PARVO AND MAGNOCELLULAR PARALLEL PATHWAYS

AUTHOR

Thomas Salmon: Northeastern State University, USA

PEER REVIEWER

Scott Steinman: Southern California College of Optometry, USA

THIS CHAPTER WILL INCLUDE A REVIEW OF:

- Retinal neurons
- Introduction to the parvocellular (parvo) and magnocellular (magno) systems
- Anatomic differences between parvo and magno neurons
- Comparative anatomy of parvo and magno systems
- Parellel pathways in humans

RETINAL NEURONS

PHOTORECEPTORS	• 4 types (rods, L-cones, M-cones, S-cones) • Simple, circular receptive fields • Graded potentials • Hyperpolarize when stimulated by light
HORIZONTAL CELLS	• At least 2 types (H1 and H2) • Receive input from multiple photoreceptors • Simple, circular receptive fields • Graded potentials • Hyperpolarize when stimulated by light

RETINAL NEURONS (CONT.)

BIPOLAR CELLS	• At least 9 types (on-/off-center midget, on-/off-center diffuse, S-cone bipolar cells, others) • Receive input from multiple photoreceptors and horizontal cells • Center-surround receptive fields (spatial antagonism) • Depolarize when stimulated (opposite to photoreceptors) • Midget cells – colour opponency, high spatial resolution • Diffuse cells – non-opponent • Characteristics also vary depending on whether they are located in the central or peripheral retina
AMACRINE CELLS	• Spatial antagonism • Action potentials • Transient response (motion perception) and sustained response types
GANGLION CELLS	• At least 18 types (on-/off-center midget (parvo), parasol (magno), small bistratified cells, other) • On-/off-center midget bipolar cells - on-/off-center midget (parvo) ganglion cells • Midget cells – fewer dendritic connections • On-/off-center diffuse bipolar cells - on-/off-center parasol (magno) ganglion cells (Schwartz Fig. 12-11) • Parasol cells – transient, larger dendritic trees • S-cone bipolar cells -> small bistratified ganglion cells (konio; Schwartz, 2004 Fig. 12-13) • Action potentials to support longer transmission distances

Quoting from Schwartz, 2004 at the end of Chapter 12 (p. 280):

> *The photoreceptors have simple requirements for activation: diffuse light falling on their receptive fields elicits a response. At more proximal locations within the retina, the requirements for neural activation are more stringent. Ganglion cells, for example, are responsive only to stimuli that manifest spatial contrast.*

From a teleological point of view, the retina is designed largely to extract contrast information from the visual world. This is consistent with the singular role that spatial contrast plays in our visual experience.

INTRODUCTION – PARVO & MAGNOCELLULAR SYSTEMS

Scientists have discovered that at least two major neural pathways connect the retina and visual cortex. These **retino-cortical tracts** are known as the parvo and magnocellular systems. The **parvo** (L. *parvus* - small) cellular system is closely associated with central vision. The **magno** (L. *magnus* - large) cellular neurons are closely associated with peripheral vision. Recently, another pathway, the konio pathway has been discovered.

When discussing parvo and magno functions, it may be tempting to equate parvo functions with cone vision and magno with rod vision, but this is incorrect. All of the phenomena we will discuss today are characteristics of cone vision under *photopic* conditions. Recall that cones are present in the periphery—in fact, over 90% of the retinal cones are found in the periphery, not the fovea.

ANATOMIC DIFFERENCES – PARVO & MAGNO NEURONS

Depending on the species of animal studied, parvo (or parvo-like) ganglion cells are sometimes referred to as **beta, X, midget or P cells**. Parvo ganglion cells (mostly foveal) have smaller dendritic trees and receive synapses from fewer cells (small spatial summation). In the fovea, one parvo ganglion cell receives a synapse from one midget bipolar cell, which is connected to one cone.

In the periphery, magno ganglion cells predominate and have large dendritic trees that receive input from many photoreceptors (large spatial summation) via the diffuse bipolar cells. Depending on the species, the magno ganglion cells are sometimes called **alpha, Y, parasol or M cells**.

Although the majority of foveal ganglion cells are parvo neurons, there are some magno cells in the fovea. Conversely, although most of the ganglion cells in the periphery are magno cells, some parvo cells are present there. This is summarized by Figure 29-1 below, which was redrawn from Adler's (9th Edition), 1992: Figure 24- 20.

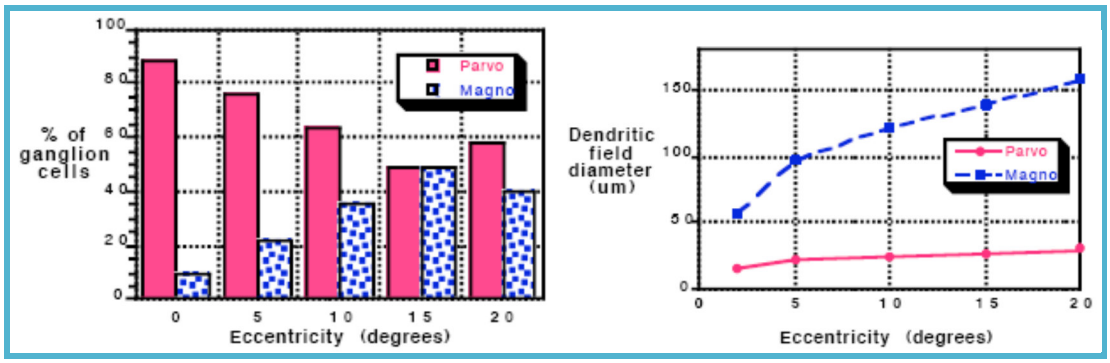

Figure 29-1: *Relative numbers and dendritic field sizes of the parvo and magno ganglion cells*

The parvo/magno distinction is obvious in the LGN. Neurons in the LGN are organized into six layers and the two lower (ventral) layers contain giant neurons that are considered part of the magno system (labelled M in Figure 29-2).

Layers 3-6 contain smaller neurons that are considered part of the parvo system (P in Figure 29-2).

Magno Layer 1 receives input from the contralateral (opposite side) retina and Layer 2 receives input from the ipsilateral (same side) retina. Parvo Layers 3 and 5 receive input from the ipsilateral retina and Layers 4 and 6 receive input from the contralateral side.

Neurons in the konio pathway are located between LGN Layers 2 and 3 (K in Figure 29-2).

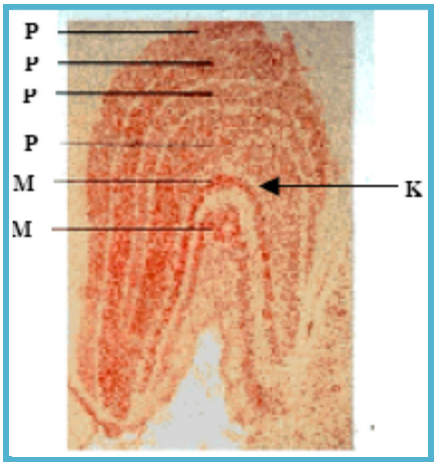

Figure 29-2: *Coronal section showing layers of the LGN*

COMPARATIVE ANATOMY – MAGNO AND PARVO SYSTEMS

Studies of other animals (frogs, monkeys, cats) have been used to better understand the division of retinocortical pathways into these two distinct, parallel systems.

FROGS

Frog studies show that their ganglion cells include two classes that can be distinguished based on their response to certain features in the visual environment. Some ganglion cells are more active when the frog sees small black spots. These ganglion cells were called “bug detectors.”

Other ganglion cells are most stimulated when the frog sees large objects, such as a moving shadow. This shows that there is a distinction between neurons that specialize in small detailed, high spatial frequency vision and those that specialize in low spatial frequency vision.

CATS

Research with cats has also shown that their ganglion cells can be divided into two classes based on the response to visual stimuli. Some studies tested cats using sine wave gratings. Certain neurons, identified as X-ganglion cells, showed a **linear response** to gratings positioned within their response fields.

In simple terms, a linear system is one in which the total response is equal to the sum of the responses to sub parts of the stimulus. In a linear system, the input from different parts of the receptive field sum for the total response.

In contrast to the linearly responding cells, certain neurons, identified as Y-ganglion cells, showed a **non-linear response**. This showed that there are two different approaches to neural processing.

Schwartz, 2004 Fig. 13-3 illustrates the difference between linear and non-linear neural responses. The right column shows an annular receptive field for one ganglion cell. A light stripe falling on the center of the receptive field stimulates (positive response) the ganglion cell (top). This is shown by the increased response in the upper-left plot. A light stripe falling in the peripheral portion of the receptive field inhibits (negative response) the ganglion cell, as shown in the lower plot. If a light stripe falls half on the center and half on the surround, then, assuming a linear response, the output should be neutral, as shown in the middle-left plot. This illustrates a linear response and is the way X-cells respond to gratings.

The middle column shows that even when a neutral response is expected, the Y-ganglion cell still shows an excitation response. In fact, no matter where the grating is placed in the receptive field, it causes excitation. This was interpreted as evidence of non-linear neural processing in those cells.

MONKEYS

Rhesus monkey studies also show that ganglion cells, LGN cells, striate cortex and higher cortical neurons appear to be organized into two distinct pathways. The cells in these two pathways show different responses to colour, and temporal and spatial stimuli, as summarized in Table 29.1 (modified version of Schwartz, 2004 Table 13-1).

Table 29-1: *Characteristics of the parvo and magno pathways*

	PARVO NEURONS	MAGNO NEURONS
COLOUR DISCRIMINATION	Yes (colour opponency)	No
NEURON RESPONSE	Sustained	Transient
AXON DIAMETER	Smaller	Larger
SIGNAL TRANSMISSION	Slower	Faster
TEMPORAL SENSITIVITY	Low frequency	High frequency
SPATIAL SENSITIVITY	High resolution (20/20)	Low resolution (20/200)
RETINAL INPUT MOSTLY FROM	Fovea	Periphery
SPATIAL LINEARITY	Linear	Some non-linearity
SENSORY SPECIALIZATION	Colour / spatial detail(what/details)	Motion (where/danger!)

COMPARATIVE ANATOMY – MAGNO AND PARVO SYSTEMS (CONT.)

The response of the different types of ganglion cell and LGN neurons (parvo or magno) to colour is illustrated in Schwartz, 2004 Fig. 13-4.

- Parvo cells show different responses depending on wavelength. For example, some parvo neurons show inhibition (decreased action potential frequency) for short wavelengths and excitation (increased rate) for long wavelengths; that is, **colour opponency**.
- Magno cells do not show colour opponency, therefore they can't discriminate wavelength and cannot contribute to colour perception. (Schwartz, 2004 Fig. 13-5)

Temporal response to stimulus presentation (Schwartz, 2004 Fig. 13-6) is summarised below:

- Parvo cells fire as long as the stimulus is present—**a sustained response** (Schwartz, 2004 Fig. 13-6A)
- Magno neurons show a rapid burst of electrical activity when the stimulus turns on and when it turns off. This is called a **transient response** (Schwartz, 2004 Fig. 13-6B)
- Parvo neurons may respond better to relatively stable lighting, which would be associated with lower temporal light changes, and better sensitivity *to low temporal frequencies*
- It appears that the transient response of the magno cells respond better to rapid changes in illumination. This would be associated with *high temporal resolution and better motion perception*

Speed of transmission is summarised below:

- Parvo cellular axon diameters are smaller and they transmit electrical signals slower
- Magno cellular neurons have larger diameter axons. Large diameter cables transmit electrical signal faster, and this is true for neurons as well. This would contribute to faster motion perception

Receptive or spatial summation fields sizes are summarised below:

- Parvo receptive fields are smaller, therefore they support better spatial resolution (better VA). The parvo cells in the LGN are mostly connected to foveal ganglion cells
- Magno cells have larger receptive fields, which allows for greater spatial summation and better sensitivity in low light

It appears that these two parallel pathways in the visual system are specialized for certain types of visual perception:

- The magnocellular system is more oriented toward general detection or alerting and is referred to as the **'where' system**. It's faster and more sensitive to movement. It may be more important in detecting dangers that arise in our peripheral vision
- Once an object is detected, the detailed visual information (spatial details, colour) seems to be carried primarily by the parvo system. It is called the **'what' system**

Selective damage to certain parts of the LGN caused visual anomalies that would be expected for a system designed to support two distinct functions:

- Damage in the Layers 3-6 (parvo cells) cause reduced colour perception and poorer visual acuity. Sensitivity to high-frequency flicker, however, is preserved
- Lesions in LGN Layers 1-2 (magno cells) cause poor detection of high-frequency flicker and greater difficulty in detecting large objects. Colour perception and high spatial resolution are unaffected

PARALLEL PATHWAYS IN HUMANS

Because of the similarities between man and monkeys, scientists assume that these principles also apply to the human visual system. Psychophysical tests have been devised to isolate and study the magno and parvo cellular systems.

ISOLUMINANT GRATINGS

One technique uses **isoluminant** (same luminance) gratings that stimulate only the parvo system, while leaving the magno system unstimulated (Schwartz, 2004 Fig. 13-7). Alternate bars of different colours (for example, red and green bars) are shown, but the luminance (not radiance) of the bars is the same. The stripes should be invisible to the magno system, since they are all of the same luminance and differ only in colour. This can be used to test the parvo system only since the magno neurons cannot detect the stripes.

INCREMENT SENSITIVITY

Another strategy is to use coloured (spectral) increment sensitivity testing (Schwartz, 2004 Fig. 13-8). The stimulus contains two important features:

- A monochromatic spot (one-wavelength hue) must be detected against a white background
- In addition, the stimulus is flickering at 25 Hz

Starting with a very small luminance increment (ΔI), increase the luminance until the person detects the colour and the flicker. These occur at different luminance levels (different thresholds) that vary as a function of wavelength.

At some wavelengths the person is more sensitive to colour and detects it first, then sees the flicker (440 nm). (Recall threshold and sensitivity are inversely related.) At other wavelengths the eye detects the flicker first (more sensitive to flicker), then colour (600 nm). This suggests separate parvo (colour vision) and magno (flicker detection) systems at work.

Quoting from Schwartz, 2004 (p. 293): “Discrete thresholds for colour and flicker suggest the existence of two independent physiological pathways. The colour curve presumably represents thresholds for the colour-coding sustained parvo pathway, and the flicker curve represents thresholds for the transient magno pathway.”

SELECTED READING/REFERENCES

- Schwartz SH. **Visual Perception - A Clinical Orientation, 3rd Edition**. Appleton & Lange, Stamford, Connecticut, 2004
- Adler FH and Hart WH. **Adler's Physiology of the eye: Clinical application**. 9th Edition. Mosby, USA. 1992