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# *Parallel Organization of the Primate Visual System*

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# Parallel Organization of the Primate Visual System

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## Introduction

The primate visual system contains hierarchical processing from the retina to higher visual cortex.

There is also a prominent parallel component to the organization.

Several parallel channels convey information from the retina to the brain.

X or P cells convey one class of information.

Y or M cells convey a different class of information.

W cells are different, less prevalent, and less well understood.

W cells project primarily to brainstem structures.

The parietal and inferotemporal parts of visual cortex process different information.

Parietal cortex concerned with motion and spatial relationships.

The cortical areas in this region make up *the motion pathway*.

Inferotemporal cortex is concerned with color and form.

The cortical areas in this region make up the *color and form pathway*.

The relationship between the P and M channels and motion and color and form pathways is important.

It appears that there is a close association between P cells and the color and form pathway and the M cells and the motion pathway.

This suggests that the visual system is split from the retina to the highest cortical centers.

Important for understanding visual function, sensory processing in general

## Parallel organization in subcortical visual projections

The retina in all vertebrates contains distinct classes of retinal ganglion cells.

First well-described in the cat as X, Y, and W cells.

X cells are largest population.

Smallest receptive fields and highest resolution for spatial frequency.

Slowly adapting responses.

Not very sensitive to high temporal frequencies (fast flicker).

Linear summation within the receptive field.

In primates this class conveys most information about color.

Y cells have different properties.

They have large receptive fields and lower resolution for spatial frequency.





They have rapidly adapting responses.

They are sensitive to high temporal frequencies (fast flicker).

Non-linear summation within the receptive field

In primates this class has very little color selectivity

W cells include all other retinal ganglion cells

Probably several distinct classes

Very slowly conducting axons

Usually large receptive fields

Complex response properties (e.g., direction selectivity)

Similar cells classes exist in monkey

Properties differ from those originally described for the cat, so they are called P and M cells instead of X and Y.

P cells are similar to the X class of retinal ganglion cells

M cells are similar to the Y class of retinal ganglion cells

Named for their projections to the lateral geniculate nucleus (LGN)

P cells project only to the parvocellular layers of the LGN

M cells project only to the magnocellular layers of the LGN

The parallel organization is very obvious in the LGN

The properties of LGN neurons closely mimic their inputs

Segregation is maintained in the projection to striate cortex (primary visual cortex)

Parvocellular LGN sends axons to layer 4C$\beta$

Magnocellular LGN sends axons to layer 4C$\alpha$

## Parallel organization in higher visual cortex

The parietal and inferotemporal regions of visual cortex subserve different functions

Parietal cortex concerned with spatial relationships and motion

Inferotemporal cortex concerned with object and pattern identification

The distinction is supported by clinical observations

Parietal damage can leave people unable to make spatial judgments or motion judgments, without affecting object identification

Inferotemporal damages can create and inability to recognize objects visually, although patients can locate the objects very well

The distinction is supported by physiological observations

Neurons in the parietal regions are characteristically sensitivity to the direction of stimulus motion, and insensitive to stimulus color, size or shape

Neurons in inferotemporal cortex are often very selective for stimulus shape.

Inferotemporal cortex includes face-selective and hand-selective neurons

The distinction is supported by psychophysical observations

The part of the visual system sensitive to color does not see motion well

It is very difficult to see the motion of color edges when the colors are exactly the same intensity.

The separation of function is probably not complete.

There is overlap in the physiological properties of neurons in the two regions

There are anatomical connections between the two regions

The differences are not likely to be specifically motion, or specifically color and form

**Associations between M and P cells and parietal and inferotemporal cortex**

Proposed that M cells feed the motion pathway and P cells feed the color and form pathway

Implies a parallel segregation that is continuous from the retina to higher cortex

This suggestion is supported by basic consistency between the properties of neurons between M channel and motion pathway and P channel and color and form pathway.

M and P channel response properties are roughly consistent with needs for motion and color and form assessment

Supported by anatomical segregation in striate cortex and area V2

Distinct compartments can be seen in both areas using a stain for the metabolic enzyme cytochrome oxidase (CO)

In striate cortex there is a regular array of CO columns that run through the thickness of cortex

Called "blobs" — the superficial and deep layers of striate cortex contain both blobs and "inter-blob" regions.

In V2 there is a regular alternation of CO rich and poor stripes.

CO-rich stripes can be thin or thick.

The normal sequence is ... thin CO-rich stripe — CO-poor stripe — thick CO-rich stripe — CO-poor stripe ...

These CO regions appear to support the segregation of the P and M channels.

The M channel feeds striate cortex layer 4Cα, and from there leads to layer 4B and then to the thick CO-rich stripes in area V2.

Layer 4B in striate cortex and the thick CO-rich stripes in area V2 both project to the middle temporal visual area (MT), which is an important component of the motion pathway.

The P channel feeds striate cortex layer 4Cb, and from there leads to both the CO-blobs and CO-interblobs in the superficial layers.

The CO-blobs in striate cortex project to the thin CO-rich stripes in V2.

The CO-interblobs in striate cortex project to the CO-poor stripes in V2.



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The thin CO-rich stripes and the CO-poor stripes in V2 both project to area V4, which is an important component of the color and form pathway.

This anatomical organization suggests that the motion pathway is dominated by M channel inputs, and the color and form pathway is dominated by P channel input.

The evidence is not conclusive.

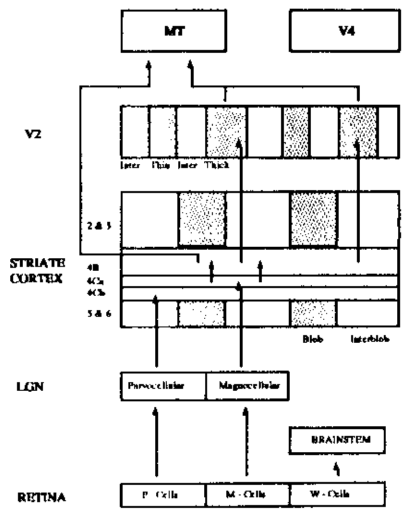
Anatomical methods do not show precise microcircuitry

Leave the possibility of substantial "cross-talk" at every level

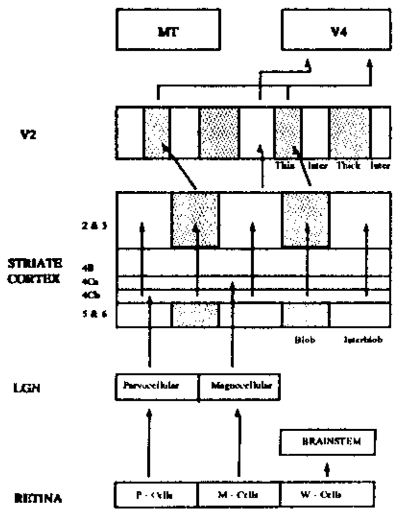
Physiological correspondence is not conclusive

Similarities could arise from cortical processing of inputs from either channel.

Magnocellular Pathway




Parvocellular Pathway




**Direct tests of the relationship between the P and M channels and the higher cortical pathways.**

The relationship between the P and M channels and the motion and color and form pathways has been examined using direct physiological methods

Selective inactivation of individual LGN layers permits direct measurement of the contribution of the layers to responses in higher visual cortex
Individual layers can be reversibly inactivated by injecting small quantities of local anesthetics or synaptic blockers

M and P contributions to the middle temporal visual area (MT) in the motion pathway.
All neurons in MT are affected by blocking the M channel at the level of the LGN
Usually the neurons become completely unresponsive
Most neurons in MT are unaffected by blocking the P channel at the level of the LGN.
MT is dominated by M channel input, in keeping with the suggestion from the other observations
M and P contributions to area V4 in the color and form pathway
Most neurons in V4 are affected by blocking the P channel at the level of the LGN
Most neurons in V4 are also affected by blocking the P channel at the level of the LGN.
V4 receives a major input from the P channel, in keeping with the suggestion from the other observations.
V4 also receives a major input from the M channel, which would not necessarily be expected from other observations.
Thus, the organization is not completely parallel.
It appears that there is one more-or-less independent channel: M cells — motion pathway.
The color and form pathway depends on inputs from both the M channels and P channel.

**Behavioral assessment of the contributions of the P and M channel**
Contributions of P and M channel to vision can be tested with LGN lesions
Small injection of neurotoxin can selectively lesion the magnocellular or the parvocellular layers.
Magnocellular lesions do not make an animal unable to see motion
Animals have trouble seeing high rates of flicker and low spatial frequencies (large objects or coarse patterns).
Vision is little affected when the stimulus is moving slowly or has predominantly high spatial frequencies.
Results are consistent with sensitivity of M cells to high temporal frequencies (fast flicker) and low spatial frequencies (coarse patterns).
Animals with magnocellular lesions can judge directions and speeds of motion well





if they are for objects with high spatial frequency and low temporal frequency
Parvocellular lesions do not make an animal unable to see form
Animals are severely impaired on color vision.
Animals are not able to resolve the highest spatial frequencies (fine patterns).
Animals can still judge shape, if highest spatial frequencies are not needed for the recognition.
Results are consistent with the P channel carrying most of the information about color, and having sensitivity to higher spatial frequencies than the M channel.
Behavioral tests support the idea that there is only a partial segregation of function into two parallel systems.

**Summary**
A clear-cut parallel organization exists throughout the primate visual system.
The relationship between P and M cells and the motion and color and form pathways is not one-to-one.
The motion pathway is dominated by M cell inputs.
However, both and M and P contributions are evident in the color and form pathway.
The system is likely to be further sub-divided in the future.
W-cells are a sizable proportion of retinal ganglion cells, and project mainly to subcortical structures.
The color and form pathway is a likely to contain two more-or-less distinct subdivisions.
Although no subdivisions of the motion pathway are obvious, motion is used for many different functions, and there may be anatomical segregations that support the differences.

# Neural Correlates of Attention in the Primate Visual System

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## Introduction

Neural mechanisms related to attention and behavioral state are much less well understood than those related to sensory or motor signals.

Effects of attention have been seen in many brain regions.

Effects of attention have been seen in relatively earlier stages of sensory processing.

Effects of attention on the activity of individual neurons are complex and diverse.

## Changes in Neuronal Activity Related to Attention

The experimental approach invariably involves recording from trained, behaving animals.
- Effects of attention cannot be observed in anesthetized animals.
- Effects of attention cannot be understood in freely-behaving animals.
  - It is impossible to assign changes in neuronal activity to attention when the sensory input is uncontrolled and changing unpredictably.
  - It is impossible to assign changes in neuronal activity to attention when the motor output is uncontrolled and changing unpredictably.
  - Animals are trained to perform tasks that act to control sensory input and motor acts.
  - For studying the visual system, tasks almost always include fixing gaze on a spot, so that visual stimuli fall on known parts of the retinas.

Saccadic enhancement was one of the first effect of attention demonstrated in the visual system.
- It was first described in the superior colliculus.
  - The superior colliculus is a visual structure in the brain stem (also called the optic tectum).
  - In primates it is important in the generation of saccades (jumps in eye position from spot to spot).
  - Neurons in the superficial layers of the superior colliculus receive input directly from retinal ganglion cells.
    - Respond strongly to the onset of small spots of light.
- Responses to a spot of light are stronger when the animal is about to move its gaze to the spot.
  - Responses are weaker if the same spot appears in the same place when the animal does not subsequently move its eyes to the spot.
  - The enhanced response when the animal is about to use the spot for a target is called "saccadic enhancement."
- Saccadic enhancement is considered to be an effect of attention.
  - The sensory stimulation is the same in both conditions.
  - The difference occurs well before an eye movement.
  - No motor activity is seen in the neurons when the animal makes eye movements in the dark.
- Saccadic enhancement has also been seen in other visual structures.
  - It is found in the frontal eye fields in cerebral cortex, which are also important for making eye movements.
  - It is found in the parietal cortex, which is important for assessing spatial relationships and locations in the world.

A related effect of attention is seen using tasks that require peripheral attention.
- Saccadic enhancement occurs only when the animal is about to make an eye movement.
- Peripheral attention tasks require the animal to attend to a spot while looking at another spot, making no eye movement.
  - This is not a natural form of behavior, but animals can be trained.
  - They are usually required to release a level when the peripheral target dims slightly.
  - Responses are compared between when the animal is attending to the peripheral spot and when it attends the spot it is looking at.
- Many neurons in parietal cortex and the frontal eye fields respond more strongly when the animal attends to the peripheral stimulus.
- This effect is considered to be an effect of attention.
  - The stimulus stimuli are the same in both conditions.
  - There is no movements occurring at the time the responses are measured.





Changes in Neuronal Activity Associated the Difficulty of a Task.
- Saccadic enhancement and peripheral attention treat attention as a binary quantity (it it either present or not present).
- More continuous and complex representations are associated with attention.
- Neurons can change the sharpness of their tuning depending on the difficulty of the task the animal is performing.
  - Desimone's laboratory has examined this effect in area V4.
  - Animals were required to detect whether the orientation of a bar changed between two presentations.
  - Orientation tuning curves could be generated by measuring responses to bars in different orientations.

The difficulty of the task could be changed by changed the orientation difference that occurred.

Some V4 neurons had different orientation tuning curves depending on whether the animal was performing the easy or difficult version of the task.

This effect of attention is not simply on or off depending on whether the animal attends.

Changes in Neuronal Activity Associated Short-Term Memory

Neurons in many regions change their level of activity depending on what the animal is required to remember.

Typical tested using a delayed match-to-sample task.

At the start of each trial the animal is briefly shown a sample stimulus.

After 2 to 15 seconds the animal is shown a stimulus and must decide whether or not it is the same as the sample.

Neuronal responses are measured during the delay period, when no stimulus is present.

Some neurons are more activity while the animal is remembering a particular sample.

Cells that are activated by remembering different colors are found in inferotemporal cortex.

Cells that are activated by remembering different orientations are found in area V4.

Cells that are activated by remembering different locations in space are found in the substantia nigra.

Cells in inferotemporal cortex are activated when an animal remembers particular complex objects.

These cells were only activated by familiar objects, not novel ones.

May contribute to recognizing familiar objects.

These neuron probably contribute to remembering information for short periods.

Probably contribute to maintaining a stable internal representation of the world.

Summary

Effects of attention are found at many levels of processing in the visual system.

Effects are not binary (on/off) depending on whether the stimulus is attended.

Effects are poorly understood.

**Correlating the Behavior of Individual Neurons with Organism's Capability**

The sensitivity of neurons can be compared with the sensitivity of individual neurons.

Orientation selectivity of individual neurons in striate cortex is sometimes comparable to the





sensitivity of the animal.

Perception does not appear to depend on averaging the activity of large groups of neurons.

Direction selectivity of individual neurons is comparable to that of individual neurons in the middle temporal visual area (MT).

The behavior of the animal can be predicted to some extent by the activity of individual neurons in MT.

The animal is more likely to report seeing motion in a neuron's preferred direction on trials when that neuron is more active.

Variability of the neuron's activity does not appear to depend on changes in the stimulus.

**Microstimulation Experiments**

Microstimulation can be used to demonstrate that neurons contribute to perceptual decisions.

Microstimulation in MT has shown that neurons there contribute to assessment of direction of movement.

Microstimulation with low currents biases animals to report that they see the direction that is preferred by the neurons that are stimulated.

It is likely that this approach can be used in other sensory structures.

**Summary**

Effects of attention are widely distributed in the nervous system.

They have been found to take many different forms and levels of complexity.

Neuronal mechanisms related to attention and memory are far less well understood than those related to sensory and motor signals