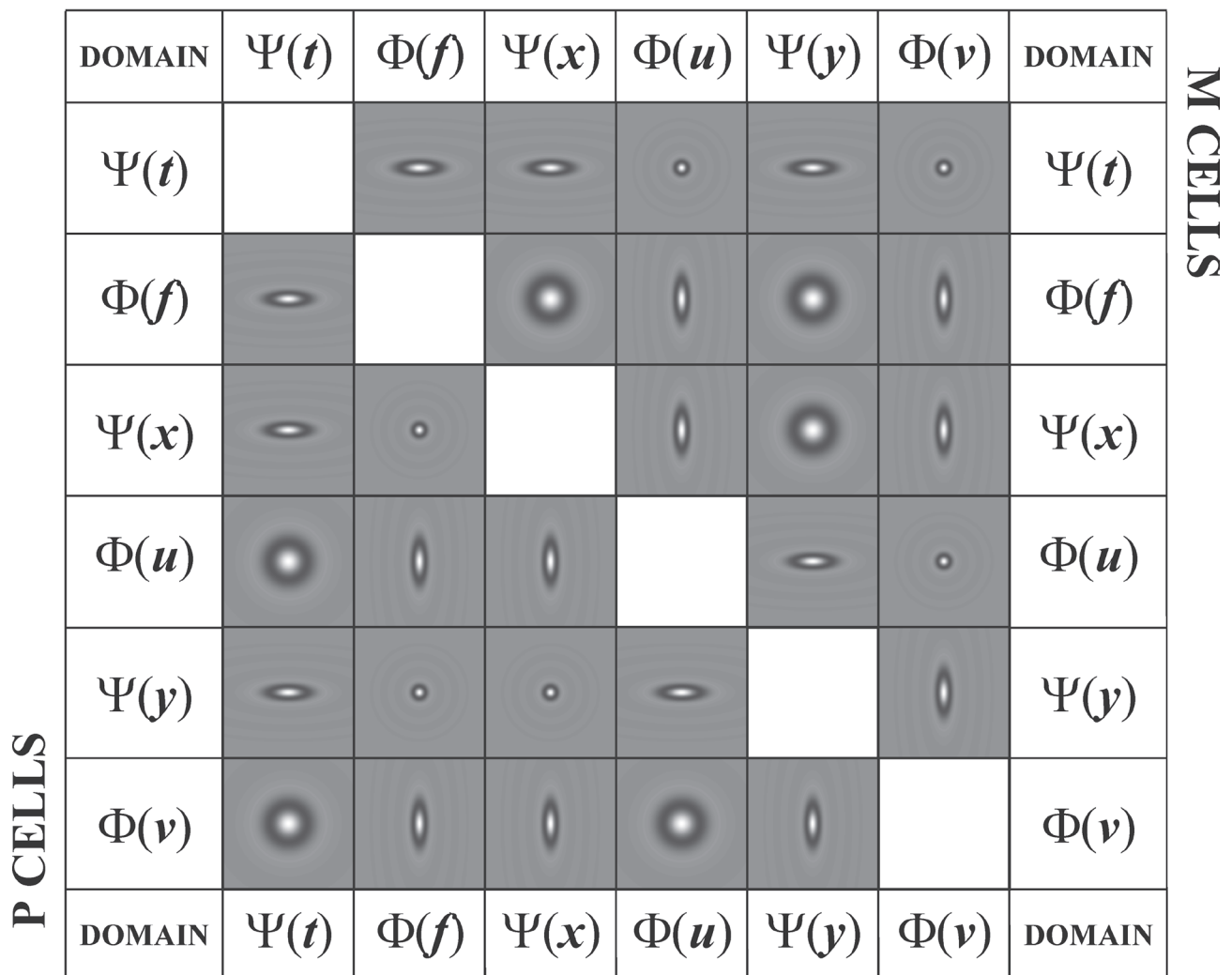

Figure 4. Schematic representation of M and P cell responses in the Fourier Space. The actual cell amplitude response is a hypervolume that can be represented as a function of the three space-time dimensions – time and two dimensions of space – and their Fourier transforms. In the figure, the M and P cell responses are represented by their orthogonal two-dimensional projections. It is assumed, based on measurements of spatial properties (receptive field sizes: de Monasterio & Gouras, 1975; Croner & Kaplan, 1995), that M and P cell responses spread in each domain in a three-fold difference basis

6D JOINT ENTROPY

Figure 5. Schematic representation of M and P cell precisions in Fourier Space. The actual cell 6D joint entropy is a hypervolume, but it can be visualized by the means of its orthogonal two-dimensional projections. M and P cells differ by a three-fold difference in their receptive field sizes all across the retina (de Monasterio & Gouras, 1975; Croner & Kaplan, 1995; Silveira & de Mello Jr., 1998). For linear systems this implies a similar three-fold difference in the spread of their spatial frequency tuning curves. Finally, it is assumed in this schematic representation that M and P cell joint entropies also differ by a three-fold difference in the remaining dimensions, time and temporal frequency. The matrix representation makes easier to understand that the M pathway works with high precision in the domains of time and spatial frequency, while the P pathway do the same in the domains of space and temporal frequency. Modified from Silveira (1996) and Silveira and de Mello Jr. (1998).

Another condition that affects retinal ganglion cell physiological properties is light adaptation. The scarce information available indicates that when retinal illumination decreases, M and P cell responses become less localized in space and temporal frequency, and more localized in spatial frequency and time, changes that are similar to the effect of increasing eccentricity (Silveira & de Mello Jr., 1998).

Conclusion: the M And P pathways and the cortical streams of visual information

As presented in the previous sections, the M and P cell responses are 3D functions and have 3D spectral transforms (Figure 4). Consequently, the joint entropies for M and P cells are 6D hypervolumes that can be represented in a 6D Fourier Space (see Figure 5). Each projection of these hypervolumes in any of the coordinate axes reflects the 1D uncertainty in that particular domain. Orthogonal two-dimensional projections of M and P joint entropy hypervolumes have been previously presented, assuming a three-fold difference in each dimension (Silveira, 1996; Silveira & de Mello Jr., 1998). The analysis of these projections reveals that the M pathway sends highly precise information to the visual cortex concerning time of occurrence and spatial frequency content of visual patterns, while the P pathway does the same concerning the spatial location and temporal frequency content of visual patterns (see Figures 4 & 5).

The visual coding required for perception of objects, motor planning, and motor control will vary with the function performed (i.e. no single brain representation of the space-time fulfill all requirements). For instance, good spatial frequency discrimination can be critically important for some tasks such as recognition of a tree by its foliage, or precise representation of spatial coordinates might be essential to reach and grasp an object. Thus, to build a representation of the visual world adequate to the task to be performed is essential to perception and action (Milner & Goodale, 1995) or planning and control of action (Glover, 2004). This cannot be done by using a single retinal ganglion cell class to convey the information from the photoreceptor array to the visual cortex, because each retinal ganglion cell class is bound to a particular joint entropy combination. Having two or more cell classes such as the M and P cells, and perhaps one or two K cell classes, each one performing the analysis of the visual environment with a particular 6D trade-off, may optimize a solution for this problem. What is needed is to use their output in different ways according to the task to be performed. The right place to put together the information arising from different retino-geniculo-cortical pathways is the multilayered structure of V1. The information may be combined in V1 and sent to the different cortical streams as required to build visual representations for perception and action, each one with a trade-off in the information space which is optimal for each task.

A necessary step for a comparison between subcortical and cortical cells along the retino-geniculo-cortical pathways and further down along the dorsal and temporal cortical streams of information is a complete characterization of the joint entropies of these pathways. Ideally, independent measurements of (a) spatial impulse function (receptive field profile), (b) spatial frequency response, (c) temporal impulse function, and (d) temporal frequency response for a series of M and P retinal and thalamic neurons at a range of eccentricities are needed, as well as for a series of cortical cells that receive the output of the M and P channels. This is scarcely available at the moment. To plot joint entropy values for the nine cells of Figure 3 we had to make heroic efforts, searching for published data and asking for complementary information from authors. In the cat, the work of Palmer and colleagues suggested that cortical cells response is more precise than predicted by the linear combination of α and β cell responses (Palmer, Jones, & Stepnoski, 1991). As far as this review of the literature goes, similar data is not available for primates. It is a definite goal of our laboratory to collect this kind of data from different primates in the near future.

Acknowledgments

References

Croner, L.J., & Kaplan, E. (1995). Receptive fields of P and M ganglion cells across the primate retina. *Vision Research, 35,* 7-24.

Daugman, J.G. (1980). Two-dimensional spectral analysis of cortical receptive field profiles. *Vision Research, 20,* 847-856.

Daugman, J.G. (1983). Six formal properties of two-dimensional anisotropic visual filters: structural principles and frequency / orientation selectivity. *IEEE Transactions on Systems, Man, and Cybernetics, 13,* 882-887.

Daugman, J.G. (1984). Spatial visual channels in the Fourier plane. *Vision Research, 24,* 891-910.

Daugman, J.G. (1985). Uncertainty relation for resolution in space, spatial frequency, and orientation optimized by two-dimensional visual cortical filters. *Journal of the Optical Society of America A, 2,* 1160-1169.

Daugman, J.G. (1989). Entropy reduction and decorrelation in visual coding by oriented neural receptive fields. *IEEE Transactions on Biomedical Engineering, 36,* 107-114.

de Lima, S.M.A., Silveira, L.C.L., & Perry, V.H. (1996). Distribution of M retinal ganglion cells in diurnal and nocturnal New-World monkeys. *Journal of Comparative Neurology, 368*, 538-552.

de Monasterio, F.M., & Gouras, P. (1975). Functional properties of ganglion cells of the rhesus monkey retina. *Journal of Physiology (London), 251,* 167-195.

Gábor, D. (1946). Theory of communication. *Journal of the Institute of Electrical Engineering, 93,* 429-457.

Gábor, D. (1992). Holography, 1948-1971. Nobel Lecture, December 11, 1971. In S. Lundqvist (Ed.) *Nobel Lectures, Physics 1971-1980.* Singapore: World Scientific Publishing.

Gielen, C.C.A.M., van Gisbergen, J.A.M., & Vendrik, A.J.H. (1982). Reconstruction of cone-system contributions to responses of colour-opponent neurones in monkey lateral geniculate. *Biological Cybernetics, 44*, 211-221.

Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences, 27,* 3-78.

Gouras, P. (1968) Identification of cone mechanisms in monkey ganglion cells. *Journal of Physiology (London), 199,* 533-547.

Hartley, R.V. (1928). Transmission of information. *Bell Systems Technology Journal, 7,* 535-563.

Kilavik, B.E., Silveira, L.C.L., & Kremers, J. (2003). Centre and surround responses of marmoset lateral geniculate neurones at different temporal frequencies. *Journal of Physiology (London), 546,* 903-919.

Kremers, J. (1999). Spatial and temporal response properties of the major retino-geniculate pathways of Old and New World monkeys. *Documenta Ophthalmologica, 95,* 229-245.

Kremers, J., Silveira, L.C.L., & Kilavik, B.E. (2001). Influence of contrast on the responses of marmoset lateral geniculate cells to drifting gratings. *Journal of Neurophysiology, 85,* 235-246.

Kremers, J., Silveira, L.C.L., Yamada, E.S., & Lee, B.B. (1999). The ecology and evolution of primate colour vision. In K.R. Gegenfurtner & L.T. Sharpe (Eds.), *Color Vision: From Molecular Genetics to Perception* (pp. 123-142). Cambridge: Cambridge University Press.

Kremers, J., Weiss, S., & Silveira, L.C.L. (2004). Spatiotemporal properties of the magno and parvocellular neurones of the lateral geniculate nucleus of the marmoset (*Callithrix jacchus*). *Neurociências, 1,* 138-149.

Kuffler, S. (1953). Discharge patterns and functional organization of the mammalian retina. *Journal of Neurophysiology, 16,* 37–68.

Kulikowski, J.J., & Bishop, P.O. (1981). Fourier analysis and spatial representation in the visual cortex. *Experientia, 37,* 160-163.

Kulikowski, J.J., Marcelja, S., & Bishop, P.O. (1982). Theory of spatial position and spatial frequency relations in the receptive

fields of simple cells in the cat's striate cortex. *Biological Cybernetics, 43,* 187-198.

Lee, B.B., Pokorny, J., Smith, V.C., & Kremers, J. (1994). Responses to pulses and sinusoids in macaque ganglion cells. *Vision Research, 34,* 3081-3096.

Lee, B.B., Kremers, J., & Yeh, T. (1998). Receptive fields of primate retinal ganglion cells studied with a novel technique. *Visual Neuroscience, 15,* 161-175.

Marcelja, S. (1980). Mathematical description of the responses of simple cortical cells. *Journal of the Optical Society of America, 70,* 1297-1300.

Marr, D., & Hildreth, E. (1980). Theory of edge detection. *Philosophical Transaction of the Royal Society of London B, 207,* 187-217.

Milner, A.D., & Goodale, M.A. (1995). *The Visual Brain in Action.* Oxford: Oxford University Press.

Mollon, J.D., & Jordan, G. (1988). Eine Evolutionäre Interpretation des Menschlichen Farbensehens. *Die Farbe, 35,* 139-170.

Palmer, L.A., Jones, J.P., & Stepnoski, R.A. (1991). Striate receptive fields as linear filters: characterization in two dimensions of space. In A.G. Leventhal (Ed.), H.R. Cronly-Dillon (Ser. Ed.), *Visual and Visual Dysfunction, Vol. 4 The Neural Basis of Visual Function* (pp. 246-265). Houndmills, England: Macmillan Press.

Peichl, L., & Wässle, H. (1979). Size, scatter and coverage of ganglion cell receptive field centres in the cat retina. *Journal of Physiology (London), 291,* 117-141.

Pollen, D.A., & Ronner, S.F. (1981). Phase relationships between adjacent simple cells in the visual cortex. *Science, 212,* 1409-1411.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., & Flannery, B.P. (1992). *Numerical recipes in C - The art of scientific computing.* Second Edition. Cambridge, England: Cambridge University Press.

Purpura, K., Kaplan, E., Tranchina, D., & Shapley, R.M. (1990). Light adaptation in the primate retina: analysis of changes in gain and dynamics of monkey retinal ganglion cells. *Visual Neuroscience, 4,* 75-93.

Rodieck, R.W., & Stone, J. (1965). Analysis of receptive fields of cat retinal ganglion cells. *Journal of Neurophysiology, 28,* 833-849.

Silveira, L.C.L. (1996). Joint entropy loci of M and P cells: a hypothesis for parallel processing in the primate visual system. *Revista Brasileira de Biologia, 56,* 345-367.

Silveira, L.C.L. (2004). Parallel visual pathways from the retina to the visual cortex – how do they fit? *Behavioral and Brain Sciences, 27,* 50-51.

Silveira, L.C.L., & de Mello Jr., H.D. (1998). Parallel pathways of the primate vision: sampling of the information in the Fourier space by M and P cells. In L.M. Chalupa & B.L. Finlay (Eds.), *Development and Organization of the Retina: From Molecules to Function* (pp. 173-199). New York: Plenum Press.

Silveira, L.C.L., Grünert, U., Kremers, J., Lee, B.B., & Martin, P.R. (2005). Comparative anatomy and physiology of the primate retina. In: J. Kremers, J. (Ed.) *Structure, Function, and Evolution of the Primate Visual System* (pp. 127-160). Chichester, England: John Wiley & Sons.

Silveira, L.C.L., Saito, C.A., Lee, B.B., Kremers, J., da Silva Filho, M., Kilavik, B.E., Yamada, E.S., & Perry, V.H. (2004). Morphology and physiology of primate M and P cells. *Progress in Brain Research,* 144, 21-46.

Silveira, L.C.L., Yamada, E.S., Perry, V.H., & Picanço-Diniz, C.W. (1994). M and P retinal ganglion cells of diurnal and nocturnal New-World monkeys. *NeuroReport, 5,* 2077-2081.

Solomon, S.G, Lee, B.B., White, A.J.R., Rüttiger, L., & Martin, P. R. (2005). Chromatic organization of ganglion cell receptive field in the peripheral retina. *Journal of Neuroscience, 25,* 4527-4539.

Solomon, S.G., Martin, P.R., White, A.J.R., Rüttiger, L., & Lee, B.B. (2002). Modulation sensitivity of ganglion cells in peripheral retina of macaque. *Vision Research, 42,* 2893-2898.

Wang, Y., Qi, X., Jing, X., & Yu, D. (1988). Extended Gabor function model and simulation of some characteristic curves of receptive field. *Scientia Sinica B, 31,* 1185-1194.

Wang, Y., Qi, X., Yao, G., & Wang, M. (1993). Neural wave representation in early vision. *Science in China B, 36,* 677-684.

Yamada, E.S., Silveira, L.C.L., & Perry (1996). Morphology, dendritic field size, somal size, density and coverage of M and P retinal ganglion cells of dichromatic *Cebus* monkeys. *Visual Neuroscience, 13,* 1011-1029.

Yamada, E.S., Silveira, L.C.L., Perry, V.H., & Franco, E.C.S. (2001). Morphology and dendritic field size of M and P retinal ganglion cells of the owl monkey. *Vision Research, 41,* 119-131.s