# Excerpts from

# PROCESSES IN ANIMAL VISION:

## including,

# ELECTROCHEMISTRY OF THE NEURON

This material is excerpted from the full β-version of the text. The final printed version will be more concise due to further editing and economical constraints. A Table of Contents is at the end of this paper.

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# 9. Cytology & Topology of More Complex Neurons [1]

## 9. More Complex Neurons

Based on the fundamental neuron defined in the previous chapter, it is now possible to define a series of more useful neurons that can be related to those real neurons defined by the anatomists and cytologists**.** This chapter will address these application-oriented neuron configurations with respect to their cytological and topological features. Although, the description can be applied to a wide variety of neurons, the emphasis here will be on those found in vision.

> **The discussion will continue to be based on the fundamental premise of this work that all neural activity is electrolytically based and that the only chemical reactions associated with neural signaling relate to the electrostenolytic processes providing electrical power to the individual conduits forming neurons.** No requirement or situation has arisen suggesting the need for chemical neurotransmitters between neurons even though many specific chemicals are found in the vicinity of elements of the neural system.
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> **The discussion will also continue to be based on the premise that the fundamental functional unit of the neural system is NOT the neuron but the neural conduit and the proper juxtaposition of two neural conduits to form an Activa.** The neuron is the smallest living cell associated with the neural system. However, it is sometimes an incomplete functional unit since the myelin wrapping of the conduits is generally supplied by a distinctly separate cell. **Section 10.4.4** discusses this rationale in more detail.

Five functional types of neurons have been defined in this work that relate to the visual system.

+ Signal detection neurons
+ Signal manipulation neurons
+ Hybrid neurons
+ Projection neurons
+ Neuro-muscular neurons

The only other significant class of neurons appears to be the neuro-secretory neurons related to genesis, growth and metabolism. The functional aspects of the neuro-secretory and neuro-muscular neurons will not be explored here.

The only type of signal detection neuron of interest here is the photoreceptor cell. These will be mentioned briefly for continuity. They are discussed in detail in **Chapter 4**. The signal manipulation neurons include the greatest functional variety of neurons and these will be discussed in detail. The hybrid neurons consist of two types, those that encode electrotonic (analog) signals into pulse signals and those that perform the inverse function. The first are defined as ganglion cells and the latter are defined as stellate cells. Projection neurons are those types that receive pulse signals at their input terminals and regenerate those signals at their output. The vast majority of the neurons in any neural system receive and deliver electrotonic (analog) signal waveforms. It is only the hybrid and projection neurons that treat pulse type signals (action potentials).

The above classification scheme supports a variety of signaling paths within the neural system. This includes the signal paths from sensory cells at the extremes of the peripheral nervous system to the brain as well as

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those within the brain, and those that return from the brain to the muscular-skeletal system. It also includes signaling paths within the central nervous system. The retina is appropriately considered a part of the central nervous system. In many morphological aspects, it is virtually identical to the rest of the cortex and the mid-brain. The hybrid and projection neurons are used to transmit signals among these cerebral units.

The majority of the discussion concerning individual types of neurons will not address how they are connected to nearby neurons. It will be assumed that this is accomplished by electrolytic, or gap, junctions. The details of the junction between neurons will be addressed in **Sections 9.4 & 10.4**. This discussion will also focus on the quiescent or static parameters of the neurons. Their dynamic parameters will be examined in detail in the second half of **Chapter 10.**

Initially, this work attempted to model the neurons as general purpose circuits of unknown complexity, similar to man-made operational amplifiers. This was found to be unnecessary when the simplicity of the circuitry of each neuron was determined. The active element of each circuit was then analyzed as to their electronic form, e. g., voltage controlled or current controlled devices. It was quickly determined that all of the active devices within the neural system could be characterized as of the current type and consisted of PNP class of active semiconductor electronic devices. ***Based on this work, there was no need to emulate the active devices of the neural system by complex networks of man-made active devices as found previously in the literature***. The complete neural system can be represented by a highly replicated network of strings of remarkably simple individual circuits.

The various neuron configurations defined in this Chapter can generate signal waveforms in excellent agreement with the data base in the vision literature. These waveforms will be discussed and compared in the second part of **Chapter 10**.

## 9.1 Categorization of neurons by function

Although there are many idiosyncrasies associated with the structure of visual neurons, leading to difficulty in determining their proper morphological classification, **Table 9.0** will define the more significant functional types to be addressed in this Chapter. A Type Designator will be assigned to them for ease of cataloging. They will then be discussed in order of complexity, beginning with the type most similar to the fundamental neuron discussed above.

**TABLE 9.0**
**Common names of neurons associated mainly with vision**

| Class | Type | Common Name | Purpose/Feature(s) |
|---|---|---|---|
| **In *Chordata*** | | | |
| SIGNAL DETECTION | | | |
| Receptor | AT | Photoreceptor | Adaptation amplifier: strip line form, exponential internal feedback, collectors in parallel . |
| | AD | | Distribution amplifier |
| SIGNAL MANIPULATION | | | |
| Signal Process | AB | Bipolar | Primarily isolation amplifiers |
| | AL | Horizontal ___/ | Differential amp. with two inputs, internal feedback |

| | | | |
|---|---|---|---|
| | AL | Amercine / \ | Differential amp. with two inputs, internal feedback |
| | AL | Pyramid / | \Differential amp. with two inputs, internal feedback |
| ? | AS? | Interplexiform | External feedback amp. from amercine to horizontal |
| Signal transfer | BS | Synapse | Isolation amplifier |
| SIGNAL PROJECTION | | | |
| Signal Encoding | AG | Ganglion | Encoding: Analog input, pulse output, inter. f'dback |
| Signal Decoding | AR | (Brain) | Decoding: Pulse input, analog or pulse output |
| Signal Regen. | AN | Node of Ranvier | Regeneration of action potentials |
| MUSCLE ACTIVATION | | | |
| Signal Conversion | AM | End Plates | Decodes at high current level |

**non-*Chordata***

SENSORY

Receptor — Retinular Cell

INTERNEURONS

Signal Processing | Eccentric Cell provides both of these
Signal Modulation | functions in simple animals like Limulus

**Other**

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[[ integrate into the above table ]]

| Class | Type | Suprathreshold (all or nothing) | Subthreshold (sustained or electrotonic) |
|---|---|---|---|
| | Projection | X | |
| | Myloneurons | X | ? |
| Interneurons | | | |
| | Sensing | | X |
| | Processing | | X |
| | Encoding | (output) | (input) |
| | Decoding | (input) | (output) |

The horizontal, amercine, pyramid and interplexiform cells (if the latter exist) form part of a large group

defined as signal manipulation neurons in this work. The signal manipulation capability of the eccentric cell of *Limulus*, and some other primitive animals, are special. They can be placed in this group with regard to their signal manipulation capabilities but they also exhibit a signal encoding function and are also classified as hybrid cells.

The morphological descriptor's monopolar and bipolar do not relate well to the electrical performance of neurons and will not be used in this Chapter. The Bipolar name will be used to define a neuron primarily with respect to its location in the retina between the photoreceptor cell and the ganglion cell in a signal path. This neuron usually exhibits an electrically monopolar waveform; i. e., proceeding in only one direction from its resting potential when subject to an input stimulus.

Because of the fact that an active device may be formed upon the juxtaposition of any two membranes associated with neural conduits, amplification, in the broad sense, may occur at two different locations in the nervous system. It may occur inside a given neuron and also between two adjacent neurons. The Nodes of Ranvier are examples of multiple amplifiers within a single cell.

The circuit associated with the Activa of Type AN (the N for Node of Ranvier), will be discussed briefly in **Section 9.3** because of its prototypical role in all signal projection and hybrid neurons within and outside of the eye.

## 9.2 The analog, or electrotonic, neurons

The neurons exclusively involved in processing analog signals within the retina are, in order of complexity, the bipolar, lateral and photoreceptor cells of vision. They perform signal detection and a variety of signal manipulation functions. Similar analog neurons occur in the mid-brain, the cortex and elsewhere in the neural system. The primary signal manipulations involve the summing and differencing of voltage mode signals. All of the signal detection and manipulation neurons are derived from the basic topology of the bipolar neuron (which corresponds to the fundamental neuron of the previous Chapter when the poda impedance is minimal in value and insignificant in function).

In the following discussion, it will be seen that some of the signals are reversed in polarity as they pass along the signal path. This functional process removes any correlation between the nature of the signal and the concept of hyper- or de-polarization with respect to the signal at a given point. It will be shown that the direction of the potential change due to increased excitation of the eye by photons depends on the circuit under discussion. For the photoreceptor cells, increased excitation always results in a negative going potential change, a hyperpolarization. For the bipolar cells, the same excitation causes a negative going change, a depolarization. For the lateral cells and the ganglion cells, the situation is more complex and only anecdotal evidence (based primarily on after effects as detected by Bidwell's disk, etc.) is available. In general, it appears that the lateral cells produce a negative going change in output potential, a hyperpolarization, in the presence of increased excitation of the M- spectral channel. For illumination concentrated in the S- or the L-channel, the same increase in illumination results in a reduction in output potential, a depolarization.

### 9.2.1 Bipolar Cells

The bipolar cell is the simplest extension of the second order cell defined in **Chapter 8** and therefore one of the simplest of neuron types. They are also the basic templates from which all of the other neurons can evolve. In the general case, the bipolar neuron acts as an isolation amplifier in the overall signal processing environment. In this mode, it is configured to accept multiple input signals and generate multiple output

signals without causing impedance problems in the cells associated with it.

### 9.2.1.1 The Topology of the Bipolar Cell

The general morphology of the bipolar cell is straight forward although it is sometimes difficult for investigators to definitively describe the end structures associated with the dendrites and axons. The general cytology and topology of the bipolar cell is shown in detail in **Figure 9.2.1-1(a)**. This figure can help in understanding the morphology as well as the topology of the cell. The dendritic conduit of the cell is shown on the left. The wall of the conduit consists of several zones reflecting different types of BLM. Most of the wall acts as a simple insulator to the flow of all fundamental charges, ions and large molecules. It is probably made up of a symmetrical bilayer membrane at the molecular level. In areas juxtaposed to various other neurons, the cell wall consists of a zone(s) of asymmetrical bilayer membrane exhibiting an electrical characteristic typical of a diode. The area of this diode is a parameter controlling the reverse cutoff current of the diode and therefore its impedance. Two active connections to other neurons are shown as well as one potential or failed connection. Also shown is a zone of the BLM associated with the electrostenolytic process establishing the quiescent potential of the dendroplasm with respect to the surrounding matrix. Finally a zone is shown where the dendritic conduit is juxtaposed to the axon conduit. This juxtaposition comprises the Activa within the neuron. The axon conduit is shown to consist of a similar set of zones of BLM. The majority of the BLM is probably symmetrical at the molecular level and an insulator. One area is shown supporting an electrostenolytic function for biasing the axoplasm. Two areas are shown as connecting to following neurons.

The juxtaposition of the two conduits and the associated electrical path to the surrounding matrix through the podaplasm allows the Activa to function as an active electrical device when it is properly biased. It appears from the literature that, in the bipolar neuron, the base connection of the internal Activa is connected to the surrounding fluid environment via a low impedance path. This condition removes internal feedback as a factor in the operation of the bipolar neuron. However, the poditic battery or an additional electrostenolytic process associated with the poda may be important in establishing the overall bias structure of the cell. The dendrite is seen to exhibit one or more input sectors along its surface and it is conceivable that in certain physical locations the surface of the dendrite is a continuous Activa providing synapses anywhere along its length that is needed. Such a continuous or quasi-continuous surface is found in the photoreceptor neuron. In the figure, three conceptual inputs are shown:

+ an input from the output sector of a photoreceptor cell,
+ an input from the output sector of a second photoreceptor cell, or alternately from a horizontal cell, and
+ a failed input due to the failure of the two diodes to establish a common base region, e. g., achieve the ideal juxtaposition.

The last case is merely illustrative. If the two diodes do not establish a common base, no transistor action can occur and the diode associated with the dendrite will exhibit a high input impedance relative to the possible current from the potential input since it is reverse biased relative to the interneural plasma in that area. In the other two cases, the diodes of the dendrite are reverse biased but current is transferred into the dendroplasm by transistor action. In the absence of transistor action, a sector of the dendrite may act as a power source wherein the battery provides a potential to the dendroplasm relative to the surrounding interneural plasma. However, it cannot act as an input sector due its high impedance to input currents.

### 9.2.1.2 The Electrical Circuit

**Figure 9.2.1-1(b)** shows the electrical circuit of this cell. This circuit is a non-inverting current repeater for all input signals. The current delivered by the collector into the axoplasm is essentially identical to the current entering the emitter of the Activa. However, the delivered current may be at a higher impedance level, thereby providing power gain.

In the absence of input current, the circuit of the bipolar neuron is usually biased near cutoff by the various batteries and electrostenolytic processes involved. The axoplasm is therefor at its highest potential under quiescent conditions, i. e. fully polarized. Upon the application of a signal, the axoplasm becomes depolarized, the voltage relative to the interneural plasma drops.

The output current from the Activa is the sum of the input currents from all of the individual input sectors. Because of the presence of the load impedance associated with the axon power source, and possibly the output connections, the axoplasm exhibits a voltage relative to the surrounding medium. This voltage can be used to generate a current passing through any of the output sectors of the axon. If the contact with the proximal cell is intimate, transistor action will occur and signal amplification can occur at this junction, i. e., an impedance change although the current amplitude will remain the same. In general, the signal voltage at the emitter of the proximal cell will represent the logarithm of the current entering the cell.

In other simple cells of this type, a second type of output is conceivable, and has been widely proclaimed. The cell could emit a chemical substance into one or more synapse regions in response to the voltage of the axoplasm. This is not believed to occur in the retina.

The Bipolar Cell is representative of the simplest type of neuron. It accepts multiple input signals via transistor action which effectively isolates the sources of those signals from each other and the cell. Similarly, it generates a voltage in the axoplasm that can be used to drive multiple output sectors without causing the signals in proximally related cells to become cross coupled. It does not provide signal inversion and the output voltages appear to be depolarizing. No chemically based neurotransmitters are required to support the transfer of a signal to subsequent circuits. This situation will be addressed in more detail in **Section 9.4.**

### 9.2.1.3 Signal summation in the dendroplasm

The topology of the basic bipolar neuron suggests the answer to another question. In active semiconductor devices of the current (as opposed to the field) junction type, it is possible and common to have multiple emitters associated with a single base. The effect of this arrangement is to provide a degree of isolation between the signals applied to the individual emitters. This does not appear to be the case in the bipolar neuron. The total input current into the dendroplasm is the sum of the currents from the individual input zones. The current associated with each zone is a function of the impedance of each of the zones and the voltage of the previous conduit axoplasm. Because of the topology of the upper frame, the lower left frame shows multiple input signal paths converging on a single emitter of the Activa. Each signal path provides a current that is summed at the emitter of the Activa.

### 9.2.1.4 The Π Network Model of the Bipolar Cell

At a more basic level of schematic, an active semiconductor device, such as the Activa, is frequently represented by a fundamental circuit configuration of electrical engineering, a Π-network. Such a network is capable of accommodating and displaying all of the significant circuit elements within a given device regardless of frequency or application. The basic Π-network for this circuit configuration is shown in **Figure 9.2.1-1(c)**. Note that the impedance, $Z_2$ between terminals 1 and 3 (which would complete the  symbol) is so

high it is normally not shown in low frequency networks such as neurons. This element is basically an open circuit at frequencies below a megahertz for signal manipulation neurons.

For purposes of emphasis, the two intrinsic voltage sources related to the membranes are shown explicitly. These voltage sources are internal to the Activa and distinguish it from a man-made transistor. They basically relate to the fundamental characteristics of an asymmetrical bilayer membrane immersed between two electrolytes, a critical element in the formation of an Activa. ***It is important to note that these intrinsic BLM potentials are not necessarily the same or equal to the plasma potential they are commonly associated with.*** In fact, each zone of a membrane may exhibit a different intrinsic membrane potential. In most cases, it is the potentials established by the electrostenolytic processes that control the operation of the circuit and not the intrinsic membrane potentials.

### 9.2.1.4.1 The unbiased Activa

In the absence of any external biases applied to the Activa, the input circuit consisting of the current path between terminals 1 and 2 can be represented by a small intrinsic potential and a diode. The output circuit can be represented by a similar battery and diode in series as shown between terminals 3 and 4. In this condition, the circuit between terminals 1 and 2 represents a high impedance in both directions. Similarly, the circuit between terminals 3 and 4 can be considered a high bidirectional impedance. There is no current through the current generator connected between terminals 3 and 4.

### 9.2.1.4.2 The biased Activa

If a significant positive voltage is applied to terminal 1 with respect to terminal 2, a current will flow through the input circuit. The value of this current will be controlled by the forward impedance of the input diode. In the absence of any external bias between terminals 3 and 4, no current will flow in the output circuit nor will there be any voltage between these two terminals except that due to the intrinsic potential associated with the output membrane.

If the bias between terminals 1 and 2 is removed and terminal 3 is made negative with respect to terminal 4, insuring that the diode is reverse biased, the impedance of the output diode will be high as represented by its reverse biased condition. No current will flow through the diode.

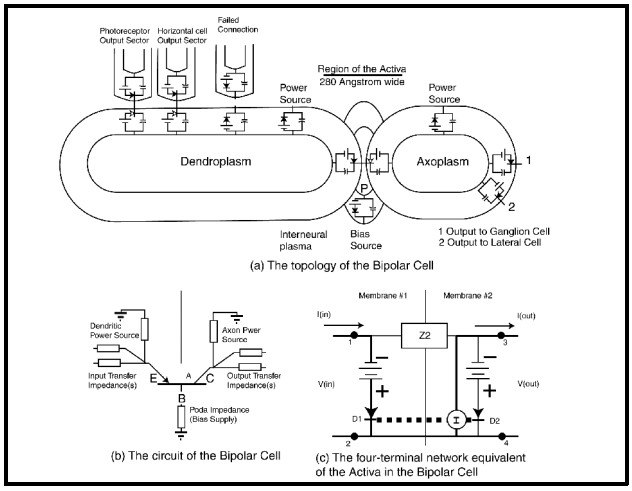


**Figure 9.2.1-1** The topology of the bipolar cell. (A); the topology showing the interface with the surrounding circuits. (B); the schematic circuit of the bipolar cell. (C); the four-terminal network representation of the Activa within the bipolar cell.

If a positive bias is applied to the input circuit and a negative bias is applied to the output circuit, a unique phenomenon occurs. A current appears in the output circuit essentially equal to the input current (typically greater than 99%) regardless of the potential between terminals 3 and 4 as long as it is maintained negative. This is the phenomenon of “transistor action” and it is suggested by the dashed line coupling the input diode to the output current generator. Note this generator is in parallel with the reverse biased output diode. The output circuit retains it’s high impedance

characteristic regardless of the current through the generator.

It is important to note that the output current is of the same magnitude as the input current and flows in the same direction along the signal path as long as the input current forward biases the input diode. It is this fact that leads to the device exhibiting a transfer characteristic between its input and output that looks like a single diode. However, this transfer characteristic is only obtained when the device is biased as above. Otherwise, it exhibits a high impedance between terminal 1 and 3 under any condition.

### 9.2.1.5 The bias point of the bipolar neuron

The output potential of the bipolar neuron becomes more negative for increased levels of illumination applied to the eye. In the absence of illumination, the bipolar neuron is biased to a quiescent point compatible with the quiescent point of the photoreceptors connecting to it and the dynamic range required to support those photoreceptor cells.

## 9.2.2 The lateral and interplexiform Cells

In this work, a lateral cell is defined as a neuron with two distinct input structures that makes it capable of performing analog subtraction between two input signals. Such a neuron can assume a variety of morphological forms while still maintaining this fundamental capability. Lateral cells are frequently described by the morphological designations of horizontal, amercine and pyramid cells.

### 9.2.2.1 The definition and absence of interplexiform neurons

The interplexiform cell has been carried in this discussion to represent a cell that supports external feedback between cells of the retina. Discussions of such a cell have appeared occasionally in the literature. In the course of this study, no definitive need for or example of a cell supporting external feedback has appeared. Therefore, this type designation will be dropped. On the other hand, the occurrence of internal feedback within a neuron is nearly universal and quite important.

### 9.2.2.2 The horizontal, pyramidal and amercine neurons

The horizontal cells and amercine cells belong to a distinctive class of cells, the lateral signal processing cells (or the lateral cells), used for signal processing in the retina and exhibiting a possibly unique characteristic in the neural system, at least outside of the brain. This class also includes the pyramid cell. These cells frequently vary in their degree of arborization. However, their basic functional characteristics are the same.

#### 9.2.2.2.1 The topography (morphology) of the lateral cells

These cells exhibit two independent input structures that are not summed algebraically at the dendritic input to the Activa. They exhibit two input structures that appear similar to a histologist but seem to enter the cell at distinctly different locations. One is the conventional dendrite structure normally connected to the emitter of the Activa. The second neurite, the pseudo-dendrite or *podite*, is a similar structure but it connects to the base structure of the Activa. This characteristic provides a new dimension of circuit flexibility to the neuron.

Shepherd[2] shows a good electron-micrograph of a cell of this class which he credits to his co-workers, Hersch and Peters. Unfortunately, it is imbedded in a surrounding structure that is not related to the functional aspects of the cell itself. The cell is labeled a pyramidal cell with an apical dendrite and a basal dendrite (podite) as well as the normal axon hillock and other conventional structures, **Figure 9.2.2-1**. The plane of the micrograph does not appear to contain the Activa. However, it is reasonable to say the dendrite and the axon are separated by structures related to the podite. To demonstrate the unique functional role of the two arborizations, it is necessary to examine their role in the cytology of the cell at x50,000 or better under an electron microscope.

The above figure can be compared with **Figure 9.2.2-2** showing the proposed idealized structure of the same type of cell at the cytological level (although at a slightly different orientation).

There is little discussion in the literature concerning a variety of lateral cell morphologies found near the pedicels of the photoreceptor cells at the distal edge of the inner nuclear layer. It is generally written that these cells are typified by the horizontal neuron with two fully arborized neurite structures. The same cannot be said of the lateral cells found proximally to the bipolar cells in the inner nuclear layer. At least six different types have been described in a single paper in the literature. These cells are frequently described as pyramid cells, amercine cells with no axon, and fully arborized lateral cells similar to the horizontal cells. It will be seen that these variations in morphology are due to the different functional role of these types of neurons

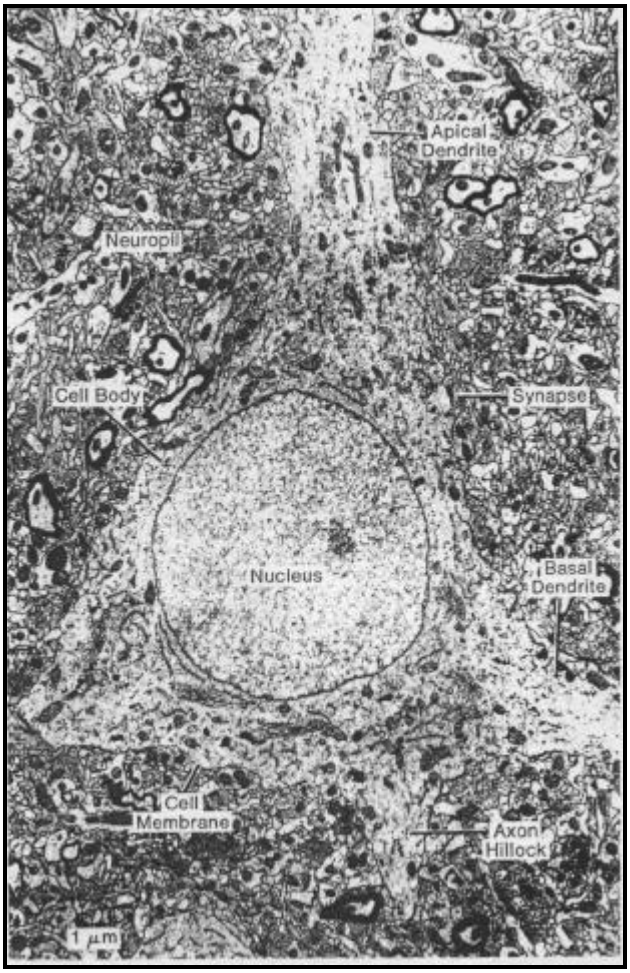


**Figure 9.2.2-1** CR Electron micrograph of a pyramid cell. Note the apical dendrite at the top, the basal dendrite (podite) at lower right and the axon exiting via the hillock at the bottom. In Shepherd, 1988, courtesy of Hersch & Peters.

[2]Shepherd, G. (1988) Neurobiology. NY: Oxford University Press pg. 43

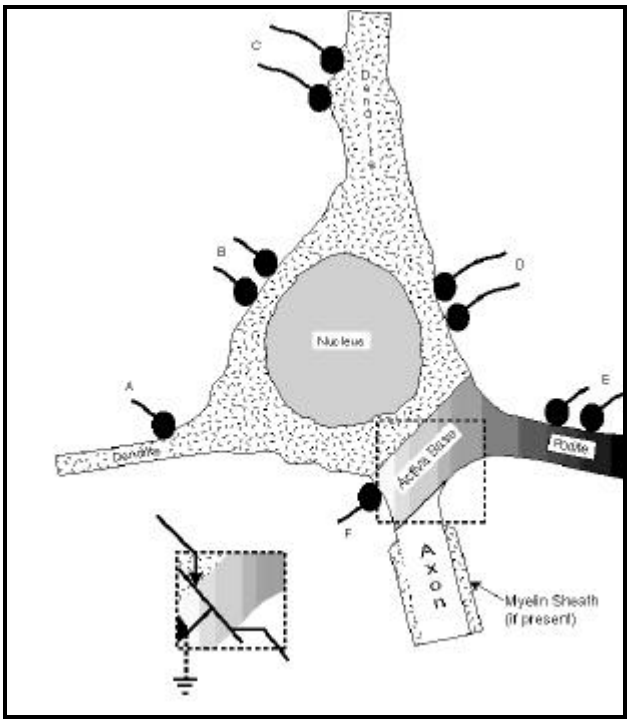


**Figure 9.2.2-2** The cytological organization of a pyramid cell. The structure labeled podite corresponds to the basel dendrite of the previous figure. The expanded inset shows the electrical topology of the active base region separating the dendritic structure from the axonal structure in the area of the hillock. A variety of synapses are shown interfacing with this cell. Note the synapses labeled E and F support inverting signal paths.

Dacey & Lee show several beautiful three-dimensional mappings of cells in this class, **Figure 9.2.2-3**. They carefully differentiate between the arborization of the dendritic conduit and the arborization of the poditic conduit which attaches to the soma at a distinctly different location.

## 9.2.2.2.2 Location of the lateral cells within the retina

From an overall signal circuit point of view, the difference between the horizontal cells and the amercine cells is their location in the retina. The conventional wisdom being that the horizontal cells are located in the distal area of the inner nuclear layer of the retina and are connected to the output of the photoreceptor cells and the input of the bipolar cells. The amercine cells are located at the proximal edge of the inner nuclear layer, connecting to the output of the bipolar cells and the input of the ganglion cells. Both cells may also interconnect with members of their own subclass in order to provide additional signal summation over large regions of the retina.

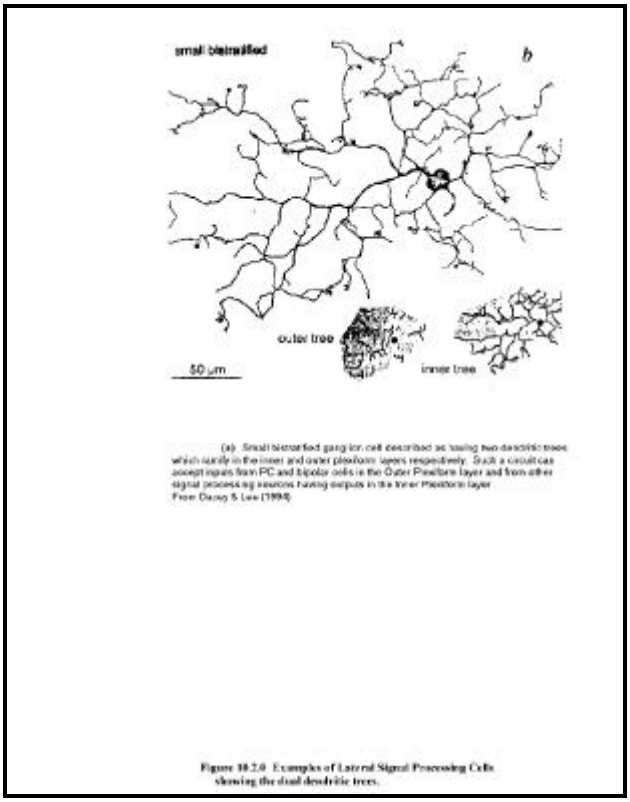


**Figure 9.2.2-3** Examples of lateral signal processing cells showing the dual neurite (dendrite and podite) arborizations.

The morphologist occasionally sees and occasionally sketches another type of lateral cell but he has no clear way to describe their electrical topology. It may be the morphologist is seeing these cells because of a preconceived notion or input from others that an external signal feedback path is needed in the retina. These cells are described as having their inputs in the proximal edge of the inner nuclear layer and their outputs in the distal edge of the inner nuclear layer. These are the interplexiform neurons addressed in **Section 9.2.2.1**.
The tendency in the literature is to ascribe to these cells a roll in external feedback within the retina. Although this may be the case, no requirement has been found in the later parts of this work to justify an external feedback path within the retina. Much more work will be needed to confirm the existence and true topology of an interplexiform neuron.

Some lateral cells do not exhibit a highly arborized input structure. This is particularly true of the so-called amercine cells located at the proximal edge of the inner nuclear layer. It also appears to be particularly true of the higher chordates, such as the primates, who have poorly developed second lateral processing matrices. These neurons are frequently labeled amercine cells. The name amercine cell is misleading since it is derived from the Greek for “no axon.” Both the horizontal and amercine cells are atypical morphologically because their internal topology is different. In many cases, the dendritic regions and axonal regions lay side by side within a single structure relative to the cell nucleus; or the axonal length is merely short because it is connecting to a nearby dendrite. This is particularly common in cells located at the proximal edge of the inner nuclear layer. It appears that this may be a feature related to their signal processing role. Some of these cells

appear to be involved in time difference signal processing. This processing involves collecting signals from remote neurons and subtracting it from other signals collected locally.

### 9.2.2.2.3 The functional characteristics of the lateral neurons

The lateral neurons exhibit intrinsic *internal feedback* due to the impedance of the poda circuit. ***This feedback is normally negative in these neurons*** (as opposed to the positive internal feedback found in the ganglion cells to be discussed below).

Briefly, the purpose of this class of cells is to perform algebraic summation in a circuit configuration capable of signal inversion (resulting in algebraic subtraction). Depending on the impedances involved, the cell can do this summation in the algebraic realm resulting in common addition and subtraction; or the cell can do this summation in the logarithmic domain resulting in *signal multiplication and division.*

By combining these operations, these cells are able to exhibit the wide range of output signals and resulting psychophysical conditions found in the literature.

A variety of morphological layouts for these types of cells can be found in the literature. **Figure 9.2.2-4(a)** illustrates the basic topological design. The cell is topologically similar to a bipolar cell except the poda region is expanded and includes signal input points. Thus, the podal region has taken on the same characteristics as the dendritic portion. The cell frequently appears in the literature to have two independent dendritic trees which will be differentiated here by describing them as the dendritic tree and the poditic tree.

There are also cartoons of many lateral cells in the literature which appear to have both input structures and output structures located along the same arm of the neuron, and often along both arms of the neuron.

**Figure 9.2.2-4(b)** presents the circuit diagram of a nominal Lateral Signal Processing Cell. It is only slightly modified slightly from the physical configuration of the Bipolar Cell. The main circuit difference consists of the poditic conduit providing a signal connection on the surface of the podalemma to the base terminal of the Activa. The functional difference is much greater than the physical difference for a number of reasons. Whereas the poda impedance in the bipolar neuron is of negligible value and significance, it plays a significant role in the lateral cell:

+ The presence of a significant poda impedance introduces negative feedback into the circuit with respect to any signal applied to the emitter terminal. This feedback normally introduces a

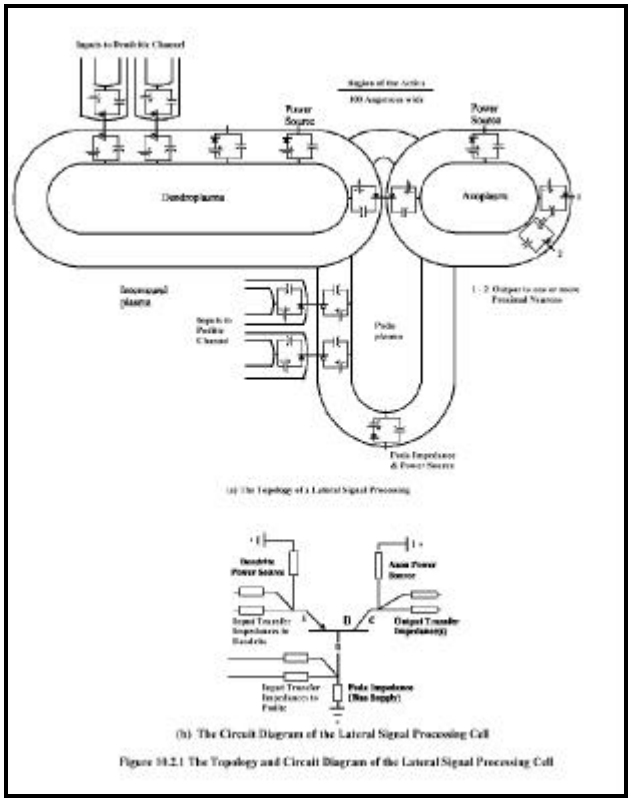


**Figure 9.2.2-4** The topology and circuit diagram of the lateral cell. (A); the topology of the cell. (B); the circuit diagram of the lateral segnal processing cell.

loss in amplification with respect to the input signal over what would otherwise be obtained.

+ The presence of a significant poda impedance allows a signal to be introduced into the base terminal of the Activa. This alternate input signal can be derived from a voltage divider network between the poda impedance and the source impedance of this alternate signal. Although this signal does not suffer from any diminution due to negative feedback, it may be suffer degeneration due to the ratio of the base input impedance and the emitter input source impedance.

+ The signal introduced through the base terminal is in phase opposition to any signal introduced via the emitter terminal, e. g., the net output is the difference between these two input signals.

+ The calculation of the net signal output is complicated by this differencing due to the phase of the two signals and the complex effective input signal amplitudes due to feedback on one hand and degeneration on the other.

The overall performance of this circuit is highly dependent upon the impedances found in the various circuit elements, the bias voltages applied and the recognition that the Activas involved are operating under large signal conditions. The detailed composition of the various membrane walls is an important characteristic of the overall cell. By varying the makeup of the phosphoglycerides in the membranes as a function of location, locations can be optimized as insulators, power sources, load impedances, signal input points and signal output points. The topology provides a great degree of flexibility with regard to the voltage sources. The principal criterion is that a given location of the neuron wall must be forward biased if it to act as a signal output point and it must be reverse biased if it is to act as a signal input point. This bias is not determined by the membrane alone at that location; it is the net voltage applied to that membrane due to its internal as well as other voltage sources. This fact illuminates *the importance of not disturbing the cell or its surrounding interneural plasma* if results are desired that reflect normal cell operation.

## 9.2.2.2.4 An alternate morphology of some lateral (amercine)cells

As will be discussed in detail in the following sections, some lateral cells associated with the 2nd lateral processing matrix may not require a significant level of arborization in either their dendritic or poditic input structures. Where they are employed in spatial filtering, they may only be differencing signals already aggregated by preceding bipolar cells. This limited role allows the employment of a simpler morphology for the cell.

**Figure 9.2.2-5** shows an alternate topology illustrating how easy it is to obtain a structure that appears to have no axon; in which a portion of a dendrite (or in this case a podite) and a portion of an axon are wrapped within a single exterior cell wall for an extended distance. Clearly, the topology will accommodate almost any morphology. As an example, the axon region could be folded back along the dendrite also, resulting in a structure that had both inputs and outputs at each end--a configuration frequently shown in the literature. Each arm would then appear to a morphologist to have both input and output points along it. Only higher magnification examination would uncover the true nature of the structure, possibly using electron beam microscopy (as opposed to conventional electron microscopy) on living cells to expose the points, channels and directions of electron flow.

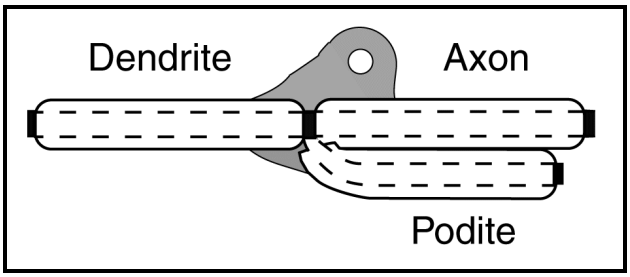


**Figure 9.2.2-5** A common lateral neuron packaged to emulate a morphologically axon-less (amercine) neuron.

### 9.2.2.3 Operation of the lateral neurons

The fundamental role of the lateral neurons is to perform analog subtraction between two input signals. These signals may be relatively simple, as in the case of the amercine cells discussed below, or complex. If the lateral cells themselves exhibit complex arborizations, the signals due to the multiple connections with preceding cells will be summed within the respective neurite plasma before participating in the signal subtraction of the lateral cells. As discussed above, the precise value of the output potential of the axoplasm is complicated because it involves so many circuit variables. However, within the operating range of the circuit, the output is essentially the algebraic difference between the amplitude of the dendritic signal amplitude and the poditic signal amplitude, each modified by a fixed coefficient. As best determined from the literature, it appears that these coefficients provide equal weighting to the aggregated signals from each spectral photodetection channel over a small area of the retina. Over larger areas, more complex relationships are found due to the finite velocity of analog electrolytic signals.

#### 9.2.2.3.1 Signal differencing in the axoplasm

Following the potential summation of signals within the plasma of each neurite, the signals are applied to the respective emitter or base terminal of the Activa.

#### 9.2.2.3.2 Spatial filtering in the spatial domain

If the effective input impedance in one of the branches is high and relatively constant compared to the input impedance of the Activa itself, then the current applied to the Activa terminal will be essentially given by the voltage applied divided by that impedance; i. e., the circuit will generate an output current that is essentially linear with respect to the applied voltage. The device will perform linear algebra on this signal. If on the other hand, the input impedance is low relative to the input impedance of the Activa itself and the signal is of large amplitude, the Activa will generate an output current that can be described as proportional to the logarithm of the applied voltage. The device will perform logarithmic algebra on this signal. This characteristic applies to both the emitter and base input signals, although the impedance of the poda bias circuit must also be considered.

#### 9.2.2.3.3 Spatial filtering in the time domain

Significant spatial signal filtering can occur in the retina in the process of converting the initial changes in illumination with either position or time into temporal signals. This filtering can occur through at least three mechanisms. It can occur in any stage where there is significant capacitance present. It can occur in any summation circuit where the signals to be summed or differenced arrive at different times due to the time delay intrinsic to long axons. It can also occur due to the limited temporal response of the photoexcitation/de-excitation process as a function of excitation level.

If the input impedances described in the above paragraph are of significant size, there comes a point where it becomes necessary to consider the capacitance shunted across them, as well as the capacitance in the poda bias circuit. This situation relates to many of the time dependent characteristics of the retina. It will be seen to be important in both the signal processing cells and, in some species, the ganglion cells.

A large capacitance shunting a large impedance, the pair in series with a second impedance, represents the standard pre-emphasis or lead network of electronics and is associated with pulse sharpening. It has the effect

of calculating the derivative of a waveform and adding the calculated waveform to the original waveform. The resulting waveform tends to rise faster and fall faster than its parent.

Although it has been assumed that the capacitance between the emitter of the Activa and the ground has been assumed to be small, this cannot be guaranteed with respect to the capacitance of the poda bias circuit. Therefore, it is quite conceivable to have the podite input consist of a capacitance shunting a large impedance, the pair in series with a second impedance consisting of a relatively high impedance shunted by a large capacitance. This so-called lead-lag network is more difficult to manipulate algebraically. However, it is easy to see that it can provide a lead network (sharpening) in certain temporal frequency regimes and a lag network (smoothing) in other regimes. These effects are commonly observed in the data in the literature, although frequently not discussed by the investigator. The typical case is seen in the paper by Purple & Dodge and discussed in Appendix D.

In most cases of routine interest, it appears the bandwidth limitations associated with the original signal created by the photodetection/de-excitation process are more important than the presence of excessive shunt capacitance.

The potential for spatial filtering in the time domain due to variable transit times between the signals applied to the 2$^{nd}$ lateral processing matrix are more important (at least in parts of the animal kingdom). By employing amercine cells to collect signals from bipolar cells separated spatially by finite multiples of a specific distance, a comb filter can be created. Such a comb filter can be used to accentuate or deprecate the signals related to a given spatial frequency or pitch in object space. It is generally recognized to be an important process in the visual system of the feline family. Large and small cats may use this capability to eliminate or discount repetitive structures such as grass in their visual field. Knowing this, a zebra may evolve stripes of the appropriate pitch to become nearly invisible to the large cats at a reasonable distance.

### 9.2.2.4 Bias point of lateral neurons

The lateral neurons are normally biased to effectuate a nominal quiescent collector current in the absence of photon excitation to the eye. This results in a quiescent collector (axoplasm) potential that is near the middle of the operating range of the collector. This allows the collector potential to rise or fall depending on the net current through the Activa in response to the differencing process carried out between its emitter and base input circuits.

### 9.2.2.5 Summary

The horizontal and amercine cells are good examples of neurons of the more general class of lateral processing cells. Like the pyramid cells, they are characterized topologically as having two independent input structures, the dendritic structure and the poditic or pseudo-dendritic structure. The poditic structure introduces an inversion of the signal waveform which can be accompanied by signal amplification. Both structures are capable of incorporating lead networks and at least the poditic structure is capable of providing a lag network as well. These cells differ significantly in their degree of arborization of each input structure. Morphologically, it may be difficult to identify the axonal structure of some cells as it may be enclosed within a common external cell wall with the dendritic or poditic structure over most of its length. This condition is the origin of the name amercine cell.

The lateral cells are the first cells in the visual pathway to utilize internal feedback in a major way. Because of the impedance in the poda circuit, there is a common signal path between the input and output signal regions. This common path introduces feedback between the dendritic input and the axonal output. Depending on the impedances within the overall circuit, this feedback may be positive or negative. Normally, the impedance is

not large. If the poda impedance is large, the waveform at the output can be significantly different from that at the input. The normal effects of a large podal impedance will be seen in paragraph 9.4.

The ability of the lateral processing cells to perform inversion of the signal applied to the base terminal is the key to their signal processing capability. These cells are the source of the psychophysical data relating to center on/surround off, center off/surround on and similar observations. They are also key to the generation of the photopic and scotopic spectral functions. They are the source of the null conditions that define the Hering axes and certain null points along the spectral locus. They are also responsible for calculating critical threshold parameters of motion and optical polarization in non-humans.

## 9.2.3 The Photoreceptor neuron

The photoreceptor cell of vision plays the most complex role of any cell in the visual system. Because of its importance, it is treated in detail in **Chapter 4**. It is responsible for providing maximum signal amplification of weak signals without overloading on strong signals. It is also responsible for providing an essentially fixed amplitude electrical signal to later neurons for further processing. To accomplish these roles;

+ it includes multiple Activa,
+ it includes uniquely structured Activas, and
+ it is closely integrated with the surrounding metabolic environment.

This section will be divided into several subsections in order to address each of the functional characteristics of the photoreceptor cell.

### 9.2.3.1 Photoreceptor cell topology

**Figure 9.2.3-1** provides a complete functional description of the photoreceptor cell (PC) of animal vision and the approximate electrical topology of the cell. As indicated elsewhere in this work, the description at this level applies to all animal eyes. Although the morphology of the cell, and particularly the associated structure known as the Outer Segment, may change dramatically, the functional characteristics remain essentially the same. The topology of the overall cell is strongly constrained by the available topography in this region of the retina.

The figure illustrates the three primary regions of the cell, the dendritic, poditic and axonal regions; along with the closely associated disk structures. The axonal region is seen to include a signal receiving sector, a power source sector and a signal transmitting sector. The podal section is shown as consisting of a simple bias source and may be even simpler than this; it may consist of only an ohmic connection to the IPM. The dendritic region is the most complex and consists of either multiple individual signal receiving sectors or a continuous structure capable of receiving input signals, regardless of where the

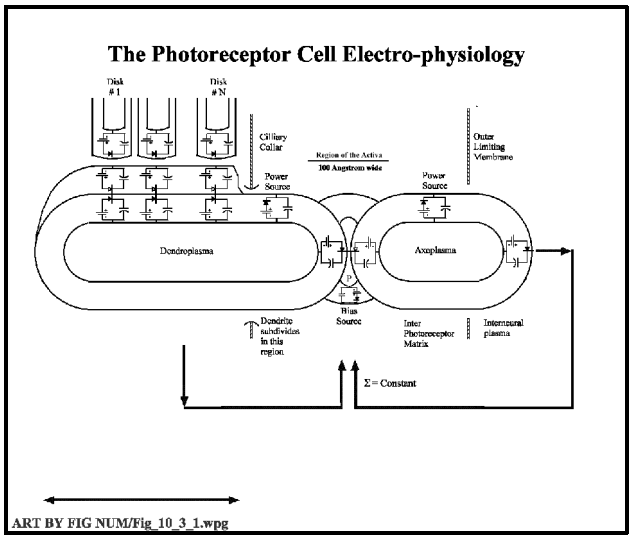


**Figure 9.2.3-1** The photoreceptor cell and its electronic topology

associated disks are located, and a power source region. A second unique feature of this signal receiving structure is that it does not receive a signal in the form of an electrical current. Since the signal in the disks is stored as (bound) electrons in an excited state and not in a conductive band, the signal transfer to the dendritic region must be by energy means and not conductive means. To accommodate this situation, the input structure is configured as an energy sensitive transistor structure, not unlike a photo-transistor. It acts as a mechanico-electrical transducer. As seen in the figure, this is accomplished by creating a bilayered cell structure in the area of the disks. As in the case of other mechanico-electrical transducers, the base connection is left open. There is no requirement for an electrical connection between the base and the external (or internal) environment.

It is important to note in the figure that there are two kinds of diodes shown, the normally forward biased or conducting diodes, indicated by the solid symbol, and the normally reverse biased or non-conducting diodes with the open centers in the symbol. The open center, reverse biased diodes are always shown as sharing a common base with a forward biased diode. Under these conditions, a normally reverse biased diode may still exhibit a current due to "transistor action."

Although difficult to show without complicating this two dimensional figure, the actual dendritic structure subdivides in the area of the CC so that individual dendritic elements (commonly described as cilia but of much greater importance than that name implies) can be folded into the furrows along the sides of the disks.

The figure may need a slight modification. It can be conjectured that the bilayer is formed where the walls of microtubules come into intimate contact with the exterior cell wall. Under this assumption, the microtubules are the actual electrical channels that carry the signal current. If this is the case, the area labeled dendroplasm might be more accurately named the microtubule plasma and there may be a separate dendroplasm that is used to support cell housekeeping functions.

For orientation purposes, the location of the Outer Limiting Membrane (OLM) and the Ciliary Collar (CC) is also shown. It is not clear whether the power source associated with the axoplasm is to the right or left of the OLM. Only detailed modeling and electrical measurement will be able to determine whether the Axon derives its power via the Inter Photoreceptor Matrix (IPM) or the Interneural Plasma (IP). A similar situation may arise with respect to the dendritic power source and the CC.

Functionally, the energy of the disks is transferred to the mechanico-electrical transistors of the dendrites where, again due to transistor action, approximately 3500 electrons flow in response to each energy packet that creates a single electron in the open base region of the transistor. *This virtually noise-free amplification is the source of the extreme sensitivity of the eye*. The electrons generated due to the action of each disk, is accumulated in the plasma of each cilia and further summed as the cilia converge into the electrical channel leading to the juxtaposition of the dendritic and axonal regions. The resulting charge (current) is applied to the input diode of the Activa located at this juncture. This input diode is also subject to the net electrical potential between the dendroplasm and the podaplasm. Normally, it appears the sum of all of the relevant individual battery potentials provides a net bias on the Activa that maintains its quiescent current at very close to zero. This zero current under quiescent conditions would cause the electrophysiologist to describe the axon to be fully polarized, or at its maximum level of hyperpolarization if he could determine the maximum level of hyperpolarization. In simple words, the Activa is at cutoff and the axoplasm is at the highest potential with respect to the external medium that the power source can generate under no load (or zero current) conditions.

Under irradiation of the OS, and in the absence of any feedback due to the poda, the same current appears in the axoplasm at a (generally) higher impedance level determined by the resistive component of the diodes associated with the power source and the output sector of the axon. The resistive component of the power source would be called the load resistor in conventional electronic circuits. The resistive component of the output sector would normally be considered the input impedance of the transfer network appearing at this

point. This transfer network could be either a passive network or an active device depending on the physical circumstances at that location.

It is both the quiescent voltage **and** the effect of the signal current that is applied to the input of this transfer network. The overall circuit is defined as direct coupled since there is no capacitor blocking the transfer of DC levels at any point in the photoreceptor cell.

## 9.2.3.2 Detailed circuit of photoreceptor cell

**Figure 9.2.3-2** shows the electrical circuit of the photoreceptor cell in conventional electrical terms. The branching of the dendritic circuit is shown only symbolically by the branches emanating from the CC. The circuit is seen to be a conventional differential amplifier with the one input connection open and excited only by quantum mechanical processes. The current flowing in the common emitter circuit is seen to control the operation of the circuit. If the two bases were set to the same voltage, the current from the common bias circuit would divide evenly between the two transistors and this would establish the quiescent output voltage and current for each transistor. However, the open base essentially cuts off the quiescent current in that transistor. This situation forces all of the bias current to pass through the active transistor and therefore changes its quiescent operating point to a lower voltage level, a low level of polarization.

As indicated briefly above, it is probable that the poda bias circuit is of very low impedance, consisting of the battery and a very low resistance diode. Under this condition, the circuit will operate without exhibiting any signal compression in the output signal waveform compared to the input waveform. If the resistive component of this circuit was considerable, positive feedback would be introduced. This would probably result in additional signal gain, and also some increase in the rate of initial signal rise and some saturation in the output waveform. Based on the literature, these characteristics are not observed in the PC output.

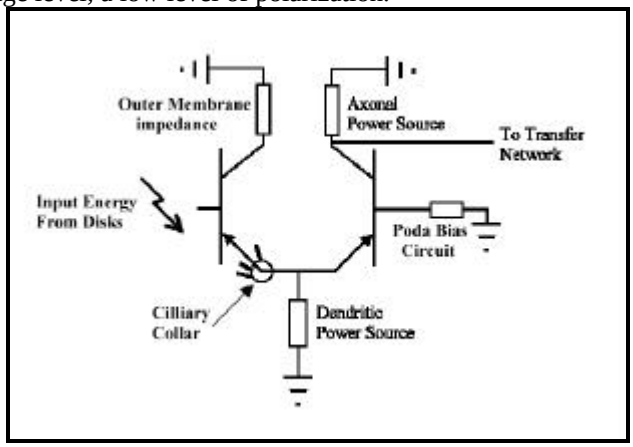


**Figure 9.2.3-2** Circuit diagram of the photoreceptor cell

Each electron induced into the open base lead will allow approximately 3500 electrons to pass through that transistor. The bias current is essentially fixed: hence, the current through the output transistor is actually reduced by the same amount. This causes the output voltage of the output transistor to rise, i. e., the output signal drives the axoplasm to a point of Hyperpolarization.

An important confirmation of this circuit hypothesis is provided by Baylor et. al.[3] They showed that if the OS was removed from the IS in a living cell, the electrical current collected from the broken connection was of the same magnitude as the *maximum* current that could be measured by collecting all of the current appearing to emanate from the OS (actually from the dendritic structures surrounding the disks)under saturating conditions.

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[3]Baylor, D. Lamb, T. & Yau, K.-W. (1979) The membrane current of single rod outer segments. J. Physiol. vol. 288, text-figure 2 on page 594

This corresponds to breaking the circuit just to the right of the ciliary collar (CC) in Figure 9.3.2 and connecting that point to the ground potential. The current measured is exactly what would be expected and this is the maximum current available from the dendritic power source. This situation is a clear indication that the power source of the dendrite is physically located within the IS portion of the photoreceptor cell. As a subject for verification, it can also be predicted that the output transistor went to cutoff and its output voltage also went to maximum, i. e., maximum polarization.

It should be pointed out that care is required in measuring the "signal" current associated with the PC. Note carefully that the "signal" current measured in the dendritic structure, to the left of the dendritic bias circuit is equal in magnitude and opposite in electrical sign to the "signal" current measured to the right of the bias circuit in the axonal portion of the circuit. The "signal" current in the dendritic structure is not the output signal. The output signal is the signal presented to the transfer network and associated with the axoplasm.

The photoreceptor cell is a good example of a neuron which contains multiple Activa types, multiple Activa of the same type, and possibly a continuous form of Activa. The photoreceptor cell is not actually sensitive to light. It contains a quantum mechanical/electrical transducer located within the inner segment of the cell. This transducer is in intimate contact with an extracellular structure, the Outer Segment, which contains the photo-(quantum)mechanical transducers. The disks within the Outer Segment are the true photoreceptors of vision.

### 9.2.3.3 Bias point of the adaptation amplifier of the photoreceptor neuron

Due to the open connection at the base of the Activa of the adaptation amplifier, there is no quiescent current through the adaptation amplifier in the absence of photon excitation of the eye. With excitation, current flows through the Activa. The output signal is taken at the emitter of the Activa. The emitter shares an impedance with the emitter of the distribution amplifier is a configuration that attempts to hold the current through this common impedance constant. While the emitter current rises during photon excitation, the voltage across the emitter impedance remains fixed. As a result, the current through the emitter of the distribution amplifier is reduced with photon excitation.

### 9.2.3.4 Bias point of the distribution amplifier of the photoreceptor neuron

The collector (axoplasm) potential of the distribution amplifier is normally biased to a quiescent value in the absence of photon illumination. This potential is determined by the difference between the base terminal potential and the emitter terminal potential of the Activa. Upon photon excitation of the eye, the potential of the axoplasm rises (becomes more negative) toward its cutoff potential. This potential is the intrinsic axoplasm potential (associated with electrostenolytics) and not the intrinsic axolemma potential. Note the intrinsic axoplasm potential is not its quiescent potential. The increase of the axoplasm potential to its intrinsic value does not imply any kind of "overshoot" or unusual condition with respect to the axoplasm potential.

### 9.2.4 Typical changes in signal amplitude among analog neurons

In summary, the act of increasing the illumination applied to the eye causes characteristic changes in the signal levels of each type of analog neuron in the retina. The emitter current of the adaptation amplifier increases. The pedicel potential of the photoreceptor becomes more negative. The axoplasm of the bipolar cell also becomes more negative. The axoplasm of the lateral cells can become either more positive or more negative depending on the predominant spectral range of the incident illumination.

## 9.3 The pulse and hybrid signaling neurons

The pulse and hybrid neurons are concerned with the transmission (projection) of neural signals over distances too great to be accomplished effectively by analog signaling. They are found in signal paths between the retina and the mid-brain (both LGN and Pretectum), between the mid-brain and the cortex, within the cortex, and elsewhere in the neural system.

## 9.3.1 The ganglion neuron of the retina and mid-brain

Ganglion neurons, by whatever name, are found wherever it is necessary to transmit neural signals more than a few millimeters. They are introduced as a matter of power efficiency at the expense of some time delay. In the visual system, they are typically found at the output of the retina and at the output of the mid-brain sections delivering signals to the cortex or the neuro-musculature of the eye.

The ganglion cell is a neuron that depends on internal feedback and capacitive loading for its normal operation. Its normal function is to encode an analog signal into a pulse stream using time delay modulation. Its normal operation involves accepting an analog (electrotonic) signal at its input and generating a pulse (Action Potential) signal at its output. It accomplishes this with the same morphological, topological and electrical element features as in the Bipolar Cell but it employs different values of the parameters, **Figure 9.3.1-1**.

**Figure 9.3.1-1** shows the ganglion cell in its typical topology. It is receiving an input directly from one Bipolar Cell and an input from a Lateral Cell. The output is shown connecting directly to a synapse in the Lateral Geniculate Body of the Brain--and possibly to a second location elsewhere in the Brain. The axon may be significantly longer than shown in this figure relative to the dendrite shown. If it is longer, there are two distinctly different situations to be addressed, the introduction of myelination and the introduction of Nodes of Ranvier.

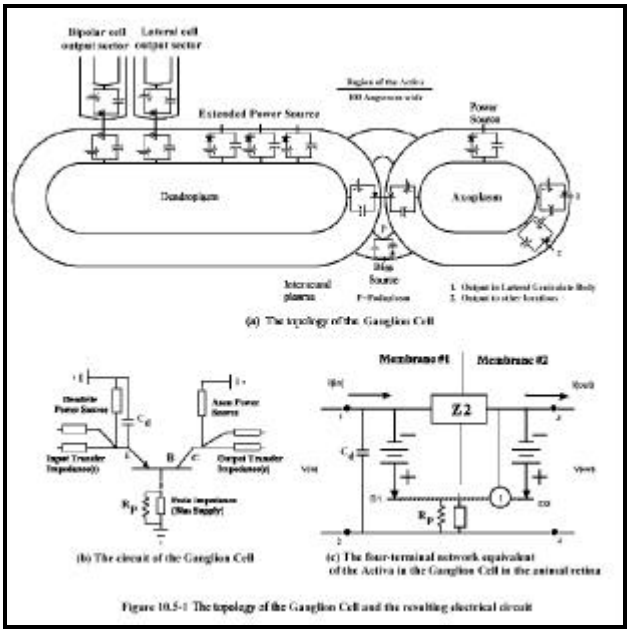


**Figure 9.3.1-1** Ganglion cell topology and circuit diagram. (A); the topology of the ganglion circuit. (B); the electrical schematic of the cell. (C); the four-terminal equivalent circuit of the Activa within the cell circuit.

There are two parameters that are key to the operation of the Ganglion Cell; the poda impedance and a large capacitance (relative to the ones encountered so far). In the Ganglion Cell, the poda impedance is so large that it actually distorts the Activa transfer function due to internal feedback. If this distortion is large enough and the biases are properly arranged, the output characteristic of the Ganglion Cell will be bimodal. If, in addition, there is a large capacitance shunting either the emitter or the collector terminals of the Activa, the circuit will not only be bimodal, there will be sufficient phase shift related to the feedback to cause the net feedback to be positive. This positive internal feedback will put the circuit in a position to oscillate in response to a sufficiently large input signal. It may only oscillate once, or it may oscillate continuously between these two modes. If it oscillates continuously, its frequency will be determined by the time constant of the circuit containing the capacitor and the time constant of the transfer impedance closest topologically to the capacitor. The figure emphasizes these two features by showing them explicitly in (b) and (c) and implicitly in (a).

Note in (a) that an extended power source sector in the wall of the dendrite will automatically provide a significant shunt capacitance between the dendroplasm and the interneural plasma. This capacitance is shown as $C_d$ in (b) and as $C_e$ in (c). A similar result could be obtained in the axon region (not shown). At present, there is no data in the literature that indicates whether the capacitance needed for action potential generation is in one location or the other. The resistive component in the poda lead is not as easily shown graphically in (a). The smaller the sector of the external poda membrane or the longer the poda conduit, the larger the resistive component of the diode characteristic. Thus $R_p$ is shown explicitly only in (b) and (c).

In normal operation, the Ganglion Cell is biased to the cutoff condition under quiescent conditions. The axoplasm is therefore at a high voltage (it is highly polarized). If an electrotonic signal is applied to the input, nothing will happen until the voltage between the emitter and the base is raised sufficiently to begin to turn on the Activa. At that time the collector voltage will begin to fall in proportion to the input current. When the emitter to base voltage becomes large enough to reach the negative impedance of the operating characteristic, the current will change abruptly to the point controlled by the impedance mentioned above. In the absence of a capacitor, it will stay at that point until the emitter to base voltage is reduced, at which point the output current will snap back to a low value according to the operating characteristic. Details of this process can be

found in Appendix B (B.3).

This is the typical situation for the Ganglion Cell in the absence of sufficient capacitance. This characteristic has been observed in ganglion cells and some lateral signal processing cells under non-*in-vivo conditions, i. e.*, generally where a plasma has been tampered with. It is this operating cycle that is addressed by Tasaki[4] in his Two Stable State Theory although his theoretical foundation does not recognize the negative impedance characteristic of an Activa with a podal impedance. Absent the concepts of an Activa and internal feedback, his electrical circuit, with arbitrary variable resistors, and his explanation of the measured I-V characteristic (figure 7) is less than satisfying. His description of what constitutes an action potential apparently includes any square wave.

Inoue et. al.[5] present data, compatible with the theory presented here, on how this bimodal neural response is affected by pharmacological and temperature changes.

If there is sufficient capacitance in either the emitter or collector to ground circuits, the circuit will operate as above except the circuit will now oscillate once the emitter to base voltage has exceeded a certain value. The width of the pulse will be determined by the circuit parameters within the cell. The time between pulses will be determined by the capacitor and the input current to the cell. These characteristics are clearly seen in the literature.

It is obvious that the so-called refractory period of a ganglion cell is not a real or fixed parameter. It involves the sum of the time intervals due to a series of individual steps (see **Section 8.5.2.4**). Under normal operating conditions, a small step input current will never cause the cell to generate an output pulse. If a very large step input current is encountered, the cell will generate an output pulse almost immediately, limited by the electrical rise time of its internal components. For in between conditions, the delay before the first pulse from a ganglion cell is a direct function of the input current, the input capacitance and the temperature. Furthermore, the input current occurs at a finite time after any radiation falls on the associated photoreceptor in the signal path. This delay is a direct function of the radiant level and the temperature. To explore the time dependency of the output further, see Appendix A.

The output of the ganglion cells in response to photon excitation of the eye is described differently than in the case of the signal manipulation neurons. The primary concern is the pulse-to-pulse interval between the action potentials produced. Discussion of hyper- or de-polarization is seldom found in the literature. For those cells designed to accept monopolar signals from the bipolar cells, the interval between action potentials is typically decreased for higher levels of photon excitation. This results in a higher average pulse frequency for the action potentials if the illumination level is held high for a short interval but not long enough for the adaptation amplifier to become effective. However, in any case, it is not the frequency of the action potentials that is related to the signal. In the case of the ganglion cells designed to accept bipolar signals, the pulse interval and related pulse stream average frequency are more complex. In the case of the P-channel, increased photon excitation in the M-channel is generally found to reduce the pulse-to-pulse interval and therefore increase the average pulse stream frequency. Conversely, increased photon excitation in either the L- or S-

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[4]Tasaki, I. (1968) Nerve excitation: A macromolecular approach. Springfield, Ill: Charles C. Thomas also in Tower, D. (1975) The basic neurosciences, vol. 1 NY: Raven Press pg. 177-195

[5]Inoue, I. Kobatake, Y. & Tasaki, I. (1973) Excitability instability and phase transitions in squid membrane under internal perfusion with dilute salt solutions. Biochem. Biophys. Acta. vol. 307, pp. 371-377

channel is seen to extend the pulse-to-pulse interval and therefore lower the average pulse stream frequency.

In terms of polarization, the action potentials always are positive going with respect to the negative potential of the axoplasm during the quiescent period of the circuits operating cycle. In this sense they are depolarizing. The net amplitude of the positive going change may exceed the original net negative potential of the axoplasm. Although this results in a net positive potential for the axoplasm relative to the surrounding matrix, this short term potential is not directly related to the intrinsic potential of the average axolemma or of the intrinsic potential of the zone of the axolemma dedicated to electrostenolytics. The magnitude of this "overshoot" is a function of the ratio of some of the impedances used in the oscillator circuit of these neurons.

Rodieck has provided a survey of the morphology of the ganglion cell in the retina and identified five major varieties including a total of at least 12 types[6]. Of these varieties, some project to the pretectum, some to the magnocellular region and some to the parvocellular region. The latter two project via the LGN. The axons of all midget ganglion cell types are known to project to synapses with parvocellular layers. Separate studies indicate that the parasol ganglion cells project to synapses with the magnocellular layers. Information on the cell types projecting to the Pretectum is incomplete in the literature. Rodieck shows a figure based on a Macaque and indicates that some parasol cells do project to the Pretectum in that case.

### 9.3.1.1 The introduction of myelin in connection with the axon

As indicated above, a lengthening of the axon of the ganglion neuron relative to the bipolar neuron can introduce capacitance in shunt with the other impedance elements of the output circuit and lead to oscillation in the ganglion circuit. However once a critical level of capacitance is reached, additional capacitance is not desirable. It requires the Activa to switch more current between the input and output circuit to achieve the same level of action potential amplitude. To avoid this problem while achieving maximum axon length, a portion of the axon is wrapped in myelin. This process has the effect of thickening the dielectric between the axoplasm and the surrounding plasma and thereby lowering the effective capacitance per unit length of the axon.

### 9.3.1.2 The introduction of the Node of Ranvier in connection with the axon

Wrapping a significant part of the axolemma in myelin is an effective way of allowing the axolemma to be increased in length. However, it is not an adequate modification if the action potential is to be projected over distances beyond a few millimeters. In that case, active signal amplification is necessary. This can be provided by analog amplifiers while accepting the degradation of the signal waveform implicit in transmitting a pulse waveform over a relatively simple electronic transmission line, e.g., one without equalization stages to compensate for the normal phase distortion per unit length. The alternate approach is to regenerate the waveform. This actually involves replacing the received signal waveform with an alternate waveform, typically of similar waveshape. This regeneration of the waveform is the purpose of the Node of Ranvier. The process can be repeated indefinitely along the neuron since there is no accumulated waveform distortion in this approach.

The Node of Ranvier is a driven monopulse oscillator such as those discussed in **Section 9.3.3** below. This oscillator is unique in that it is introduced between sections of interaxon formed by subdividing the axon of a single cell. The resulting ganglion cell takes on a greater degree of complexity. However, the complexity is a result of replication and not new techniques. See **Section 9.3.4.** The difference between a ganglion with and without Nodes of Ranvier is a subject of interest in morphology. However, if the questions of genesis and

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[6]Rodieck, R. (1998) The first steps in seeing. Sunderland, MA: Sinauer Associates, pg. 271-291

metabolism are set aside, the difference is trivial based on cytology and signaling performance.

### 9.3.1.3 Bias point of the parasol (luminance channel) ganglion neurons

The ganglion cells associated with the luminance channels (and probably the individual direct channels to the mid-brain associated with the individual photoreceptors of the foveola) are biases to be inoperative in the absence of photon excitation of the eye. Upon excitation of the bipolar cells converging on a given luminance channel ganglion cell, these cells transmit a signal to the ganglion cell and it generates action potentials with a period determined by the intensity of the net excitation. This excitation from the bipolar cells is a positive going change in potential. As in the case of the bipolar neurons, it is the sum of the excitations received from the individual bipolar cells that is impressed upon the emitter circuit of the ganglion cell. In some cases, the sum excitation may differ slightly from the actual excitation applied to the emitter input. This is due to the presence of a pre-emphasis circuit associated with the input impedance of the cell. This circuit tends to emphasize the signal during rapid changes in signal amplitude. It can be important in reducing the time interval before the occurrence of the initial action potential.

### 9.3.1.4 Bias point of the midget (chrominance channel) ganglion neurons

The ganglion cells associated with the chrominance channel (and other differencing channels where appropriate) are biases to be operative and generate a continuous series of action potentials in the absence of photon excitation to the eye. This continuous series has a nominal pulse-to-pulse interval of about 33 milliseconds. Upon a net change in excitation from the preceding lateral cells converging on the ganglion cell, the time interval between the action potentials will change. This interval may be increased or decreased depending on the net change in potential of the emitter terminal of the ganglion cell.

### 9.3.1.5 Signal input via the poditic conduit

Although not a well-developed situation in the literature, there are indications that some ganglion cells do have arborized poditic conduits that accept signals. These signals would be treated as out-of-phase with respect to the dendritic inputs. They could therefore subtract from the critical signal amplitude needed to initiate generation of an action potential. If an exceptionally large signal, it could be considered inhibitory. Normally, it would merely cause a delay in action potential generation in both the luminance and chrominance channels.

## 9.3.2 The stellate neuron of the mid-brain and cortex

Stellate neuron is the name given to those neurons designed to accept action potentials and to generate an output potential related to the time interval between the pulses in such a pulse stream. They effectively decode the pulse stream, generated by the ganglion neurons and regenerated by the projection neurons, in order to recover a facsimile of the original analog signal presented to the ganglion neurons. In this respect, the cells operate in a manner analogous to a ratio detector circuit in a FM radio. The ratio detector circuit is slightly different from the frequency discriminator circuit used in higher quality FM radios that are optimized for receiving music.

Depending on the quiescent bias between the emitter and the base of the Activa within the stellate neuron, the average output level may be at the intrinsic axoplasm potential due to electrostenolytic action, or it may be at a less negative quiescent value caused by continual current flow in the collector circuit of the Activa. If it is at the intrinsic level, the signal output is necessarily a positive going one, a de-polarization, for increase signal

input levels. If the quiescent level is less negative (closer to zero) than the intrinsic electrostenolytic level, the output signal can be either more positive (de-polarizing) or more negative (hyperpolarizing) depending on the signal applied to the input of the circuit.

### 9.3.2.1 Cytology of the stellate neuron

The cytology of the basic stellate neuron is similar to that of the basic ganglion cell compared to the fundamental neuron typified by the bipolar neuron. The output impedance associated with the stellate neuron consists of a larger capacitance than found in the bipolar neuron. In this case, there is little or no feedback through the poda impedance and the circuit is not subject to oscillation. The capacitance is so high, that the circuit accepts individual current pulses injected into the axoplasm by the Activa and does not dissipate the resulting change in voltage within the time interval expected for the following action potentials. Thus the average voltage of the axoplasm becomes a facsimile of the average current caused by the injection of a unit charge in response to each action potential arriving at the stellate neuron divided by the pulse interval between those action potentials.

### 9.3.2.4 Bias point of the stellate neuron

The bias point of the stellate cells as a group is undetermined at this time. The bias point can have two different values depending on the configuration of the output circuit of the stellate cells and the input circuits of the following neurons.

In general, the input circuit of the stellate neurons receiving luminance (or other monopolar) signals will be biases so that no output signal is impressed on the input circuits of the following neurons in the absence of photon excitation to the eye. This is because of the time interval in the denominator of the above mathematical expression. Under this condition, the Activa will normally be in cutoff and the axoplasm will normally be at the intrinsic potential of the electrostenolytic process supporting that conduit.

Conversely, the input circuit of the stellate neurons receiving chrominance (or other bipolar) signals will be biases so that no output signal is impressed on the input circuits of the following neurons in the absence of photon excitation to the eye. However, the output circuit must be ready to reproduce either a positive going or negative going output. Therefore, the output circuit must be at a potential below that of the intrinsic potential of the electrostenolytic source for that conduit. This requires the Activa within such a neuron to be conducting during the quiescent interval.

### 9.3.3 The projection neurons

Projection neurons are used throughout the neural system. They are specialized in that they accept only action pulses at their input and generate action pulses at their output. They contain Activa circuits that are configured as driven monopulse oscillators. In the absence of adequate input stimulation, these circuits remain in their nominal quiescent condition. For low levels of excitation, they may produce a low level signal that is a reproduction of the input signal. However, this output is not the normal, higher amplitude, and characteristic action potential of the circuit. The peak in the nominal action potential of this circuit occurs following a significant time delay relative to the peak in the excitation waveform. The rise time to this peak is determined by the product of a resistive and capacitive impedance in the projection neuron circuit. Following switching at a time near the peak in the waveform, a different combination of resistive and capacitive impedances determines the fall time of the decay characteristic of the action potential.

### 9.3.3.4 Bias point of the projection neuron

Being that the projection neurons operate strictly as signal regenerator circuits, they are biased to produce no output signal in the absence of excitation from one or more preceding projection or hybrid neurons. The individual Activas are normally biased to cutoff with their axoplasm at, or very near, the intrinsic axoplasm potential determined by their electrostenolytic supply source. They require a positive going pulse at their input to drive them into conduction. If the positive going pulse is of sufficient amplitude, the circuit will be driven into oscillation. Upon adequate excitation, these circuits generate a single monopulse or action potential and then return to their quiescent condition.

## [[ new part 9.4

## 9.3.4 A neuron containing a chain of Activas

In the past, the conventional wisdom was that the axon of most neurons consisted of a continuous core with the signal propagated along the axon in a continuously decaying manner similar to an electrical cable. The purpose of the Nodes of Ranvier was essentially unknown and the purpose of the myelin sheath was usually related in vague language to the insulation surrounding an electrical cable. More recently, it has been recognized that the signal along an axon is regenerated at each Node (with the mode of signal transmission described as salutatory) and that the axon actually consists of semi-independent regions connected at the nodes; in the fashion of a string of sausages. **Figure 9.3.4-1** illustrates this from an electron microscope image. This image clearly shows that the core of the axon is not continuous at the node, there is a juxtaposition of membrane walls. The active region of the Node, the area of the Activa, is approximately 100 Angstrom wide and 100 Angstrom in height (probably a diameter).

Similar figures can be found in Waxman, Figure 2-6, 2-18 & 2-19. Also 2-20 is of interest.

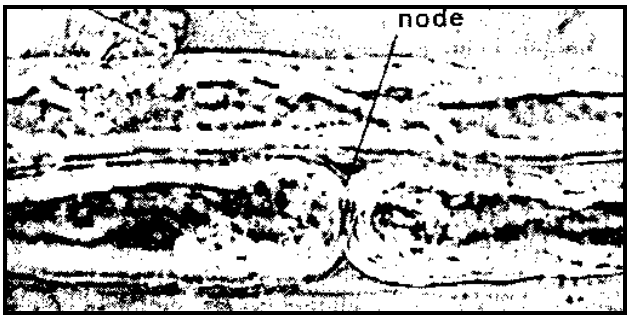


**Figure 9.3.4-1** CR Ranvier's Node isolated in living tissue by dissection. The internal synapse between the two segments of the axon is clearly seen. It is also clear that the point of contact is extremely small and that this region has direct conductive contact with the medium surrounding the nerve at this "void" in the myelin sheath. From Ottoson, 1953.

**Figure 9.3.4-2** presents two cartoons of the above electron micrograph. In this case, the axon of the neuron is subdivided into a number of sections that are electrically isolated by membranes. Section n has a steady state electric potential which is determined by the integration of all of the potentials along its membrane, except where it is insulated from the surrounding interneural plasma by the myelin sheath. It may exhibit a transient electrical potential due to its receiving a charge (current) at its distal end which is not shown. In **Figure 9.3.4-2(a)**, the two sections are close but not in intimate electrical and diffusional contact. The region between the two membranes can be designated a pseudo-synapse or just synapse at the discretion of the reader. A current may pass from the axoplasm of section n into the synapse area if the overall electric potential applied to the membrane n is appropriate. In theory, this or an equal current may similarly pass on into the axoplasm of section n + 1 if its internal electric potential is appropriate. However, this condition is extremely unlikely in light of the diode characteristic of the post synaptic membrane. No signal amplification will occur under this condition in any case, only a transmission of the charge (current). Over a number of sections, the signal level will continue to decay due to the finite resistivity of the axoplasm and the inevitable shunt capacitance through the exterior

wall and/or myelin sheath.

If the two sections are brought closer together until the two membranes are in intimate contact and their diodes share a common cathodic area, the situation changes. In this case, a current will flow out of axoplasm n if the diode in membrane n is forward biased. In addition, this same current will flow into the axoplasm of section n + 1 even if the diode associated with that section is reverse biased, *by means of transistor action*. Signal amplification (in the impedance changing sense) will occur under this condition. However, two additional critical parameters are required for amplification of the signal voltage. To regenerate the action potential, positive feedback must be implemented between the post and the pre-synaptic terminals. This can be done by providing a significant amount of reactive impedance (a capacitance) shunted across either terminal and the INM and the introduction of an impedance between the junction area and the surrounding INM. **Under these conditions, the received action potential will be regenerated at full amplitude in the post synaptic interaxon.** With the signal regenerated in voltage at each node, but without a significant change in the current, the signal can propagate indefinitely in a salutatory manner.

To provide the flexibility needed to arrange the various electric potentials, it is very desirable that the common cathodic area between the two membranes can be contacted electrically and circuit elements introduced between the cathode and the interneural plasma. As indicated earlier, this can be done in two ways: The interneuron plasma located in the narrow region of the synapse can be considered an impedance in itself; alternately, a separate membrane can be used to isolate the cathode connection from the interneuron plasma. This membrane will create another zone of plasma and an additional set of electrical circuit elements associated with it. The second case, illustrated in Figure 9.4.2(b), is clearly the most flexible but it may not be needed in most situations.

Notice in both frames of **Figure 9.3.4-2** that the region of membrane associated with each section that is not isolated by the myelin sheath can provide regions of electrical activity independent of the junction area. This provides an additional degree of freedom since the membrane in this area can effectively control the steady state electric potential of the entire section. Alternately, the membrane in this area can be completely passive electrically.

The configuration of **Figure 9.3.4-2** is ideal for the purposes of a projection neuron, it allows for an indefinite number of essentially identical axonal sections to be employed, with the original action potential generated at the dendrite/axon interface being regenerated at each Node of Ranvier.

With this topology and circuitry in mind, portions

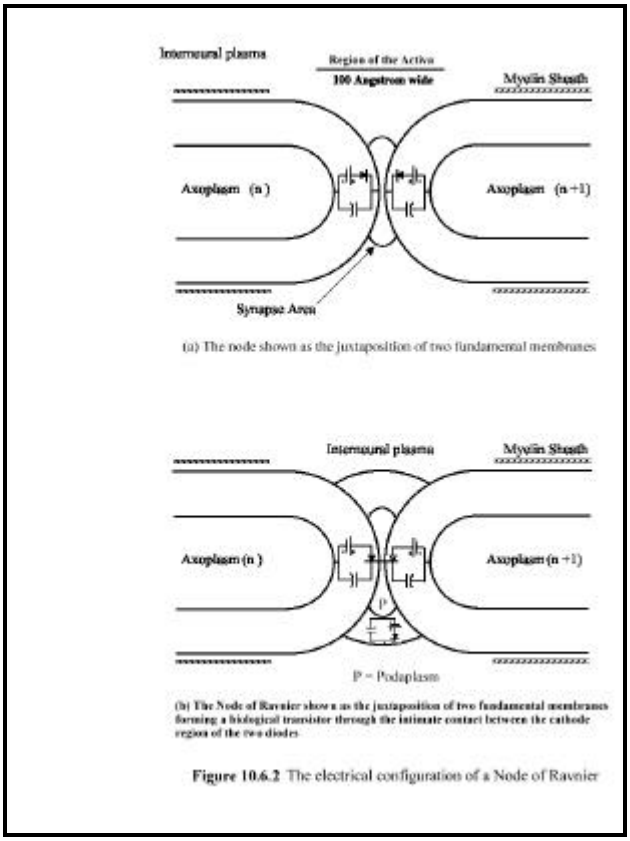


**Figure 9.3.4-2** The electrical configuration of the Node of Ranvier. (A); the Node shown as the juxtaposition of two membranes. (B); the Node shown with a distinct poditic conduit.

of Tasaki's[7] text make very interesting reading because the effects of pharmacological treatments become clearer. However, his treatment of a series of interaxons and Nodes of Ranvier as a passive cable of only resistors is far too elementary.

He notes that the effect of an anesthetic on the myelinated portion of a neuron is virtually nil. It is only when it is applied to the area of a Node of Ranvier (or other terminal area) that the anesthetic has an impact.

**Figure 9.3.4-3** is an optional figure [similar to that in (c) of figure 10.4.4-2] illustrating the configuration of a neuron containing a chain of similar Activas. This configuration will be discussed more completely in **Section 10.4.4**. The neuron can be considered a projection neuron in the absence of a hybrid (analog to pulse) circuit at its head end or a ganglion cell (with such a hybrid circuit). In either case, it consists of a series of Nodes of Ranvier.

As indicated in the earlier discussions, Nodes of Ranvier and other driven monopulse regenerators need not have a significant current through the Activas during the quiescent period. They are typically biased to cutoff during this period. The literature is ambiguous whether all Nodes of Ranvier involve a poditic conduit or whether, in some cases, the base region of the Activa is in direct (although restricted from an impedance perspective) electrical contact with the surrounding interneural matrix. As long as the impedance is appropriate and not excessively high, the difference is trivial. However, if the base region is in direct contact with the interneural matrix, the Node of Ranvier is analogous to the Synapse to be discussed next.

Note that the interneuron conduit between two Nodes of Ranvier is Janus-like. It appears to be a dendrite to the previous Node of Ranvier and to be an axon to the following Node of Ranvier. It is in fact a simple conduit with two regions of electrostenolytic activity and a perpetual potential difference between its extreme ends for biasing purposes. Except during an action potential, little power is consumed since no signal current flows along the conduit. During an action potential, both electrostenolytic regions may be active. Note that the electrostenolytic activity of these regions reduces or eliminates the necessity of an external current flowing in the INM from the region of one Node to the other in order to complete the conventional closed current path.

[7]Tasaki, I. (1982) Physiology and electrochemistry of nerve fibers. NY: Academic Press. pp. 37-61

## 9.4 The coupling between neurons–the SYNAPSE

Although it has only been in recent times that the biological community would consider the possibility that the junction between two neurons might have an electrical aspect, they are now speaking more frequently of a "gap junction" which is electrical in nature. In the evolution of this work, the similarity between the structural form of the Nodes of Ranvier and the so-called gap junction cannot be ignored. Close study indicates that the gap junction involves the close juxtaposition of two cell walls in the same manner as in the Node of Ranvier. By application of appropriate voltages to the plasmas on each side of these juxtaposed cell walls relative to the fluid in the space between the walls, transistor action will occur[8]. This transistor action can be used for several purposes.

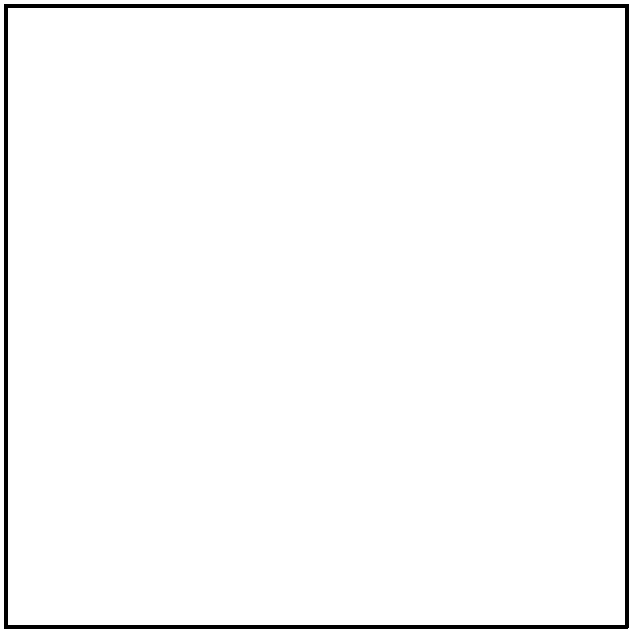

**Figure 9.4.1-1** [SEE FIGURE 10.4.4-2] A neuron containing a series of Activas.

The simplest purpose is for the creation of a nearly lossless current path between the two conduits. Positioning the two neurons so that the axon of one is in close juxtaposition to a dendrite of the other and establishing the proper potentials between them is all that is necessary. This connection allows the transmittal of an electrical signal from one neuron to the other without significant loss and no chemical action at all with respect to the signal. The only chemical action is metabolic in nature. It involves establishing the appropriate voltages. To achieve this result, the transistor formed is employed in what is conventionally called the common base configuration. This configuration does not normally exhibit any voltage amplification and the ratio of the output current to the input current is very close to 1.000. An Activa used in this "gap Junction" role will be defined as a Type BS with the S derived from the name synapse.

A second purpose for employing an Activa at the intersection between an axon and one or more dendrites is to act as a current amplifier and a distribution amplifier. This can be achieved by connecting the axon to the input of an amplifier capable of current amplification and then distributing the resultant current to the various dendrites as appropriate. In this case, the amplifier is usually embedded within a neuron and such a neuron in the retina is typically described morphologically as a bipolar cell.

At this point, it is important to define a synapse from a functional perspective. A synapse is a functional junction between the electrical circuits of an axon and a second neuron, a muscle or a gland. It is typically comprised of a common base (common podium) connected Activa and the bio-energy supplies necessary to bias the axon and input structures appropriately. The common base connected Activa provides the signal transmission path. The bio-energy supplies are provided by means of diffusion from the surrounding medium and/or the nucleus of the respective cells.

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[8]U.S. Patent --Fulton, J. (1998) Active Electrolytic Semiconductor Device

The synapse is capable of transmitting an analog or pulse signal but is not capable of signal regeneration or signal summation (addition or subtraction).

## 9.4.1 The configuration of the synapse

When reviewing the topography of a synapse in light of the earlier description of a fundamental neuron, it becomes clear that the synapse might be considered an active circuit in its own right. This assumption is true. The typical synapse of the animal neural system consists of an active electrolytic device connecting two conduit segments. It does this in a manner only marginally different from that of any Node of Ranvier. **Figure 9.4.1-2** shows the topography, the topology and the basic electrical schematic of such a synapse. In (a), the axon and the dendrite have changed places and the podalemma provided in the case of the Activa internal to a neuron has been eliminated. The only impedance connected to the base of the Activa within the synapse is now due to the constricted passage between the Activa base and the surrounding interneural plasma. The axoplasm potential is now controlled by the pre-synaptic Activa and the impedances related to the axoplasm power supply and the input impedance of the Activa forming the synapse. The current available to the post synaptic Activa is the result of injection of current through the Activa of the synapse. Frame (b) reduces these comments to the equivalent circuit of the synapse and (c) shows the four-terminal equivalent circuit of the synapse. In both of these frames, the light vertical line is the centerline between the two membranes of the junction. There is no appreciable lumped capacitance associated with any of the terminals of the Activa. Therefore, it is not susceptible to oscillation. As in the earlier cases, the impedance Z2 is significantly larger than any other impedance in the circuit and can be considered an open circuit in neural systems. The dashed line represents the "transistor action" occurring between the pre-synaptic diode and the current source injecting current into the collector circuit of the Activa. The voltage sources shown in (c) are the intrinsic voltage sources associated with the asymmetrical molecular bilayer membrane in the area of the synapse. These are distinctly different from the power sources shown in (b).

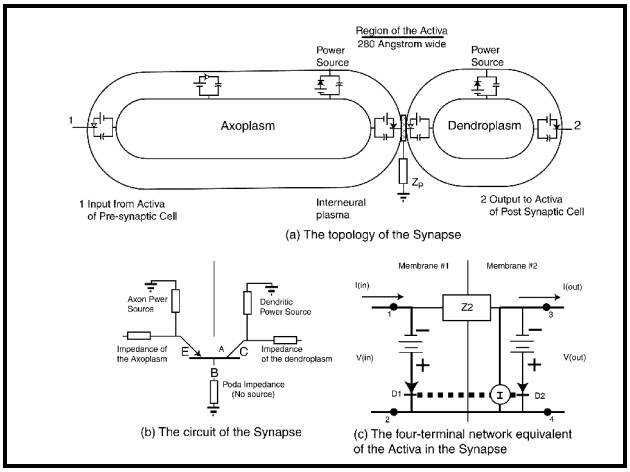


**Figure 9.4.1-2** The topography, topology and detailed circuit schematic of a synapse.

## 9.4.2 The detailed morphology of the synapse

Although discussed in greater detail in Chapter 10, it is useful to complete this discussion with a caricature of the fundamental synapse. The literature provides many copies of a simple concept of the synapse as a chemical interface between two neurons. At higher resolutions associated with electron microscopy, a more detailed caricature can be discerned. This caricature is shown in **Figure 9.4.1-3**. The lower part of the figure shows the Activa configuration described above. It provides a very efficient unidirectional flow of signal current between the two conduits. The gap between the presynaptic and post synaptic membranes is only 80-100 Angstrom and is filled with a liquid crystal of hydronium.

> It is important to note that electron-microscopists frequently complain when preparing a sample of a synapse for examination that it is necessary to fully remove a small amount of water on the surface of the axolemma to avoid problems with their vacuum system.

The upper part of the figure shows the chemical materials associated with the electrostenolytic support function. Although these chemical constituents change slightly with signal operations, this is a secondary effect due to electrostenolysis and related to "ion pumping." Although the literature equates these chemical changes to the signaling function and defines some of the chemicals as neurotransmitters, this concept is not required in this work.

## 9.4.3 The synapse as a diode

Referring to (c) in the previous figure, injection of a current into the presynaptic diode results in the generation of a current in the post synaptic circuit by transistor action. This output current does not pass through the post synaptic diode but is created by transistor action, symbolized by the heavy dashed line between the presynaptic diode and the current source, I. The current at the input and the output of the synapse is inherently unidirectional due to the presynaptic diode. It appears that the input current flows through the circuit in the direction of the arrow in the fundamental synapse. This is because the current through the base region of the Activa into the interneural matrix is less than one percent of the current in the direction of the arrow and is normally overlooked. The input and output currents differ by this small difference.

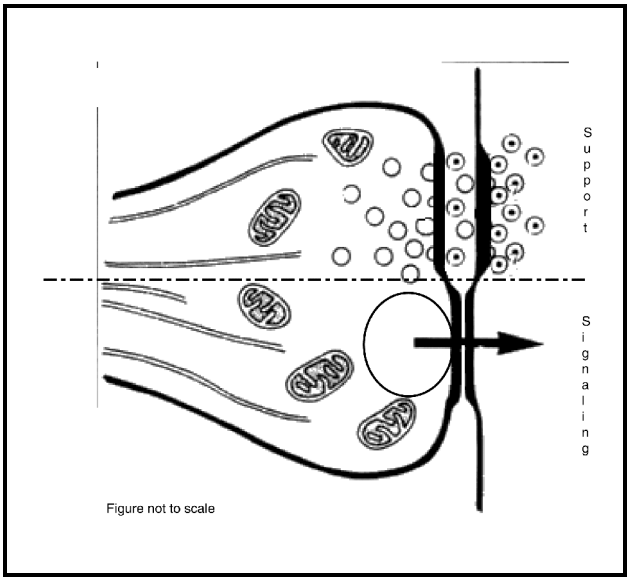


**Figure 9.4.1-3** The fundamental synapse showing both the signaling and support functions. While the support area includes a variety of chemicals, these are not involved in signal transmission. Signaling is facilitated by a three-terminal Activa that can be described as a diode limiting the flow of electrons to the direction of the arrow.

## 9.4.4 The synapse as an impedance

The current passing through the fundamental synapse is determined by two factors. The first is the size of the presynaptic diode which is formed by a small area of specialized axolemma in contact with the hydronium crystal forming the base of the Activa. The second is the potential across that diode. Ignoring the impedance between the base and the INM, this potential is the difference between the instantaneous potential of the axoplasm and the potential of the INM. IN the actual case, the potential may be marginally smaller due to the impedance between the base region and the

INM. Since the current produced in the output circuit is within one percent of the current in the input circuit, it is acceptable to describe the transfer function of the synapse by the input impedance of the presynaptic diode. This impedance is precisely that of the diode. This characteristic impedance can be defined by the reverse cutoff current of the diode. This characterization avoids the problem of defining the instantaneous impedance as a function of the potential across the diode. Note that for bias determination purposes, the static impedance of the diode at a particular potential is determining. However, for signaling purposes, it is the dynamic impedance of the diode that is important.

## 9.5 Other important features

### 9.5.1 Merging and bifurcating signal paths

The above discussion provides a variety of tools that can be used to discuss the merging and bifurcation of signal paths. Where the merging or bifurcation only employs a synapse, no regeneration is involved. The action of the circuit relies upon the following circuit elements. Alternately, if a hybrid neuron is used as the core of the merging or bifurcation process, several situations are possible. Complete description of all of the options available in both the analog and pulse domain is not called for here.

The literature suggests that all of the presynaptic axoplasms associated with the merging of signals can be represented by a voltage source. This appears to be true in both the analog and pulse domains.

#### 9.5.1.1 Merging and bifurcation in the analog signal domain

The merging of the signals from two or more axoplasms via synapses into a single neuroplasm is primarily a matter of the impedance of the individual synapses relative to the input impedance of the Activa in the post synapse circuit. In the analog domain, the result is straight forward and amounts to a summation or a differencing of signals as indicated above. In the case of bifurcation, the situation is similar. If the output of the presynaptic axoplasm is of low impedance, it can act as a voltage source and support any reasonable number of synapses without introducing crosstalk due to circuit loading.

#### 9.5.1.2 Merging and bifurcation in the pulse signal domain

In the pulse domain, the merging of the signals from two or more axoplasms via synapses into a single neuroplasm can be as simple as the analog case. However, there are more options. The options vary with a variety of circuit element impedances and ratios of impedances. They also depend on the refractory state of the subsequent action potential generator or regenerator. In the simplest case, the two pulse streams would merely be merged. The merged pulse streams would then be regenerated by the next Node of Ranvier. This would result in a single pulse stream. However, if the following regeneration circuit exhibits a significant refractory period, the pulse train might be significantly distorted. It is not clear what significance this option would have from an information theory perspective. In a second option, the two pulse streams could be decoded in a post synaptic hybrid neuron circuit, either summed or differenced and a new pulse stream generated. This pulse stream would appear orderly and could represent the difference between two signaling channels. This appears to be the situation, with possibly additional signal manipulation, that happens in the LGN and the Pretectum of the mid-brain before the signals are sent on to the cortex. A third option would be where the two pulse streams are applied to two input terminals of a projection neuron without decoding. In this case, the output would be strongly influenced by the refractory period of the projection neuron. The output pulse stream would be subject to significant distortion, including what might be called inhibition. The integrity of the information content of such a pulse stream would be questionable.

### 9.5.2 Relationship of nuclei to conduits and sheaths

As indicated earlier, while the neuron is considered the fundamental morphological unit of the neural system, it is not the fundamental functional element of the neural system. The fundamental functional structure is a series of interdigitated conduits and active electrolytic semiconducting devices. The nuclei and supporting metabolic elements of a cell are able to support a variable number of conduits and active devices based on topographic considerations. The presence of multiple Nodes of Ranvier is the quintessential example of this situation. Thus, the number of neurons is not directly related to the number of functional units in the neural system.

The method of providing myelin wrapping to a (generally axonal) conduit also differs from a one-to-one relationship. The terminology is also somewhat convoluted in this area. In the peripheral nervous system, the myelin is provided by Schwann cells. In the CNS, it is provided by oligodendroglia cells. The difference between these two cell types appears more procedural than substantive. Both cells are capable of providing a myelin wrap to a number of conduit sections. These conduits need not be associated with the same neural nucleus. Thus, neither the nuclei of the neural cell nor the nuclei of the myelin providing cell exhibit a unique relationship to a specific number of conduit segments. In this respect, figure 5.2 in Matthews[9] and the comments of Afifi & Bergman[10] are inconsistent with other literature. They both imply one nucleus for each segment of myelin wrapping by a Schwann cell in these pedagogical texts. This implication is not supported by other authors.

### 9.5.3 Biasing and the non-uniformity of axoplasm potential

The previous discussion has not concentrated on the precise voltage of the plasma within a given conduit when discussing the biasing of the Activa for two reasons. First, the precision required in specifying these potentials is not supported by the literature. A change of only a few millivolts can be significant when the average potential difference is less than 100 millivolts. Second, there is a difference in potential between the two ends of most conduits. Although the plasma does not exhibit a significant dissipative resistance, it does exhibit a significant time delay in the propagation of a potential from one end to the other. Thus, the two ends of a plasma are typically at different average potentials. This allows the bias voltage applied to an Activa at one end of a conduit to be different from the bias voltage applied to an Activa at the other end.

To specify the actual quiescent bias levels of each node of a multi-stage direct coupled electrolytic circuit requires considerable precision and very careful measurement.

## 9.6 Parametric values of Biological transistors

It is now possible to reinterpret much of the data in the biological literature so as to define the performance of individual Activa, the biological transistors of the various neurons more explicitly. The data presented here will be only preliminary since much new experimentation is expected based on the availability of this model.

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[9]Matthews, G. (1991) Cellular physiology of nerve and muscle. Boston, MA: Blackwell Scientific Publications. pg. 61

[10]Afifi, A. & Bergman, R. (1998) Functional neuroanatomy. NY: McGraw-Hill pg. 19

## 34 Processes in Animal Vision

Based on the voltages measured and the currents encountered in animal neurons, it is clear that all Activa fall in the class of **pnp** type transistors. That is they achieve "transistor action" when negative voltages are applied to their emitter and collector electrodes relative to their base electrode. The voltages used in biological transistors are in general much less than used in man-made devices, where man controls the range for convenience. However, some man-made devices of the super-gain family are limited quite severely in their operating voltage and therefore have characteristics similar to specific Activa.

The principal properties of interest are similar to those found in data sheets for solid state transistors. The 2N2904-2N2907 family of silicon-based *pnp* transistors provide a convenient model. The data sheets are broken into four main areas:

1. a selection guide among the family based primarily on their maximum operating voltage and their current gain, $h_{FE.}$

2. the small signal characteristics stressing the input and output impedances and the maximum internal feedback ratio due to resistance in the base lead as well as noise figure, collector to base time constant etc.

3. the large signal characteristics stressing the rise and fall time characteristics of the device

4. the switching characteristics stressing the rise and fall times under specific conditions as well as the delay and storage times of the device

In the case of the Activa family, category 1, corresponds well to the type of neuron in which the Activa is used, bipolar, ganglion etc. Category 2 will be seen to be most appropriate for the only Activa usually processing small signals, the piezo-electric translator Activa of the photoreceptor cell.

Category 3 is the most appropriate category for most of the Activa of the eye since they typically operate with large signals in a signal processing mode; the output Activa of the photoreceptor cell, and all of the bipolar and lateral signal processing cells. Category 3 and 4 as a group are most appropriate for categorizing the ganglion cells.

Based on this classification, a selection guide for Activa might look like **TABLE 9.6.0.**

**TABLE 9.6.0**
**SELECTION GUIDE FOR ACTIVA**

| Used In Device Type | Max. Breakdown Voltage, $BV_{CEO}$ | Current Gain min/max @ $I_0$ | Application | Comment |
|---|---|---|---|---|
| AT | *10 mV* | *3500* | Low noise amp | Super gain/critical $BV_{CEO}$ |
| AD | >100 mV | 1 (common base) | Distrib. amp | |
| BS | >100 mV | 1 (common base) | Isolation amp | |
| AL | >100 mV | XXX(com. emit.) | Signal proc. amp | Used in many configurations in lateral cells |
| AG | >100 mV | XXX | Encoder amp | Used as voltage controlled oscillator |
| AN | | | | Used in projection neurons |

As developed elsewhere in this work, the maximum open circuit voltage generated by sectors of neuron external membranes with respect to the surrounding plasma is less than 100 mV. Until *in-vitro* experiments are performed to quantify their absolute capabilities, we only know that the Max. Breakdown Voltage of most Activa exceeds this number (with the exception of the type AT above).

The following sections are provided in their incomplete form as a matter of record. As new parametric values are measured for characteristics of these different devices, the tables will be completed.

## 9.6.1 The AT type low noise Activa--used in the photoreceptor cell

The critical situation to note in **Table 9.6.0** is the unique situation with regard to the AT device type; this is the Activa used as the translator between the OS and the neural system. It must provide the highest possible gain with the lowest practical noise level. Because of the unique handling of the incoming photon energy by the transducer in the OS, the signal energy level must be at least 2.34 electron-volts, i.e. 2 times the energy of a photon from a 1.06 micron laser to interface with the L-channel and at least 2.0 electron-volts, i. e. the long wavelength skirt of the M-channel. This allows the energy threshold (known as the forbidden-gap energy, $E_G$) of the AT device type to be not less than 2.0 electron-volts in order to meet both criteria. If the threshold energy level for the excitation of a neural transistor is taken as 2.0, this level is considerably higher than the random energy level of the biological noise at the temperature of the organism, normally taken as 0.026 volts. With this ratio greater than 80 even under low irradiance conditions, the chance of thermally generated charges entering the signal path is extremely low, much less than one in a million. Therefore, charge amplification or "gain" is the principal requirement on this amplifier. Very high gains can be achieved by minimizing the overall thickness of the junction area of the Activa. However, this leads to the danger of an electrical breakdown due to the high electrical fields involved. Hence, to achieve really high gain, it is necessary to severely restrict the potential applied to the Collector relative to the Emitter. The Max. Breakdown Voltage, $BV_{CEO}$, indicates this restriction. To ensure that a similar transistor in a man-made circuit does not encounter a voltage higher than this limitation, the transistor is usually used in a circuit called a differential pair. The translator Activa of vision is also used in a differential pair type of circuit. Devices operated near their $BV_{CEO}$ frequently utilize the effect known as "Avalanche multiplication" to achieve their highest gain. This is a unique process that provides extremely high gain under very low and zero input conditions but provides only nominal gain as the operating current rises and the net voltage applied to the collector falls--a very effective and powerful form of adaptation.

Man-made super-gain transistors of the junction type are not widely used because of their delicacy and the fact that most applications do not enjoy the noise threshold conditions found in the eye. Furthermore, the Metal-Oxide-Semiconductor (MOS) class of transistor and other types of parametric amplifiers have essentially replaced the junction type transistor in low noise applications.

**Table 9.6.1** provides a summary of the small signal characteristics of the Type AT Activa. It is taken from the solid state transistor model but has been expanded to include parameters, such as the intrinsic voltage of the input and output membrane structures. These additional parameters are shown in italics.
These characteristics are marked preliminary as in the first issue of any commercial transistor data sheet. The values apply to any type AT Activa regardless of animal species. However, some of the parameters are more temperature sensitive than others and are so marked.

**TABLE 9.6.1**
**Small Signal Characteristics of the Type AT Activa (preliminary)**

| Characteristic | Symbol | Min. | Max. | Units | Comment |
|---|---|---|---|---|---|
| Maximum Breakdown Voltage | $BV_{CEO}$ | | 10 | mV | estimated |
| Current Gain-Bandwidth Product | $f_T$ | >35000 | | hertz | @ $I_e = 0$ |
| Output Capacitance** | $C_{ob}$ | 0.02 | | pF | output area ~1 $^2$ per branch |
| *Output Intrinsic Voltage* @ $I_e = 0$ | $E_{ob}$ | | | *mV* | |
| Input forbidden-gap energy | $E_G$ | | 2.0 | eV | |
| Input Capacitance** | $C_{ib}$ | 0.02 | | pF | input area ~1 $^2$ per branch |
| *Input Intrinsic Voltage* $I_e = 0$ | $E_{ib}$ | | | *mV* | |
| Voltage Feedback Ratio | $h_{re}$ | | 0 | Used in open base mode* | |
| Small signal current gain @ $I_e = 0$<br>@ $I_e = X$ | $h_{fe}$ | 2500<br>100 | 4000<br>100 | ratio | |
| Output Admittance | $h_{oe}$ | | | mhos | |
| Collector-Base time constant | $r_b'C_c$ | | | ps | @ ..... |
| Noise Figure | NF | | | dB | negligible/not applicable |

* As in all semiconductor devices utilizing transistor action, the type AT Activa is sensitive to external energy impinging on the junction region. Many transducers use a transistor in the common emitter/open base configuration to achieve very high charge transfer gains with zero internal feedback.

** Based on a nominal capacitance/area of 0.02 pF/ $^2$ and an area of 1.0 $^2$ for the active portion of each branch dendrite. There may be additional capacitance due to inactive connecting membrane.

To achieve maximum signal charge collection, the type AT device is found to occur in an essentially continuous form in each of the outer dendrites of the photoreceptor cell. Each dendritic branch collects charge from its interaction with the OS. The charge from all of the dendritic branches is collected at the emitter of the Activa operating as the photoreceptor cell distribution amplifier.

## 9.6.2 The AD type distribution amplifier Activa--in the photoreceptor cell

## 9.6.3 The AB type buffer amplifier Activa--in the bipolar cell

This Activa type is used in the low level current repeater in the bipolar cell. It may be used in a current summing mode where signals from multiple photoreceptors

### 9.6.4 The AL type signal processing Activa--in lateral cells

This Activa type may include more variation in its characteristics than other types because of the variety of applications in which it is used and possible differences in the sizes of the devices among species. This device type is used in all of the signal processing neurons (interneurons) including the horizontal, amercine, and interplexiform cells; and the various subclasses of interneurons defined in the literature.

**TABLE 9.6.4**
**Large Signal Characteristics of the Type AL Activa (preliminary)**

| Characteristic | Symbol | Min. | Max. | Units | Comment |
|---|---|---|---|---|---|
| Maximum Breakdown Voltage | $BV_{CEO}$ | | 500 | mV | estimated |
| Current Gain-Bandwidth Product | $f_T$ | >1000 | | hertz | @ $I_e = 0$ |
| Output Capacitance* | $C_{ob}$ | 0.02 | | pF | output area ~1 $^2$ per branch |
| *Output Intrinsic Voltage* @ $I_e = 0$ | $E_{ob}$ | | | *mV* | |
| Input Capacitance** | $C_{ib}$ | 0.02 | | pF | input area ~1 $^2$ per branch |
| *Input Intrinsic Voltage* $I_e = 0$ | $E_{ib}$ | | | *mV* | |
| Voltage Feedback Ratio | $h_{re}$ | | $10^{-4}$ | | the intrinsic value |
| Small signal current gain @ $I_e = 0$ | $h_{fe}$ | 100 | 400 | ratio | |
| @ $I_e = X$ | | 100 | 400 | | |
| Output Admittance | $h_{oe}$ | | | mhos | |
| Collector-Base time constant | $_{rb,\ Cc}$ | | | ps | @ ..... |

* Based on a nominal capacitance/area of 0.02 pF/ $^2$ and an area of 1.0 $^2$ for the cross sectional area of the active junction of the device. There may be additional capacitance in the circuit due to the dendritic structure associated with the device.

** Based on a nominal capacitance/area of 0.02 pF/ $^2$ and an area of 1.0 $^2$ for the cross sectional area of the active junction of the device. There may be additional capacitance in the circuit due to the axon structure associated with the device.

This type is frequently used in single Activa differencing amplifiers utilizing both the emitter (dendrite) and base (poda) inputs for signal purposes.

## 9.6.5 The AG type switching Activa--in ganglion cells

This device type is used primarily in the encoding amplifier of the ganglion cell as well as in the repeater function of each Node of Ranvier. It is basically a high current driver utilized as a pulse generator/repeater. It is optimized as a waveform repeater when there is a significant resistive impedance in the base lead. It is further optimized for operation as a voltage driven oscillator when the emitter or collector is shunted by a capacitance to the common terminal of the overall circuit and there is a significant resistive impedance in the base lead.

**TABLE 9.6.5**
**Large Signal Characteristics of the Type AG Activa (preliminary)**

| Characteristic | Symbol | Min. | Max. | Units | Comment |
|---|---|---|---|---|---|
| Maximum Breakdown Voltage | $BV_{CEO}$ | | 500 | mV | estimated |
| Current Gain-Bandwidth Product | $f_T$ | >1000 | | hertz | @ $I_e = 0$ |
| Output Capacitance* | $C_{ob}$ | 0.02 | | pF | output area ~1 $^2$ per branch |
| *Output Intrinsic Voltage* @ $I_e = 0$ | $E_{ob}$ | | | *mV* | |
| Input Capacitance** | $C_{ib}$ | 0.02 | | pF | input area ~1 $^2$ per branch |
| *Input Intrinsic Voltage* $I_e = 0$ | $E_{ib}$ | | | *mV* | |
| Voltage Feedback Ratio | $h_{re}$ | | $10^{-4}$ | | the intrinsic value |
| Small signal current gain @ $I_e = 0$ | $h_{fe}$ | 100 | 400 | ratio | |
| @ $I_e = X$ | | 100 | 400 | | |
| Output Admittance | $h_{oe}$ | | | mhos | |
| Collector-Base time constant | $r_b'C_c$ | | | ps | @ ..... |
| **Switching characteristics** | | | | | |
| Delay time | \| | | | | |
| Rise time | \| These characteristics are currently unknown | | | | |
| | \| because they are only a part of the overall | | | | |
| Storage time | \| neuron circuit and cannot be measured | | | | |
| Fall time | \| independently | | | | |

* Based on a nominal capacitance/area of 0.02 pF/ $^2$ and an area of 1.0 $^2$ for the cross sectional area of the active junction of the device. There may be additional capacitance in the circuit due to the dendritic structure associated with the device.

** Based on a nominal capacitance/area of 0.02 pF/ $^2$ and an area of 1.0 $^2$ for the cross sectional area of the active junction of the device. There may be additional capacitance in the circuit due to the axon structure associated with the device.

## 9.6.6 The AN type repeater--in Nodes of Ranvier of Ganglion Cells

This Activa is used in the pulse (action potential) repeater associated with the axon of the ganglion cells. It may be used repeatedly; in each of the Nodes of Ranvier, of a single axon.

**TABLE 9.6.5**
**Large Signal Characteristics of the Type AG Activa (preliminary)**

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| Characteristic | Symbol | Min. | Max. | Units | Comment |
|---|---|---|---|---|---|

## 9.6.7 The BS type isolation amplifier

This Activa is used to interconnect neurons throughout the neural system.. Its normal role is to provide a very efficient unidirectional connection for the flow of current between two conduits. The conduits may be at different electrical potentials.

There are suggestions in the literature that certain subtypes of this type may be formed as a lenticular array of small individual Activas. These small devices would be approximately 85 Angstrom in diameter and on 85-90 Angstrom centers. Their physical parameters would be controlled by a similar array of vesicles on the axoplasm side of the axolemma. These vesicles would also provide the electrical connection between the small Activas and the reticulum of the axon conduit.

**TABLE 9.6.7**
**Large Signal Characteristics of the Type BS Activa (preliminary)**

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| Characteristic | Symbol | Min. | Max. | Units | Comment |
|---|---|---|---|---|---|

## 9.6.8 The AR type signal recovery amplifier

**TABLE 9.6.8**
**Large Signal Characteristics of the Type AR Activa (preliminary)**

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| Characteristic | Symbol | Min. | Max. | Units | Comment |
|---|---|---|---|---|---|

## 9.6.9 The AM type muscle control amplifier

**TABLE 9.6.9**
**Large Signal Characteristics of the Type AM Activa (preliminary)**

| Characteristic | Symbol | Min. | Max. | Units | Comment |
|---|---|---|---|---|---|

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