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INFORMATION PROCESSING IN THE OUTER RETINA

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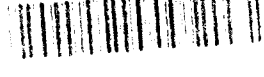

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Memorandum 4469

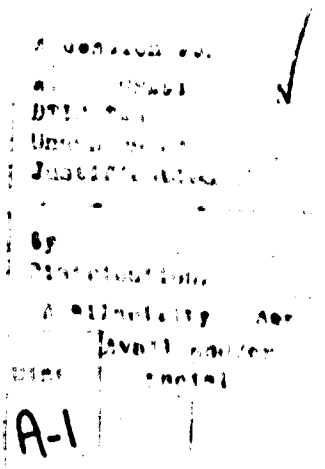
Information Processing in the Outer Retina.

Dr. S. Collins

April 18, 1991

Abstract

Analogue electronics appears to offer the most direct way to mimic the information processing which occurs in the dendrites of neurons. Unfortunately, analogue electronics suffers from a restricted dynamic range, a problem which also occurs in neurons. The study, reported in this memorandum, was therefore initiated to understand how biological neural systems overcome the problems inherent in employing components with an inadequate dynamic range. The inadequacy of the dynamic range available in neurons is most apparent in retinas which deal with an input signal covering 5 decades using components with a dynamic range of less than 2 decades. The 'predictive' encoding hypothesis which has been proposed to explain the function of the outer retina is adopted as a framework for understanding the neurological data discussed. Then, three different, independently evolved, retinas are considered to demonstrate the different implementations of the same underlying principle. The study shows that the problems posed by the limited dynamic range available in both neurons and analogue electronics can be overcome if the system is correctly designed. It also demonstrates that the McCulloch-Pitt model of a neuron, which forms the basis of artificial neural networks, is an incomplete model.



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1 Introduction

A previous study of information processing in the brain[1] suggested that at least some of this information processing occurs within the dendrites of neurons. In dendrites information is almost exclusively represented as a continuous electrotonic potential. This observation, combined with fact that the widely used model of a dendrite is the cable equation[1], also used to model metal tracks on integrated circuits, suggests that dendritic information processing is most directly mimicked by analogue electronics.

Unfortunately, analogue electronics relies upon the ability to fabricate large numbers of identical devices. In practice there are variations in any population of devices, leading to a minimum significant voltage difference. This combines with the maximum allowed voltage difference arising from the power supply to restrict the dynamic range available in an analogue circuit. The dynamic range of analogue circuits can be increased at the cost of employed more area. However, in achieving 8-bit equivalent resolution an analogue approach losses its advantage of compactness when compared to a digital implementation[2]. To maintain the advantage of compactness an analogue system must tolerate a dynamic range smaller than that available in a digital system.

Fortunately, biological neural networks have evolved to tolerate the small dynamic range available in neurons. The study reported in this memorandum was therefore initiated to discover how the biological neural networks have adapted to the limitations arising from the use of analogue signals in neurons. Understanding the information processing which is occurring within the neural systems is a prerequisite to a study into how these systems overcome the limited dynamic range available within their components. This prerequisite naturally leads to a study of sensory systems, which have been studied in detail and can be understood in terms of the characteristics of the information they receive. A particularly well studied sensory system is the retina. There are several reasons why the retina is a good subject for the present study:

- There is a theoretical basis for interpreting the information processing which occurs within a retina.
- There is a sever dynamic range problem in retinal cells. The signals received by the retina have a dynamic range of 10^6. This signal is processed by the retina despite the fact that none of its component neurons has such a large dynamic range, in fact the output neurons only operate over one decade[3]. The result is that at any instant the eye can only distinguish levels of illumination which differ by up to 2% from the overall mean level[1].
- The retina performs data compression. The fact that the retina greatly reduces the bandwidth required to transmit the data it receives is indicated by the fact that the human eye transmits the information from 10^8 receptors using an optic nerve containing only 10^6 fibers.
- All this retinal information processing is performed using local connections. Similar techniques may therefore be suitable for for implementation in analogue electronics.

[1] This ability to cope with a restricted dynamic range is the reason why Mead chose to mimic the retina in silicon[4]. Expressed in his terms, the retina provides a model for automatic gain control applied in analogue circuits to extend their useful operating range.

The memorandum begins with a description of a theory which has been proposed to explain retinal information processing. This is followed by a discussion of three very different retinas in sections 3, 4 and 5. These short descriptions outline the general applicability of this theory and the different neural 'implementations' which have been adopted. The implications of these findings are then discussed in section 6. For completeness there is an appendix discussing retinal gain control, an alternative theory of retinal information processing.

2 A Theory of Retinal Information Processing

In studies of retinal structure neurons are described in terms of the part of the field of view to which they react, their receptive field. It is frequently found that these receptive fields consist of two components a 'centre' and 'surround', supplied via neighbouring receptors. These two components have opposite effects on the 'target' neuron corresponding to the receptive field. For example, a target neuron may be excited by the input from the centre of its receptive field and inhibited by inputs from the surround. Neurons with this type of receptive field respond to the difference between the excitatory and inhibitory inputs and are said to posses an antagonistic centre-surround receptive field. Any theory of retinal information processing must explain the widespread occurrence of neurons with antagonistic centre-surround receptive fields [2].

There have been several proposals attempting to explain the function of antagonistic centre-surround receptive fields in the retina[5]. These have included:

- Attenuation of low frequencies components of the input signal. When originally proposed it was thought that the motivation for this filtering would be to compensation for optical blurring of the images. However, this hypothesis does not appear to be supported by later evidence. More recently it has been proposed that low frequency attenuation is employed to enhance edges, an important feature in images. Units with antagonistic centre-surround fields enhance edges by performing an operation sometimes referred to as a difference of Gaussians which can be used as an approximation to a Laplacian filter. Laplacian filters are widely used in vision data processing to enhance edges to help object definition[4].
- Removal of unspecified redundant information.
- Removing any d.c. bias in the signals. However, this is a qualitative hypothesis from which it is difficult to determine the neighbourhood over which the bias should be calculated.

Since all these proposals depend to some degree on the filtering properties of an antagonistic centre-surround receptive field it is possible that all these functions are performed.

A more detailed hypothesis has been proposed by Srinivasan, Laughlin and Dubs[5]. These authors have suggested that the retina is removing the linearly predictable spatial

[2] Any theory which does explain antagonistic centre-surround receptive fields may have an impact beyond the retina. Neurons responding to antagonistic centre-surrounds have been identified throughout the visual system. More generally antagonistic centre-surround is simply one form of lateral inhibition observed in many parts of the brain.

and temporal correlations from the input signal, using a technique which they refer to as 'predictive' coding. The authors suggest that this correlation removal is achieved when a prediction of the signal strength is subtracted from the signal. This removes spatial and temporal correlations if the 'prediction' is based upon the previous value of the signal at a point and in its neighbourhood. The advantage of employing this technique is that redundant information, concerning predictable components, can be removed from the signal. The resulting 'error' signal can then be represented in a smaller dynamic range [3].

To enable a comparison between this theory and neurobiological results Srinivasan, Laughlin and Dubs studied the dependence of the theoretical 'best' neighbourhood on the spatial correlations in the image and the signal-to-noise ratio[5]. They found that the 'best' neighbourhood is insensitive to the spatial correlations in the image. This is an important result which suggests that the retina will not be required to adapt to specific scenes. In contrast, the 'best' neighbourhood was found to be sensitive to the signal-to- noise ratio. The theory suggests that the smaller the signal-to-noise ratio the larger the neighbourhood which should be used in a 'prediction'. This enlarging of the neighbourhood can be interpreted as an attempt to reduce noise by increasing the sample size. Since low levels of illumination correspond to small signal-to-noise ratios, due to a large photonic (shot) noise component, the hypothesis suggests that low levels of illumination will correspond to large neighbourhoods. The 'predictive' encoding hypothesis can therefore be tested by studying the dependence of the neighbourhood on the level of illumination [4].

Predictive encoding can also be used to remove temporal correlations[5]. These temporal correlations arise from one of two sources, spatial correlation in a slowly changing scene or the finite response time of the photodetection process in a rapidly changing scene. Temporal prediction relies upon a weighted sum of previous signals at the same point. Although there are differences, arising from the continuous nature of temporal sampling compared to discrete spatial sampling, the theories for spatial encoding and temporal encoding are very similar. Again the main result is that as the noise level increases the time over which the prediction is made increases, in an attempt to reduce the noise. The theory therefore predicts that as noise increases the system will trade speed for accuracy.

Predictive encoding seems plausible and encompasses some of the earlier theories. It both indicates that the redundancy which is removed is any predictable components, in both space and time, and gives a technique to determine the neighbourhood over which to calculate a 'd.c. bias'. Also, the connectivities required for predictive coding and edge enhancement are very similar. The difference between these two approaches is simply one of underlying philosophy. Predictive encoding is based on the qualities of images, whilst edge enhancement is a feature extraction technique based on the perceived importance of a specific feature.

The predictive encoding hypothesis is interesting because it takes as its starting point the general properties of the input signal and a desire to employ a restricted dynamic range. This then leads to 'operations' which could explain the antagonistic centre-surround receptive fields observed in the retina[6]. To be fully accepted, the predictive encoding hypothesis

[3] An alternative interpretation of this technique is that it a calculates a 'local' mean. This local mean can then be treated as a d.c. offset which is subtracted from the signal.

[4] As an example of the neighbourhoods required; for a signal-to-noise ratio of 10 the 1st nearest neighbours are required, a ratio of 1 requires a neighbourhood including nearest 8 neighbours and a ratio of 0.1 requires a global mean.

[5] The motivation to reduce the dynamic range is sufficiently general that predictive encoding may rep-

needs to be tested against detailed neurological results. To this end Laughlin has continued to study the fly retina[6]. Some of his results are outlined in the following section.

3 The Fly Eye

The eye of a fly is a compound eye formed from a hexagonal array of units known as ommatidia, *little eyes*. There are various forms of compound eyes found in different insects. The fly eye is one of a class of compound eyes in which each ommatidium is optically isolated by pigmentation[7]. The result of this isolation is that the photodetectors, the rhabdoms, only receive light via the aperture of the ommatidium in which they are situated. Within the fly eye each ommatidium contains eight different detectors. These form a cluster, with six peripheral detectors, known as R1-R6, surrounding two central detectors organised with one, R8, behind the other, R7. The outer surface of each ommatidium is faceted in such a way that within each ommatidium one of the peripheral detectors looks in the same direction as the central detectors in one of the six neighbouring ommatidia.

To form an image the inputs from all the peripheral receptors which are stimulated by the same point in the field of view are superposed [6]. This superposition of stimuli from the R1-R6 neurons occurs within a hexagonal array of *cartridges* in a structure known as the lamina. Each cartridge in the lamina contains the same types of neurons, organised to a common pattern, and it is separated from its neighbours by a sheath of glial cells. It is this regular structure which makes the fly eye an accessible subject. The projection of the receptor neurons to the cartridges is not fortuitous, each neuron undergoes a twist through 180° to compensate for image inversion. This complex mapping of receptor inputs onto the lamina has the property of retaining the relative positions of the points in the field of view[7].

A full discussion of the fly eye would be prohibitively lengthy. In his studies Laughlin[6] has concentrated upon the system formed by the R1-R6 photosensitive neurons and the two large monopolar cells, L1 and L2, referred to as the LMCs, within each cartridge[8]. By concentrating upon these neurons the extent of the present discussion can be restricted.

When this group of neurons was studied, it was found that both the photoreceptors and the LMCs employ continuously varying electrotonic potential signals. Experiments indicate that the photoreceptor cells generate a transient response to stimulation followed by a plateau dependant upon the illumination level. The photoreceptors are not therefore fully

resent the fundamental principle underlying the widespread use lateral inhibition in neuron populations.

[6] Interestingly, the central detectors do not appear to take part in this convergence. This suggests that the fly has two detector systems working in parallel; a high intensity, high resolution (the centre waveguide is narrower than the others) system and a low intensity, low resolution system[7]. However, there is strong evidence that the R1-R6 neurons are necessary in tasks for which the R7 and R8 neurons appear to be adapted[8]. The role of the R1-R6 neurons may be explained by the discovery of a small area of the cartridge in which the R7 and R8 cells connect to the R6 cell in the cartridge[9].

[7] This mapping means that the cartridges are the first layer at which the eye forms an image of the field of view. In this important respect they correspond to the rods and cones in a refracting eye, such as a human eye.

[8] An interesting question which is not directly related to the current topic is; Why are their two apparently identical LMC cells? The answer appears to be related to the fact that the cells are not identical but have different thicknesses. The theory of signal propagation in axons suggests that this means they have different signal propagation velocities. Braitenberg[10] has suggested that these cells could be used as delay lines in a motion detector. No supporting evidence is given for this hypothesis.

light adapted. However, the transient responses observed do indicate that the photoreceptors are using a slow time-constant and self-inhibition to reduce the average level of activity by removing temporal correlations from the input.

The important observations concerning the subsequent conversion of the signal from the receptors to the LMCs are that the signal is inverted, amplified and has extra transients introduced. The inversion of the signal is insignificant. However, considerable effort is involved in its amplification. Both the receptors and the LMCs have a relatively small range of accessible membrane potentials, dynamic range. Without an adaptation mechanism the LMCs would be restricted to encoding signals over 2 decades compared to the 5 decades required in conditions ranging from twilight to bright sunlight. The LMC response is therefore adapted so that a constant background is represented by the same potential independent of its intensity. Any change in the background is then represented by transients which decay within a few hundred milliseconds. It is this adaptation to the average illumination level which causes the extra transient nature of the signals observed in the LMCs. These cells also adapt by decreasing the leakage current out of the cell in response to decreased illumination levels. The result is that the integration time used by the cell is increased. Thus accuracy is increased as the cost of reduced speed, in line with the prediction based on the predictive encoding hypothesis in section 2.

Laughlin considers the signal processing involved in transmitting information from the photoreceptor to the LMCs as occurring in three stages: A photoreceptor response related to the logarithm of the stimulus, followed by subtraction and amplification. The logarithmic response arises from the use of a photoreceptor mechanism which combines non-linear summation of conductance events and a gain which reduces with illumination[11]. This step is significant in reducing the calculation of ratios, involved in contrast calculations, to subtraction. Therefore, as well as reducing the dynamic range of the signal, the first two stages of the transmission process ensure that the photoreceptors encode the contrast in the scene[11]. This contrast encoding has the advantage that it eliminates the effect of the overall level of illumination when objects are observed by reflection. Thus ensuring that an object appears the same under all illumination conditions.

It is at the second, subtraction, stage of the transmission process that predictive encoding may be occurring. This stage reduces the signal to the smallest dynamic range possible within the constraints imposed by the 'wetware'. Then this signal is amplified so that the entire dynamic range available in the LMC is employed. This process ensures that the amplified signal is as robust as possible against noise. The amplification of the signal actually occurs at a chemical synapse which is the dominant noise source in the system. Since the level of amplification possible is limited by the restricted dynamic range of the LMCs, Information Theory suggested that matched coding should be used to optimise the level of amplification. Shannon and Weaver proved that a limited number of symbols carried the maximum of information if each symbol is used equally often (the equivalent technique used in digital signal processing is *histogram equalisation*). Laughlin proved that the LMCs used matched coding by demonstrating that the intensity-response function of the LMCs is the cumulative distribution of the contrast in the scene. To match the intensity-response curve to its environment the system requires a mechanism to generate a logistic intensity-response curve and adapt the slope at the mid-point to the contrast distribution in the current image. In fact this type of behaviour is widespread in retinas[9]. Analysis of the behaviour of LMCs

[9]It is sufficiently common to form the basis of a separate theory of retina adaptation proposed by Shapley and Enroth-Cugell, which is discussed in appendix A.

indicates that the non-linearity in the synaptic transmission process is sufficient to account for the matched coding behaviour.

As stated previously, the problem with any subtraction process is to determine how to calculate the value to be subtracted from the signal. A global mean could be used, but this would not account for local variations in the illumination levels. The predictive encoding hypothesis is useful in determining the neighbourhood over which the 'mean' should be calculated. Once the prediction is subtracted from the actual value the dynamic range of the signal will be reduced without loss of information[10].

Having identified the neurons of interest and the signals observed in the neurons, a complete knowledge of their synaptic connections is required to understand how these signals arise [11]. Fortunately there appears to be strong evidence for all the connections of interest between these neurons. It has been observed that as they approach the lamina the R1-R6 neurons form a circular bundle prior to forming a 'crown' around the two LMC neurons, L1 and L2 [8]. Within the crown each of the R1-R6 neurons is connected to its two neighbours in the circle by numerous, approximately 60, gap junctions and to each LMC cell by approximately 220 chemical synapses[12]. Since the responses of the R1-R6 cells are superposed within the LMC cells the discovery of these gap junctions was a surprise. Another surprise was the fact that despite the strong evidence for lateral inhibition between LMC cells there is no evidence for the existence of gap junctions to mediate this interaction[9]. It now appears that the observed lateral inhibition arises from variations in the local potential field in the lamina. Since local potential variations are difficult to generate and sustain in large systems this mechanism immediately explains why the lamina has evolved to be electrically isolated from both the ommatidia layer and the rest of the brain[13]. It appears that this local potential arises from synapses which have been observed between some of the α and β neurons in the cartridge and the glial cells which surround the cartridge. Since coupling between glial cells is a rule rather than an exception, there is the potential for the glial cells to behave like a network of resistors. (This type of network has been extensively studied and employed artificial retinas to calculate local average potentials[4].) Thus the glial cells may generate a local potential dependant upon the local neural activity. This local potential is then subtracted from the instantaneous receptor potential by a change of potential reference. The overall result is that the LMCs are stimulated by the difference between the receptor neurons potential and a local potential. Thus, the coupling between glial cells and the electrical isolation of the lamina seem to provide the substrate for the removal from the signal of spatial correlations.

The 'wetware' needed to encode the signal therefore exists in the lamina. As stated previously the shape of the surround required to perform the predictive coding is not critically dependant upon the spatial correlations of the scene. However, it is critically dependant upon the noise induced in the photoreceptors. Under conditions of high illumination the predictive encoding hypothesis suggests that the nearest neighbours can be relied upon to generate a reliable prediction. However, as the illumination level decreases the number of receptors which should be included in the averaging process should increased. In physiological terms this means that the lateral antagonism, on which the centre-surround organisation

[10] Information is not lost as long as the method of encoding is known. In artificial systems the method of encoding is part of the transmitted signal. In hardware this is unnecessary *as long as the method is unchanged.*

[11] Experiments to determine synaptic connections are difficult to perform[9], resulting in a continuous review of the evidence for the various synaptic connections.

is based, should become weaker and more widespread as the illumination level is reduced. This type of effect has been observed A more detailed analysis of the lamina shows that the antagonism present is more widespread than expected from the predictive encoding hypothesis. Laughlin has postulated that this effect is accounted for by the fact that the eye is attempting to encode moving images.

Laughlin has put forward a convincing case supporting the suggestion that the predictive encoding hypothesis can be used to interpret the information processing occurring in the fly retina. However, the general applicability of the hypothesis can only be tested by studying other retinas. To this end two other retinas are described in the following sections.

4 The Vertebrate Retina.

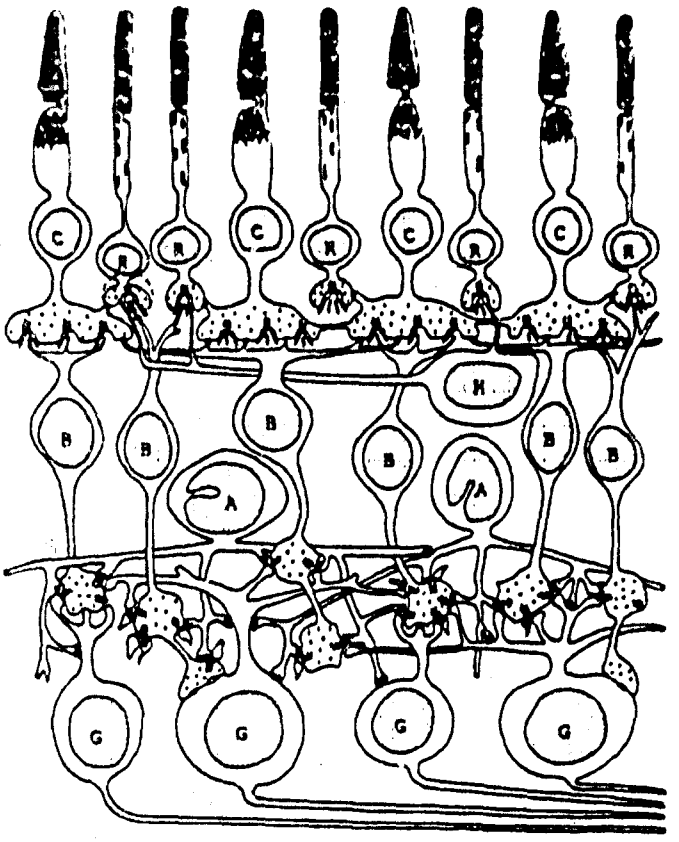
The vertebrate retina, shown in figure (1), is more complex than the fly retina. However its position and structure, a small variety of cells organised in layers, make it a relatively easy subject to study. In the vertebrate retina there are two types of photodetectors, the rods and the cones. The remainder of the retina is made up of four other types of cells known as the bipolar, horizontal, amacrine and ganglion cells[14]. Each population of detector cells performs a separate function: The rods are responsible for vision at low illumination levels, whilst the cones are responsible for high acuity, colour vision at high illumination levels[12]. In general, the bipolar cells connect the photoreceptor cells to the ganglion cells which form the output from the retina. The other two types of cells spread laterally throughout the retina forming ideal communication pathways. Of these different cell types in the retina action potentials only commonly occur in ganglion cells, with infrequent occurrence in amarcine cells[16]. The information processing of interest therefore occurs in cells which employ electrotonic potentials.

Unfortunately this classification into five cell types may be too simplistic. It is now clear that there are distinct types of *amarcine* cells distinguished by morphology, arborisation, chemistry and responses. Their precise role is unknown but they appear to be concerned with movement detection and directional sensitivity. To limit the scope of the present discussion details concerning the structure and function of amarcine cells will be omitted.

The easiest cells in the retina to study are those cells whose axons form the output of the retina, the ganglion cells [13]. Studies indicate that the ganglion cell receptive fields have large overlaps so that even a small spot causes a response in several ganglia. As with the cartridges in the fly lamina, the ganglion cells are organised to form a map of the field of view. The importance of this mapping for information processing is emphasised by the fact that it is preserved by the projections of the ganglion cells to the brain. The antagonistic centre-surround nature of the ganglion cell receptive fields was discovered using spot stimuli[14]. There appear to be two forms of antagonism used by ganglion cells. Cells

[12] Barlow states that the cones each have their own direct connection to the optic nerve. In this respect the cones are appear to be similar to the R7 and R8 neurons the fly retina.

[13] There are two main categories of ganglion cells, referred to as X-cells and Y-cells, which are characterised by differing responses to stimuli. It would appear that the X-cells concentrate on output from the fovea and are responsible for high-acuity vision whilst the Y-cells, which concentrate upon output from the periphery, are primarily motion detectors[16]. In animals with a colour vision it is the population of X-cells which contain colour specific ganglion cells.



(a)

(b)

Figure 1: A section through a primate retina: Figure (1a) shows the relationship between the various cell types. The rods (R) and cones (C) connect vertically to the ganglion cells, (G), via the bipolar cells, (B), whilst the horizontal, (H), and amacrine, (A), cells interact laterally. The triad synapse is encircled, this is the point at which the rods reaction with the bipolar cell is mediated by the horizontal cell. Figure (1b) shows the detail of the triad synapse to emphasis the interaction between the rod and the dendrites of both the bipolar and horizontal cells. (Reproduced with permission from reference [15])

referred to as on-centre cells respond with an increased firing rate when their centre is illuminated. In contrast off-centre cells respond to stimulus by slowing their firing rate.

Detailed studies indicate that the precise form of the centre-surround neighbourhoods vary between species. Cats have simple circular receptive fields, whilst rabbits have ganglion cells with receptive fields sensitive to lines and motion in specific directions. Surprisingly, frogs and toads appear to perform the most retinal processing. They use ganglion cells tuned to one of several specific stimuli, including some which are so specific they appear to be 'bug' detectors[16]. It appears that in higher animals most of the detailed interpretation of the information is performed in the higher centres of the brain, where input from other sensory systems can be used to assist any interpretation. The retina of higher vertebrates may therefore represent the result of a desire to compress data, without prejudicing later interpretation by assuming too much prior knowledge.

The next question to consider is: How are these receptive fields organised from the other cell populations in the retina? In describing the complex connectivity within the retina the best starting point is the photoreceptor cells, which react light falling on their surface[14]. The Bipolar cells which receive input direct from the photoreceptors cells have been found to possess concentric antagonistic centre-surrounds. The centres of the receptive fields are supplied directly by the photoreceptors, whilst the horizontal cells supply the surrounds. The mechanism by which the horizontal cells affect the bipolar cell response has been studied by Werblin[17]. Werblin demonstrated that the horizontal cells mediated the bipolar cell response by correlating the activity in the horizontal cells with the adaptation of the bipolar cells. By examining the response of a horizontal cell to a point stimulus it has been demonstrated that the influence of a receptor on the horizontal cell decays exponentially with distance from the stimulus. This behaviour, together with the numerous gap junctions between the horizontal cells, suggests that the function of these cells is to act like a resistive network. The mechanism underlying the influence of horizontal cells on the bipolar cells was not identified by Werblin. However, he was able to demonstrate that the affect of the horizontal cells was to subtract from the stimulus of the bipolar cell before the rod to bipolar cell synapse. This implicates the triad synapse, shown in figure (1b), where the rod, bipolar and horizontal cells have neighbouring synapses, in the mechanism. The fact that the horizontal cells do not adapt with the bipolar cells suggest that the horizontal cells are stimulated directly by the receptor cell population. The effect of the horizontal cells is a shift in the sensitivity of the bipolar cells to the level of illumination of the surround of its receptive field. Then the bipolar cell responds to central illumination levels which differ by one decade in intensity in this surrounding level. The bipolar cell therefore encodes a measure of the contrast between the centre and the surround.

Werblin[3] found that he could study the antagonistic centre-surround using uniform illumination because the effect of the surround is delayed by 200*ms* compared with the effect of the centre. Using this technique he found that at low levels of illumination the ganglion cells responded directly to the receptor cells, via the bipolar cells. The horizontal cells, which mediate the antagonistic centre-surround organisation only affected the bipolar cells, and hence the ganglion cells at high levels of background illumination. This is contrary to a prediction, based upon the predictive encoding hypothesis, in section 2.

5 The Horse-shoe Crab Lateral Eye

The compound eyes of the horseshoe-crab, *Limulus Polyphemus*, have been studied for over 50 years [14]. Since this species is an isolated example of the use of compound eyes within its group, these eyes are extremely atypical. In fact each Limulus has several structures which are photosensitive and could be termed eyes. The present discussion will concentrate on the lateral eyes, which are apposition compound eyes used by males to detect females during mating.

Examination of the lateral eyes has shown that each ommatidium contains a group of 10 – 13 photosensitive retinula cells. The cells connect to the eccentric cell, a modified retinula unique to the *Limulus* retina, which forms the output. These output neurons from the ommatidia then form the plexus, an open meshwork of retinular and eccentric neurons together with some efferent axons[19]. Although the eccentric cells form the output from these eyes, they do not generate action potentials until they have traversed the plexus.

In the earliest experiments it became evident that the retina performed a great deal of sophisticated 'data processing' [19, 20]. Initially, the neurons were expected to act independently and inhibitory behaviour between neurons was only discovered, by accident, when it was noted that stray laboratory light usually caused a decrease rather than an increase in neural activity. This effect is now known to be caused by inhibitory inputs, from the receptors stimulated by the stray light influencing the receptor under investigation. More detailed studies have indicated that the inhibition is not instantaneous. This delay in the onset of inhibition is critical in the widespread occurrence in neurons of 'on' transient bursts of activity[19]. These bursts arise because the direct stimulus of the cell generates an increased activity which is later decreased by the delayed inhibition. Once the stimulus, and hence the inhibition, is removed post-inhibitory rebound in the neuron generates an 'off' burst of activity.

Experiments and simulations indicate that the inhibition caused by a neuron depends upon its potential after it has itself been inhibited. The result is that the inhibition experienced by an neuron depends upon the inhibition it has generated in a neighbour. In an attempt to uncover the mechanism underlying this recurrent inhibition Fahrenbach[21] has studied the synaptic connections in the plexus. His results indicate that the inhibition is mediated by synapses between collaterals of eccentric cells, with a synaptic connectivity determined by a stochastic process. This makes describing and then interpreting the plexus network very difficult. The stochastic connection rules could only be revealed by detailed studies of several neurons. In general the synapses occur at the terminal arborisations, with input and output neurons intermingling. The total number of output synapses appeared to be independent of the distance of the arborisation from the parent axon. On the contrary the output synapse density decreases with increased distance of the arborisation from the parent, 13% of the nearest arborisations contained 38% of the synapses. These results suggests that the stochastic connection rule leads to the influence of a neuron decreasing

[14] These studies have been so successful that the neural network in the *Limulus* compound eye is one of the few neural networks that have been modeled exactly[18]. The equations that describe the response of individual ommatidia eye to static and moving images have been available for twenty years. With the recent advent of suitable computers, in this case a connection machine, the response of an array of ommatidia can be simulated. These simulations demonstrate that the eyes are tuned to identify other Horseshoe crabs. A result which agrees with the behavioural experiments which demonstrated that the eyes are only used to locate a mate.

with increased distance from the neuron. Thus a very different mechanism is employed to achieve the effect obtained from a resistive grid in the previous two retinas.

6 Potential Lessons

In each of the preceeding three section we have discussed a different retina. Despite the fact that these retinas represent three independently evolved systems, striking similarities emerge:

- All the systems use analog potentials to represent and manipulate information until it is communicated over long distances to the rest of the brain. It is only at this stage that it is encoded using action potentials.
- There is widespread use of lateral inhibition to form antagonistic centre-surround receptive fields. The fact that there are a variety of interpretations of the function of this feature simple demonstrates the potential usefulness of this organisational principle.
- Antagonistic centre-surround receptive fields give sufficient evolutionary advantage that three different strategies have evolved to generate these receptive fields: The fly lamina generates a local potential in the glial cells which is subtracted from the signal by a change of reference. In the vertebrate retina the horizontal cells form the resistive network, influencing the other information processing via a chemical synapse. Whilst, the strangest neural implementation is the stochastic connection probability employed in by Limulus.
- All the retinas trade speed for accuracy at low levels of illumination by extending the neural integration time.
- Inhibition is delayed to allow an on-burst of activity with a corresponding off-burst caused by post-inhibitory rebound.

It has been suggested by Laughlin and co-workers that predictive encoding is the principle underlying the widespread use of lateral inhibition, in particular, in antagonistic centre-surround. Unfortunately the theory, proposed in 1982, has not developed in light of more recent experimental results. A consequence of this is that in some situations the theory fails some of the tests proposed when it was originally developed. In particular, as discussed in section 4, the receptive fields in the vertebrate retina have been found to contract[3] as the overall level of illumination decreases, rather than expand to calculate a 'global' mean as originally predicted[5]. Closer examination of the original work suggests that this is not a failure in the underlying theory, but arises from the use of incorrect assumptions. In the original work it was assumed that predictive encoding would be used under all conditions. More recent studies suggests that predictive encoding is only used to reduce the dynamic range of signals if the signal would otherwise exceed the limitations imposed by the 'wetware'. This explains the lack of lateral inhibition at the low levels of illumination which would not be affected by the limited dynamic range in the neurons. If this is correct then, despite the errors in its original formulation[5], the predictive encoding hypothesis appears to represent the best theory for the information processing which occurs in retinas. Any

subsequent theory must retain one of the features of the hypothesis. The desired information processing must be independent of the scene. It is this attribute which enables the hypothesis to explain the 'hardwiring' of the antagonistic centre-surrounds.

Results from studies of vertebrate colour vision suggest that lateral inhibition can be used to remove other correlations from signals. Colour vision is due to pigments in the cones[16]. A single pigment would not enable unique determination of colour. This requires at least two pigments, in fact three pigments, red, green and blue, operating with overlapping bands are used. Colour is then perceived as the relative activities of cones with these different pigments. It appears these relative activities are encoded by ganglion cells using antagonism. In the simplest case of colour coding a receptive field is organised to be stimulated by one colour at the centre and inhibited by another colour in the surround. The resulting signal is then the difference between the response of cells with different pigments. The colour vision system with three overlapping sensors is a smaller version of another sensory system, the olfactory system, which also uses a range of sensors with overlapping responses. In fact Shepherd claims a correspondence between the retina and the olfactory bulb[16]. If this correspondence is correct then it suggests that the olfactory bulb and the retina employ the same information processing strategy. This would strongly suggest that the strategy employed within retinas to overcome the limited dynamic range of neurons is generally applied within neural systems.

There are several important facts which emerge directly relevant to the design of artificial analogue neural networks.

- Lateral inhibition is used extensively to reduce the dynamic range needed to represent information. The theory which has been proposed by Srinivasan, Laughlin and Dubs suggests that the lateral inhibition is used to remove predictable correlations from the data.
- The dynamic range of the signal should be reduced as soon as possible. This should be followed by amplification to increase robustness to noise.
- The amplification process should be non-linear and matched to the expected signal statistics in an attempt to use each signal level equally often.
- Considerable effort is employed within the fly lamina to ensure that related data is present locally to reduce length of any signal paths. If this is a general feature of biological neural systems then the different centres in the brain may be related to different spatial distributions, representations, of the information. Each representation could then emphasise different possible correlations in the information with transformations between representations occurring during the projection of axons between centres. These projections employ robust pulse coding of information so that information can be transmitted over long distances without being corrupted.
- The fly and vertebrate retinas[22] employ two parallel detector systems with different sensitivities. The coupling between the two sensor systems which occurs in both of these retinas suggest that the more sensitive system automatically activates the other system once it becomes saturated.

Finally, this studies emphasises that information processing can occur within a neural network without a single action potential initiation. This demonstrates the limited nature of the McCulloch- Pitt model of the neuron which forms the basis of artificial neural networks.

A Alternative theory: Retinal Gain Control

In this appendix retinal gain control is discussed as a theory for adaptation. This theory is not as complete as the predictive encoding theory discussed in the body of the text. It also appears to be incorrect as an explanation of retinal function. However, when considering techniques which can be usefully implemented in analogue neural networks, biological correctness is irrelevant. The technique is therefore included for completeness.

In 1984 Shapley and Enroth-Cugell published a paper in which they suggested that gain control within the retina was a sufficient basis to explain adaptation[23]. This new theory was proposed because the authors thought that predictive encoding may not be robust when applied to a system in motion, such as an eye. As with predictive encoding the motivation is to maintain retinal response to contrast independent of the amount of background illumination. This enables the retina to characterise objects by their reflectances. In psychophysical experiments it is found that the apparent brightness of an object depends upon the border contrast. This observation appears to be the starting point from which this theory was developed. Unfortunately it is not clear if this fact could be explained by predictive coding.

To begin it is postulated that the retinal adaptation process depends upon eye motion. Under these conditions if a receptor is viewing the 'background' and moves across a boundary it can respond to changes in the signal. This response can then be amplified. Retinal gain control suggests that if the gain of the amplification process is inversely proportional to the original illumination, the amplified signal is proportional to the contrast at the boundary independent of the overall illumination; i.e. adaptation depends upon a gain which changes with the level of illumination. Experimentally the required type of behaviour was found in some species but not in all. The authors attempted to verify their theory using results from different parts of various vertebrate retinas. This casts doubt on the validity of their results since as the authors themselves note results from one species may not be valid for others.

In studies of the fly retina, Laughlin and co-workers found that, at the highest levels of illumination, the gain of the photoreceptor to LMC synapses were constant, independent of the level of illumination[12]. The only adaptation reported ensured that the synapse operates in the regime in which it can employ maximum gain. These results appear to cast doubt upon the use of gain control as an adaptation mechanism in retinas.

Overall it is not clear if this theory can withstand scrutiny as an explanation of retina behaviour, however, it may still be applicable in an artificial system.

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Abstract

Analogue electronics appears to offer the most direct way to mimic the information processing which occurs in the dendrites of neurons. Unfortunately, analogue electronics suffers from a restricted dynamic range, a problem which also occurs in neurons. The study, reported in this memorandum, was therefore initiated to understand how biological neural systems overcome the problems inherent in employing components with an inadequate dynamic range. The inadequacy of the dynamic range available in neurons is most apparent in retinas which deal with an input signal covering 5 decades using components with a dynamic range of less than 2 decades. The 'predictive' encoding hypothesis which has been proposed to explain the function of the outer retina is adopted as a framework for understanding the neurological data discussed. Then, three different, independently evolved, retinas are considered to demonstrate the different implementations of the same underlying principle. The study shows that the problems posed by the limited dynamic range available in both neurons and analogue electronics can be overcome if the system is correctly designed. It also demonstrates that the McCulloch-Pitt model of a neuron, which forms the basis of artificial neural networks, is an incomplete model.

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