The Morphology of Alpha Ganglion Cells in Mammalian Species: a Fractal Analysis Study

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Abstract: Fractal analysis has already found widespread application in the field of neuroscience and is being used in many other areas. In this study we applied fractal analysis on two dimensional images of the α retinal ganglion cells from various species, in order to investigate the morphology of these cells and to test whether there are differences in alpha cell morphology between the species. The binary and skeletonised fractal dimension (D_{bin} and D_{skel}) were calculated for alpha retinal ganglion cells of wild and domestic animals. The aim was to determine whether the complexity of the branching pattern, which reflects the cell's function is reflected in the animal's ecology. The highest mean D_{bin} was obtained for the guanaco and Niglau antilope, while the smallest mean value was found for the ferret. On the other hand, the highest and smallest mean D_{skel} was found for the chinchilla and ferret, respectively. For the domestic animals the highest mean D_{bin} was obtained for the Guinea pig, dog and ox, while the smallest mean was found in the pig. As for the mean D_{skel}, the highest and smallest value was found for the dog and pig, respectively. The results showed that the fractal dimension represents a parameter which is of relevance for inter-species comparisons of retinal ganglion cell populations.

Keywords: Alpha retinal cells, Box-Counting method, Dendritic branching, Fractal analysis, Medical imaging, Space-filling.

1. INTRODUCTION

One of the basic principles of neurobiology holds that the function of a nerve cell is largely dependent on its structure. To understand how a neuron integrates its numerous synaptic inputs to generate an appropriate response, a complete understanding of the cell's morphology and geometry is required (Fernández and Jelinek 2001). Therefore, many quantitative parameters have been used to characterize the morphology of nerve cells. The simple models that have been used for shapes, such as spheres, ellipsoids and polyhedral, and their corresponding two-dimensional profiles, are useful for many purposes, but certainly fall short in dealing with neuronal complexity.

A new approach to this problem requires us to think about the concepts of fractal geometry. Since Mandelbrot (1983) defined the term fractal, the field of fractal geometry has enjoyed an enormous surge of popularity. The key observation is that structures growing according to stochastic processes are not really as disordered as they seem at first glance (Mandelbrot 1983). A nontrivial, scale invariant symmetry over several orders of magnitude has been found to be a typical principle of order for such growth processes, which can be quantified by the fractal dimension.

From the results and conclusions of previous research it has been shown that the concepts of fractal geometry and the use of the notion of a fractal dimension are helpful analytical tools for quantitative studies of the morphology of individual nerve cells (Smith et al. 1996). As for the morphology of two dimensional neuronal images, the fractal dimension is used to quantify the complexity of the borders of a neuron (Milošević and Ristanović 2006) or to measure how completely the branches of a neuron fill its dendritic field (Jelinek and Fernández 1998). The branching pattern of dendrites also reflects how the neuron integrates information (Koch, 1999) and is thus related to the ecology of the species (Peichl et al., 1987; Peichl, 1991).

Fractal analysis has been applied to retinal ganglion cells (RGCs) in order to discriminate among different types of neurons within a species (Morigiwa et al. 1989; Jelinek and Spence 1997; Jelinek and Fernández 1998) and to investigate classification schemes of these cells (Jelinek 1996; Jelinek et al. 2008). No study has been performed previously, at least to our knowledge, where the same type of RGCs from different species, was compared using this technique.

Therefore, the aim of the present study was to perform fractal analysis on two dimensional images of the alpha RGCs, investigating their space-filling property and straightness of the dendritic branching in order to determine consistency of dendritic pattern across eleven mammalian species. Starting from the observation by Peichl that the morphology of alpha RGCs and many of their quantitative features, are conserved in mammals coming from different habitats and having a wide variety of behaviors (Peichl et al, 1987; Peichl, 1991), we divided our sample into two groups (the wild and domestic animals) and investigated whether there are common or different morphological properties for the same

type of RGCs among the species belonging to either the 'wild' or 'domestic' group.

2. MATERIALS AND METHODS

One hundred and fifteen two-dimensional images of the α cells from eleven species were obtained using the histological procedure as described in Peichl (1989). In brief, each animal was deeply anaesthetized and the eyes enucleated. The dendritic tree morphology of the RGCs were visualised using intracellularly injected Lucifer Yellow. All cells were drawn using camera lucida projection, as seen in a wholemount preparation.

The camera lucida drawings were scanned into the computer using a scanner at 600 dpi for fractal analysis. The box-counting method was used for this analysis as it has been previously shown to be robust for neurons (Jelinek et al. 2008) and is incorporated into the public domain Image J software (http://rsb.info.nih.gov/ij/). When the box-counting method is applied to 2D neuronal images, the outcome (i.e. the fractal dimension) depends on image presentation. While the fractal dimension of binary images (silhouettes) defines the space-filling property, the same parameter for skeletonised images summarizes the straightness of the dendritic branching pattern (Smith Jr et al., 1989; Smith Jr et al., 1996; Jelinek and Fernández, 1998; Fernández and Jelinek 2001).

The box-counting method covers the image with sets of squares. Each set is characterised by the box size r of the square edge. Box sizes were taken from 1 to 1024 pixels (or 2048 pixels, when possible) as a power of 2. The number of squares $N(r)$ necessary to cover the object is presented as a function of r. The fractal dimension (D) is determined from the slope S of log $N(r)$/log r, as its absolute value (Milošević and Ristanović, 2006; Milošević et al, 2007; Jelinek et al. 2008). The fractal dimension for the binary (D_{bin}) and skeletonised (D_{skel}) image was obtained as an absolute value of the (negative) slope of the log-log relationship between $N(r)$ and r (Figs. 1A and 1B). In all cases the correlation coefficient (R) of the straight line, fitted through 11 data points, was higher than 0.995. Statistical evaluation of the correlation coefficient showed that it was different from zero with a very high significance ($p < 0.001$), proving the existence of the linear relationship between log N and log r on more than two decades of the range (Fig. 1A and 1B).

Fractal analysis was initially performed on each binary image (Fig. 2A), calculating the fractal dimension D_{bin}. Then, the cell body was removed digitally and the remaining dendritic tree skeletonised (using the same software), reducing dendritic width to a single pixel (Fig. 2B). The skeletonised image was processed by the box-counting method again, and the fractal dimension D_{skel} was obtained. One-way ANOVA and Schéffe post hoc test or Student t-test were used for statistical analysis and statistical significance defined as $p < 0.05$ (Alder and Roessler, 1972).

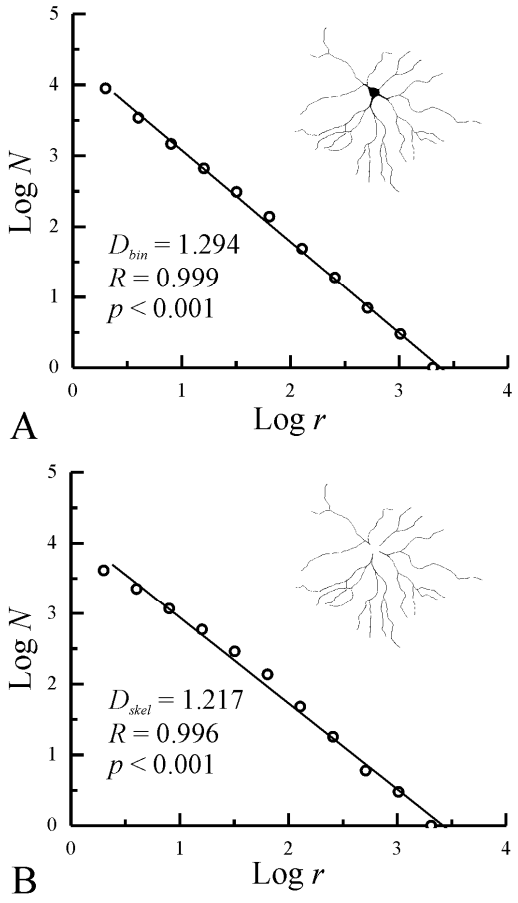

Fig. 1. Log-log plot of the relationship between N and r for the binary (A) and skeletonised neuronal image (B). The fractal dimension D is the negative value of the slope of the fitted line (in this case 1.294 and 1.217 respectively). The correlation coefficient R of the straight line fitting the data points is inscribed into the plot.

3. RESULTS

The two fractal dimensions (D_{bin} and D_{skel}) describe the two different morphological properties of 2D neuronal images (see Methods section). The frequency polygons of D_{bin} and D_{skel} for all alpha RGCs considered are depicted in Fig. 3.

These indicate that both distributions are normal. Therefore, the central tendency and dispersion measure of D_{bin} and D_{skel} in each of the eleven species were expressed by the mean and standard error.

3.1 The group of wild animals

As the next step in our investigation, we analyzed two fractal dimensions (D_{bin} and D_{skel}) between species, which belonged to the group of wild animals. Their means and corresponding standard errors are shown in Tab. 1.

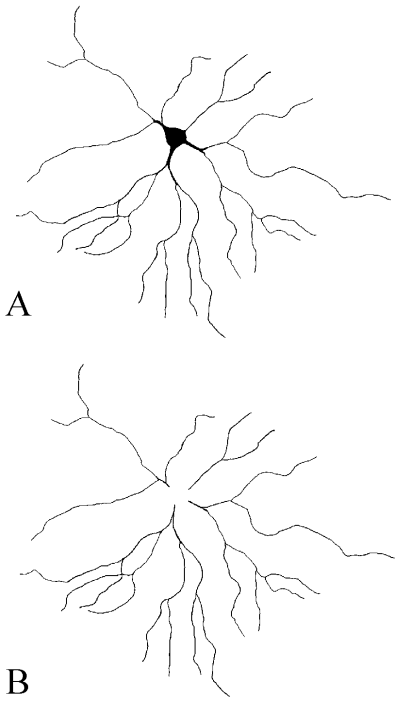

Fig. 2. Image representation for analysis of the alpha retinal ganglion cells: binary (A) and skeletonised (B) image. (Dendrites on skeletonised image are reduced only to 3 pixel width in order to clearly show this type of image.)

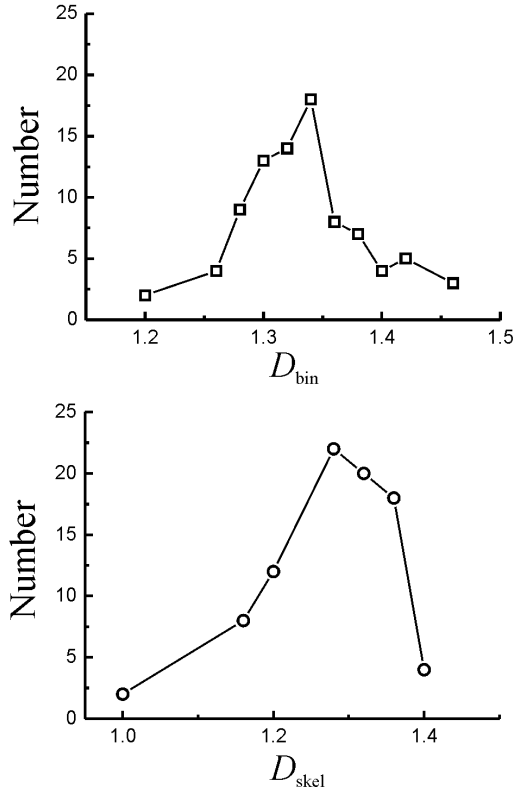

Fig. 3. Frequency polygons of the fractal dimension of the alpha RGCs cells in eleven species.

Table 1. The values of the fractal dimension D_{bin} and D_{skel} for the alpha RGCs of six species, which belonged to the group of wild animals. Each value is shown as the mean ± standard error.

Species	D_{bin}	D_{skel}
Chinchilla	1.349 ± 0.008	1.27 ± 0.01
Rat	1.354 ± 0.008	1.251 ± 0.006
Ferret	1.29 ± 0.01	1.19 ± 0.01
Guanaco	1.377 ± 0.005	1.211 ± 0.009
Niglau antilope	1.36 ± 0.01	1.205 ± 0.007
Reindeer	1.378 ± 0.008	1.222 ± 0.008

From this table it can be seen that the highest mean D_{bin} was obtained for the guanaco and Niglau antilope, while the smallest mean value was found for the ferret. On the other hand, the highest and smallest mean D_{skel} was found for the chinchilla and ferret, respectively (Tab. 1).

Table 2. Distributions of D_{bin} and D_{skel} over pairs of samples tested for significance (CH – chinchilla, R – rat, F – ferret, G – Guanaco, NA – Niglau antilope and RD – reindeer).

Pairs	D_{bin}	D_{skel}
CH - R	/	/
CH - F	***	**
CH - G	*	**
CH - NA	/	***
CH - RD	*	*
R - F	***	***
R - G	/	***
R - NA	/	***
R - RD	*	***
F - G	***	/
F - NA	***	/
F - RD	***	/
G - NA	/	/
G - RD	/	/
NA -RD	/	/

* - $p < 0.05$, ** - $p < 0.01$, *** $p < 0.001$ and / - no significance

In order to explore whether there were significant differences in the mean D_{bin} and D_{skel} among six species in the group of wild animals, a one-way ANOVA was used. In both cases the calculated F value (13.679 for D_{bin} and 8.766 for D_{skel}) was significantly different than the critical value (3.510), at a confidence level $p < 0.01$. To assess how many pairs of means D_{bin} and D_{skel} were significantly different, a Schéffe post hoc test was used. As can be seen from Tab. 2, the mean D_{bin} of the ferret is significantly different from all other species ($p < 0.001$). A significant difference between the mean D_{bin} was found between three other pairs: chinchilla-guanaco, chinchilla-reindeer and rat-reindeer ($p < 0.05$). The mean D_{skel} of both the chinchilla and rat is statistically significantly different from all other species, except that it does not include a statistically significant difference between the rat and chinchilla (Tab. 2).

3.2 The group of domestic animals

Table 3 shows the means D_{bin} and D_{skel}, and their corresponding standard errors, of the five species that belong to the group of domestic animals. In this group of species, the highest mean D_{bin} was obtained for the Guinea pig, dog and ox, while the smallest mean was found in the pig (Tab. 3). As for the mean D_{skel}, the highest and smallest value was found for the dog and pig, respectively (Tab. 1).

Table 3. The values of the fractal dimension D_{bin} and D_{skel} for the alpha RGCs of five species of domestic animals. Each value is shown as the mean ± standard error.

Species	D_{bin}	D_{skel}
Guinea pig	1.35 ± 0.01	1.22 ± 0.01
Dog	1.35 ± 0.01	1.28 ± 0.01
Cat	1.331 ± 0.008	1.228 ± 0.007
Pig	1.329 ± 0.007	1.202 ± 0.006
Ox	1.35 ± 0.01	1.23 ± 0.01

When a one-way ANOVA for the mean D_{bin} and D_{skel} of these species was performed, only the calculated F value of D_{skel} (9.968) was significantly different then the critical value ($p < 0.01$). Application of Schéffe post hoc test (Tab. 4) pointed out that the mean D_{skel} of the dog differed significantly from all other species (Tab. 4). A significant difference was found between two more pairs: cat-pig and pig-ox (Tab. 4).

Table 4. Distributions of D_{bin} and D_{skel} over pairs of samples tested for significance (GP – Guinea pig, D – dog, C – cat, P – pig and O – ox).

Pairs	D_{bin}	D_{skel}
GP - D	/	***
GP - C	/	/
GP - P	/	/
GP - O	/	/
D - C	/	**
D - P	/	***
D - O	/	**
C - P	/	**
C - O	/	
P - O	/	*

3.3 Wild vs. domestic animals

The means D_{bin} and D_{skel} for both wild and domestic mammalian species, and their standard errors, are illustrated in Fig. 4. This figure indicates clearly that the mean D_{bin} of both wild and domestic species is always higher than corresponding means for D_{skel} and moreover these mean values are significantly different ($p < 0.001$). The t-test indicated that there was no significant difference in mean D_{bin} between wild and domestic animals. The same result was obtained for the mean D_{skel}.

As the next step in our analysis, we examined all possible pairs of means D_{bin} and D_{skel} between wild and domestic species by t-test. The results of this analysis are presented in Tab. 5. From thirty possible pairs of means we found that the means of fifteen pairs of D_{bin} and the means of sixteen pairs of D_{skel} were significantly different.

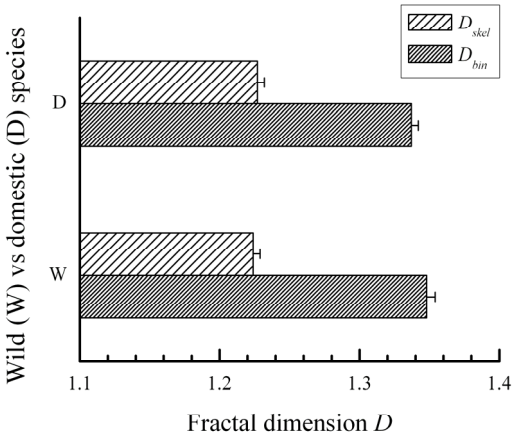

Fig. 4. Mean fractal dimensions of binary (D_{bin}) and skeletonised (D_{skel}) images of the alpha RGCs in wild and domestic mammalian species.

Table 5. Distributions of D_{bin} and D_{skel} over pair of samples, tested for significance, between wild and domestic species.

Pairs	D_{bin}	D_{skel}
CH - GP	/	**
CH - D	/	/
CH - C	/	*
CH - P	/	***
CH - O	/	*
R - GP	/	***
R - D	/	**
R - C	/	*
R - P	*	***
R - O	/	*
F - GP	***	/
F - D	**	***
F - C	*	*
F - P	**	/
F - O	***	/
G - GP	*	/
G - D	/	**
G - C	*	/
G - P	**	/
G - O	*	/
NA - GP	/	/
NA - D	/	***
NA - C	/	*
NA - P	*	/
NA - O	/	/
RD - GP	*	/
RD - D	/	**
RD - C	*	/
RD - P	***	*
RD - O	*	/

As can be seen from Tab. 5, the mean D_{bin} of the ferret is significantly different from all domestic species. Almost the same result was achieved for the guanaco and the reindeer, except that it does not include a statistically significant difference between the guanaco and the dog, as well as between the reindeer and the dog. After these three species, a significantly different mean D_{bin} was found between two more pairs: rat-pig and Niglau antilope-pig (Tab. 5).

On the other hand, the mean D_{skel} of the rat is statistically different from all domestic species. A similar result was obtained for the chinchilla, except that it does not include a statistically significant difference between the chinchilla and the dog (Tab. 5). When the mean D_{skel} of the ferret, Niglau antilope and reindeer was compared with these means of five domestic species, two pairs of means were significantly different: ferret-dog, ferret-cat, Niglau antilope-dog, Niglau antilope-cat, reindeer-dog and reindeer-pig. Finally, the mean D_{skel} of the guanaco differed significantly from the dog only (Tab. 5).

4. DISCUSSION

4.1 The alpha RGCs morphology

Since the earliest histological studies of vertebrate retinae, it has been recognized that retinal ganglion cells come in different shapes and sizes (Peichl, 1991). After Cajal's (1893) analytical paper many others were to follow describing the morphological diversity of ganglion cells in various species (Ramon y Cajal, 1911). A new quality came into the classification of retinal ganglion cells when Boycott and Wässle (1974) took eccentricity dependence into account. This provided the basis to differentiate individual cell types within the agglomerate of ganglion cell morphologies recognized previously in the cat retina, which they named alpha, beta, and gamma (Peichl, 1991). The cells changed size and detailed branching pattern in a regular way with distance from the central area, but at a given retinal location one could always distinguish between types (Boycott and Wässle, 1974).

A specific morphological type of ganglion cell, the alpha cell, was first defined in the cat retina by Boycott and Wässle (1974). Up to now, these cells are among the most extensively studied ganglion cells. The cat alpha RGCs commonly have the largest somata of all ganglion cells, some 28-38 μm diameter outside the central area, large caliber axons, and large, circular-to-oval dendritic fields with radial, relatively densely branched dendrites that rarely overlap (Peichl et al., 1987). The dendritic tree is monostratified in both the inner and outer lamina of the inner plexiform layer. Moreover, in the cat's retina, the alpha cells have been described as those cells with the largest somata and thickest axons at each retinal position of the ganglion-cell layer. The pattern of branching of the dendrites is characteristic and the dendritic field sizes increase monotonically from smaller in the central area to larger in the periphery. Alpha ganglion cells have between three and six thick primary dendrites which regularly and successively branch towards the periphery of the dendritic field. Between the branch points dendrites are rather straight and neighboring branches seldom overlap (Boycott and Wässle, 1974).

As for their functional significance, the alpha cells have been identified as the brisk-transient Y units of physiology (Cleland et al., 1975; Peichl and Wässle, 1981; Fukuda et al., 1984) with large, concentrically organized receptive fields, a nonlinear phasic ON- or OFF-center response to stationary flicker light stimuli, and a good responsiveness to moving stimuli (Stone and Fukuda, 1974). They are not color-coded and their axons have a high conduction velocity (Peichl and Wässle, 1981). The receptive-field centers of individual alpha cells match the position, shape, and size of their dendritic fields, allowing for the additional spread of the bipolar and amacrine cells that form their input (Peichl and Wässle, 1983). The dendritic stratification level in the inner plexiform layer (IPL) defines the cell's center response as being ON (inner sublamina) or OFF (outer sublamina) (Peichl and Wässle, 1981).

4.2 The alpha RGCs in mammalian retinae

After the alpha RGCs were first defined in the cat retina, this cell type has since been found in a wide range of mammalian retinae, including several orders of placental and marsupial mammals (Peichl and Wässle, 1981; Peichl et al., 1987; Peichl, 1991; Peichl, 1992). Moreover, from the qualitative and quantitative descriptions of the alpha cells, given in these studies, it is evident that this cell type may well be a basic feature of all placental mammalian retinae. In all mammalian retinae investigated, the alpha RGCs form two subpopulations according to the stratification of the dendrites in the inner plexiform layer. Previous investigations have drawn the conclusion that the morphology of the alpha cells and many features of both single cells and of the cell population, are conserved across species with different habitats and life-styles. This suggests that the alpha cells are a consistent obligatory ganglion cell type in every mammalian retina and probably subserve some fundamental tasks in visual performance (Peichl, 1991).

From the qualitative investigations of the alpha RGCs throughout various mammalian species, the alpha cell mosaics, the coverage of the retina by alpha cells, the shape of both soma and dendritic field, the density of branched dendrites, the cell stratification and axonal projections were described in detail (Peichl and Wässle, 1981; Peichl, 1991). On the other hand, in later quantitative studies both soma and dendritic field diameter, the inner to outer ratio, both central and peripheral alpha cell density and the alpha cell coverage factor have been reported.

In this study the dendritic branching of the alpha RGCs of eleven species from different life styles and habitats were analysed. In each species, the cell morphology was evaluated from five to fifteen characteristic images of the alpha RGCs, with the same stratification and similar distance from the optic disk (i.e. the eccentricity). With such selection, we have avoided any possible errors in our analysis, caused by the

differences in the dendritic branching complexity and the dendritic field size as is the case when the alpha cells with diverse stratification and various eccentricities are compared.

Different lifestyle and habitats might be correlated with different densities and distributions of retinal ganglion cells as well as with the size and optics of the eye (Hughes, 1977). We had such factors in mind when dividing the species into two groups: the wild and the domestic animals, and investigated whether there are common or different morphological properties among the species belonging to the same group or to one or the other group. Our analysis, measuring space-filling or dendritic branching pattern of the alpha RGCs performed in our laboratory has shown that these cells have significantly different morphology either between the species within the same group or between wild and domestic group. The six species classified as belonging to the wild group have different space-filling properties and straightness of individual dendrites (Tab. 2). On the other hand, the five domestic species have similar space-filling properties, whereas the straightness of their dendrites differed significantly (Tab. 4). When the wild and domestic species were compared separately, the morphology of these alpha RGCs differed significantly in one or two properties. It seems that only three pairs (chinchilla-dog, Niglau antilope-pig and Niglau antilope-ox) have similar space-filling and branching pattern (Tab. 5). Finally, an important generalization can be made: the difference in the morphology of the alpha RGCs in various mammals could be caused by possibly slightly different visual information processing in terms of electrotonic properties of the neurons that reflect the ecological diversity/similarity or degree of evolutionary divergence (van Pelt and Schierwagen, 1994).

4.3 Fractal analysis of the RGCs

Since Mandelbrot (1983) has established fractal geometry of nature as a contemporary branch of pure and applied mathematics, it was rapidly implemented in a number of diverse scientific fields (Fernández and Jelinek, 2001). Application of fractal theory in the analysis of neuronal structure is based on calculation of the fractal dimension of a neuronal image. This parameter is used to quantify the complexity of the borders of a neuron (Smith Jr et al., 1989; Caserta et al., 1995) and to measure how completely the branches of a neuron fill its dendritic field (Smith Jr et al., 1996; Jelinek and Fernández, 1998; Fernández and Jelinek, 2001). Very soon, fractal analysis became a leading technique in quantitative analysis of neuronal morphology (Milošević and Ristanović, 2006). Until now, the application of fractal analysis in neuronal morphology involves: experiments that focus on the quantification and classification of neuronal morphology, experiments that use the fractal dimension to study the cellular growth and differentiation and studies that propose models for cellular growth and differentiation (Milošević et al., 2007).

As for the retinal ganglion cells, fractal analysis has been applied in the past twenty years in order to discriminate among different types of neurons (Morigiwa et al. 1989; Jelinek and Spence 1997; Jelinek and Fernández 1998) and to investigate classification schemes of these cells (Jelinek 1996; Jelinek et al. 2008). This study shows that the fractal analysis is a suitable tool for the morphological analysis of two dimensional neuronal images. The fractal dimension represents a parameter which could be of relevance for inter-species comparisons of neuronal populations. Besides the results which verify previous studies of the alpha RGCs in mammals, our study presents a conclusion that the morphology of this cell type is not constant across the different species. From this point of view, our results can be understood as a good start point for further application of fractal analysis to investigations of the morphology of RGCs in mammals.

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