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Form and function in retinal processing

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What design principles underlie the operations of neuronal circuits? In particular, how is the form taken by neural processing related to its function? Intracellular recordings from identified photoreceptors and interneurons in the fly compound eye have produced an accurate description of the form of neural processing. A combination of modelling and experiment establishes that the first stage of neural processing codes pictures efficiently, and resembles procedures used for coding and enhancing digitized images. Redundancy is removed by neural interactions, and the residual signal, containing most of the pictorial information, is amplified. These procedures protect information from the significant amounts of noise generated at photoreceptor synapses. Similar forms of processing are seen in vertebrate retinae, suggesting a similar function.

The fly retina is an array of essentially identical optical modules, the ommatidia (Fig. 1). These map the spatial distribution of light intensity onto the photoreceptor array so that adjacent points in space are sampled by adjacent receptors. In this sense the resulting 'neural image' of receptor activity is identical to the image cast upon vertebrate retinas. Cajal and Sánchez[1] drew attention to the remarkable modular structure of insect optic lobes. The first optic ganglion, the lamina, is an array of essentially identical neural modules, the lamina cartridges (Fig. 1). Receptors sampling the same point in space project to a single cartridge[2], which in turn projects to a corresponding module in the second optic ganglion. This modular arrangement has allowed neuroanatomists and physiologists to describe the fly visual system in great detail [3–7]. There is a comprehensive description of both the photoreceptor array, and the wiring of lamina cartridges.

Such a well-defined system lends itself to the analysis of form and function. This article reviews studies of neural processing in the first neural module, the lamina cartridge. These studies describe the changes that take place when information is transferred from photoreceptors to a major class of interneurons, the large monopolar cells (LMCs) (Fig. 1). The accurate description of the form of neural coding has led to an exploration of the design principles governing the transfer of information from photoreceptors to interneurons. It has been concluded that neural coding protects pictorial information from the noise that is inevitably generated by the photoreceptors' chemical synapses. This finding is relevant to the analogous cells of the vertebrate retina, the cones and bipolars. To appreciate the need for noise protection, we should first consider the nature of pictorial information, and the way in which such information is coded by photoreceptors.

The coding of pictorial information

Pictorial information is obtained from the spatial distribution of light intensity, and from the changes that take place in this distribution with time. An eye's optics and photoreceptor array convert the distributions of light intensity into distributions of receptor potential. Many eyes must cope with the 10 000-fold range of light intensities encountered during the daytime. An important factor is the ability of individual photoreceptors, be they vertebrate cones or fly photoreceptors, to adjust their sensitivity to match the ambient light level. This form of light adaptation allows photoreceptors to exploit an invariant of natural images – contrast – so as to code light intensity simply and conveniently[8,9].

Contrast is a measure of relative intensity. The intensity at a given point is expressed as a fraction of the mean intensity level in its vicinity. For non-periodic stimuli, contrast is usually expressed as $\Delta I/I$ where ΔI is the difference in intensity between the object and a mean level, I. Most natural objects are visible because they reflect and absorb constant fractions of the light falling on them. It follows that, in areas of uniform illumination, the ratio between the intensity of one object and another remains constant, despite large changes in the level of illumination. Thus when an eye codes contrast, most objects will look the same (i.e. generate identical signals), over a wide range of mean intensities. To what extent does the fly visual system exploit this convenient invariance and code contrast?

Contrast coding has been studied in fly photoreceptors by measuring the responses generated by stimuli of fixed contrast, at a number of mean light intensities[10–12]. The stimulus is a light that alternately increases and decreases in intensity by a constant small proportion of the mean level (Fig. 2). The changes in stimulus intensity produce fluctuations in receptor potential. At lower mean intensities, the amplitude of a photoreceptor's response to fluctuations of constant contrast increases with mean intensity. At intensities corresponding to the daylight range, equal contrasts produce approximately equal responses (Fig. 2). These responses to intensity changes are superimposed on a level of depolarization that rises steadily with the mean intensity. This background signal can be as much as 30 mV under daylight conditions (Fig. 2). A constant response to constant contrast superimposed on a background signal that increases with mean

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intensity is equivalent to a logarithmic transformation of input intensity. In photoreceptors, an approximation to a logarithmic transformation is brought about by a combination of two factors. The first is a non-linear relationship between stimulus energy and response amplitude that resembles saturating dose-response curves. The second is a gain control that reduces sensitivity in response to bright light[13,14]. These two properties are found in a number of types of insect photoreceptors and vertebrate cones[8,9].

Although the photoreceptors match the gain of the visual system to the incoming light level by coding contrast, the resulting voltage signal is relatively weak. Such small signals pose considerable problems for visual processing. With a mean contrast of objects in natural scenes of 0.4, much of the pictorial information is carried by changes in receptor potential of less than 10 mV (Ref. 15). Such small fluctuations in membrane potential are vulnerable to contamination by the intrinsic noise that is inevitably generated during neural transmission and processing. To make matters worse, these contrast signals are usually superimposed on a larger background signal (Fig. 2).

A comparison between the signals in photoreceptors and LMCs[16] suggests that photoreceptor signals are protected from intrinsic noise as they are transferred to LMCs (Fig. 2). Three changes in signal are obvious from a comparison of responses in photoreceptors and LMCs (Fig. 2). The LMC signal is an inverted, amplified and more transient version of the receptor input. When the photoreceptors depolarize, the LMCs hyperpolarize, and vice versa. The larger the photoreceptor's response, the larger is the LMC's. Thus, as in the analogous bipolar cells of the vertebrate retina, information from the photoreceptors is encoded by the amplitude of the graded potential response induced in the postsynaptic cell. Action potentials are not observed at this level of processing. Recent data suggests that the photoreceptor synapses release histamine when depolarized. This unusual neurotransmitter activates a chloride conductance in the LMC[17], thus explaining the inversion of response polarity during signal transmission. As well as being inverted, the LMC responses are approximately six times the amplitude of the corresponding receptor responses (Fig. 2). This amplification is probably performed by the array of chemical synapses connecting receptors to LMCs[18].

In addition to being amplified, the LMC responses are more transient than the responses of the receptors[19] (Fig. 2). Following a change in receptor potential, the resulting LMC response is rapidly shut down by as-yet unidentified mechanisms. Because these mechanisms oppose the signals generated by the photoreceptors, they are called 'antagonistic' to avoid the problems associated with using the term 'inhibitory' in the context of a hyperpolarizing response to increasing light intensity. Manipulations of the position of stimuli show that the antagonistic components are of two general types. When a point source preferentially stimulates the photoreceptors projecting directly to the LMC, rapid components of the antagonism continue to act[16]. Since these are principally generated within the same neural cartridge as the LMC, they correspond to the self-inhibition observed in *Limulus* lateral eye[20]. When one stimulates neighbouring points in space, and hence neighbouring cartridges, one observes an additional reduction in the response of the LMC[21,22]. This antagonism has spread laterally from adjoining cartridges and is equivalent to the lateral inhibition also described in *Limulus*. The net effect of antagonism is to abolish the LMC response to the background component of the receptor signal by effectively subtracting it away. Thus, during the transfer of signal from photoreceptor to LMC, antagonism and amplification act in concert. Antagonism removes the background signal, and this allows amplification to expand the contrast signal to fill the dynamic response range of the LMC[16]. The enhanced contrast signal is more readily resolved at higher levels of processing and is less prone to contamination by intrinsic noise.

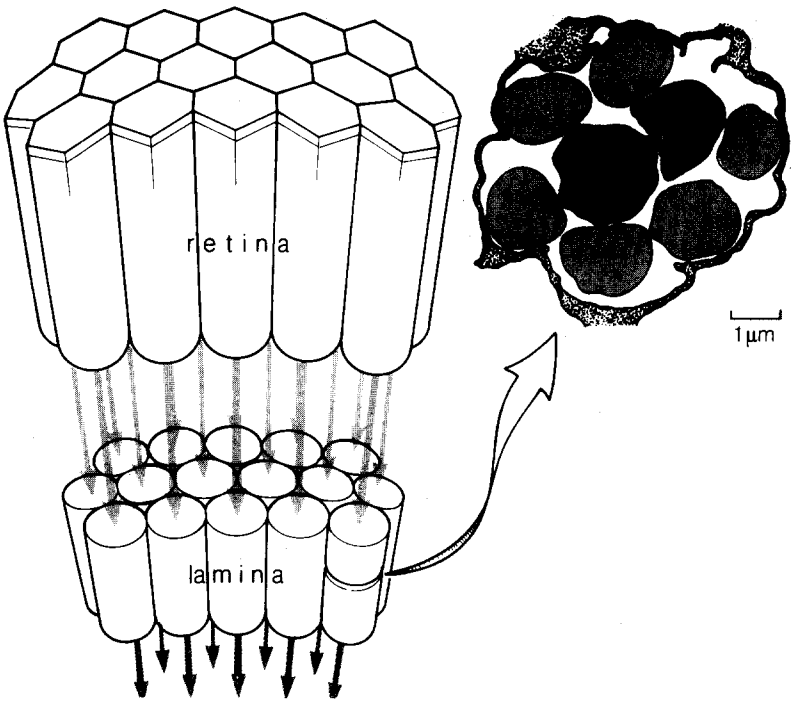

Fig. 1. *The modular structure of the retina and lamina of muscoid flies. The retina of the compound eye is an array of optical units, the ommatidia. Each ommatidium focuses light from a small solid angle of space onto a group of photoreceptors. Six of these photoreceptors terminate in the first optic neuropile, the lamina. The lamina is subdivided into cartridges: one for every retinal sampling unit in the retina. The diagrammatic cross section through a lamina cartridge shows the six photoreceptor axon terminals surrounding the two central large monopolar cells (LMCs). Each photoreceptor makes over 200 chemical synapses with each LMC[3,5]. The two LMCs project retinotopically to equivalent cartridges in the next optic neuropile. A lamina cartridge contains a number of other interneurons (not shown), and is surrounded by a glial sheath.* (Modified from Refs 3,5,7.)

Is this form of coding matched to function?

The hypothesis that this first stage in visual processing is designed to protect signals from noise has been tested by combining theory with experiment. Models are developed of coding procedures that protect pictorial information from noise. The models are tested by measuring the critical coding parameters at work in the fly retina. This measured performance is then compared with the requirements of the model. Consider first the problem of computing the background signal to be subtracted at each cartridge. The mean level of receptor output taken across the entire retina is often inappropriate at a particular cartridge. Illumination levels change across scenes (e.g. parts of a picture are in shade and parts are in sunlight). A local measure

of the mean is better, but just how localized should this estimate be? When the mean is taken over too limited an area, one begins to remove the very changes in intensity that define the presence of objects, and pictorial information is lost.

Digital image processing suggests a solution – predictive coding[23]. Predictive coding reduces the statistical correlation between the elements of a picture. Spatial correlation exists because neighbouring points in a picture are more likely to have the same intensity than widely scattered points. Temporal correlation is introduced by the relatively slow time course of the photoreceptor response. If one knows the pattern of correlation, one can estimate the signal expected at one point from other points in its vicinity. This statistical estimate is subtracted from the signal received to reduce the amplitude of the signal coded (Fig. 3). Because predictive coding removes components of a signal that can be predicted statistically from its context, no pictorial information is lost. Thus predictive coding fulfils our requirement of removing a local estimate of the background signal without removing pictorial information.

To see if the fly retina performs predictive coding, the necessary statistical weighting functions were calculated for pictures of different statistical properties and intensities[24]. These weighting functions are the areas of space and time over which the local means should be computed, and they correspond to the neural receptive fields and impulse responses required to execute predictive coding (Fig. 3). According to the predictive coding model, the weighting functions change little with the nature of the particular scene being viewed, but weighting is strongly dependent upon the signal-to-noise ratio in the photoreceptors and hence the light intensity. As intensity falls, the random variations in photon catch become increasingly prominent and de-correlate the photoreceptor signals. Consequently, the weighting functions must be extended to embrace a sample that is large enough to produce a reliable estimate. This intensity dependence provides a means for testing the model. Signal-to-noise ratios, impulse responses, and receptive fields were measured at several background intensities. The signal-to-noise ratios were used to estimate the shapes of receptive fields and impulse responses required for predictive coding. These required responses were then compared with the measured ones and it was found that retinal antagonism changes with intensity in the manner required for predictive coding (Fig. 3)[24].

Matched gain

Now consider the problem of selecting the correct gain for the amplification of the contrast signal[16]. The photoreceptor inputs can drive the membrane potential of an LMC over a range of approximately 60 mV (Ref. 16). One should maximize the amplification of the photoreceptor signal to minimize the effects of intrinsic noise. However, if amplification is too great, the input signals will often drive the LMC response to its limit, saturate the response, and so be lost. The appropriate amplification depends upon the size of the signals one usually receives. One can use information theory[25] to derive the appropriate amplification from the statistical distribution of input amplitudes[16,26], i.e. the range of contrast that a fly usually encounters. According to information theory, the response range of the LMCs is used to full advantage when all possible response amplitudes occur with equal probability. In other words, no response level is underemployed, and all contribute their fair share in carrying information. To ensure that all response levels occur equally often, the relationship between stimulus and response amplitude must take into account the probability distribution of stimulus levels.

The different levels of response will occur equally frequently when equal increments in response correspond to equal areas under the probability distribution of signal levels (Fig. 3). In this case, the relationship between input and response is equivalent to the cumulative probability distribution of signals. In essence, this procedure makes the gain of signal amplification proportional to stimulus probability. This is because the cumulative probability distribution has a slope that is proportional to stimulus probability. When gain is proportional to probability, the responses to the more likely stimuli are spread over a wider range of amplitudes. This spreading reduces the probability of observing any particular response amplitude (Fig. 3). Conversely, responses to rarer stimuli are coded with a lower gain (i.e. the slope of the contrast–response curve is lower; Fig. 3). The lower gain compresses the responses to rarer inputs into a

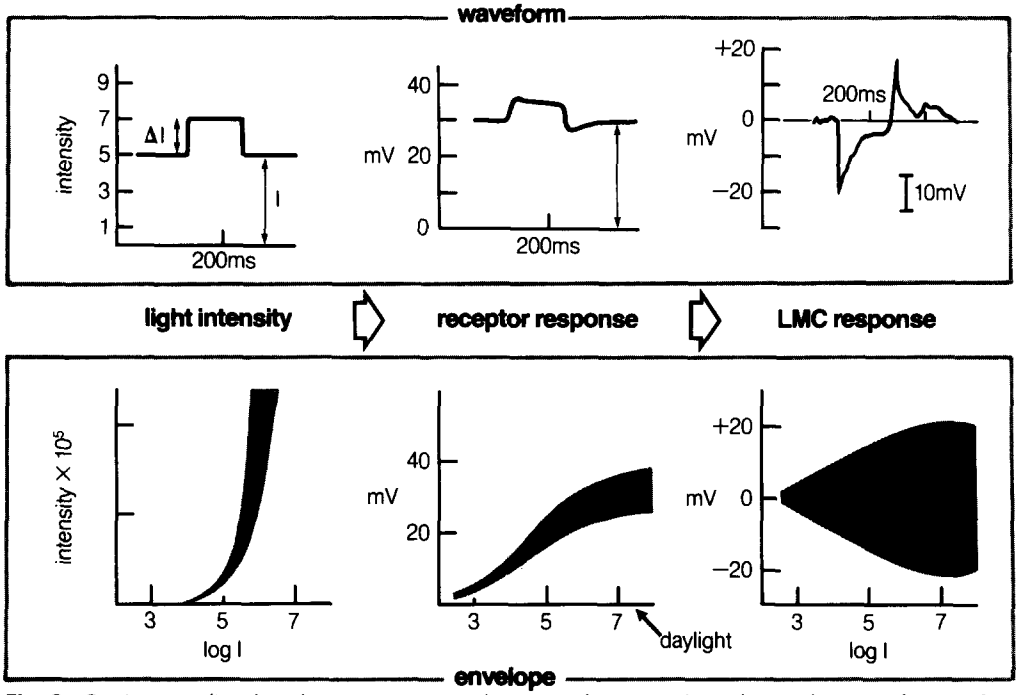

Fig. 2. *Contrast coding by photoreceptors and LMCs. The upper box shows the waveforms of an intensity signal of contrast ΔI/I = 0.4 and of the corresponding graded potential responses of a photoreceptor and an LMC. The lower box plots the envelopes of intensity signals, receptor responses, and LMC responses, as a function of log background intensity. The envelope is the range of amplitudes of signals of contrast >−0.4<+0.4. For the fly it has been estimated that approximately three quarters of natural signals fall within this envelope[26]. Background intensity (log I) is given in log (effective photons per receptor per second) – the arrow indicates full daylight. Receptor and LMC response amplitudes are plotted on a scale with zero set to the dark resting potential.* (Modified from Ref. 28.)

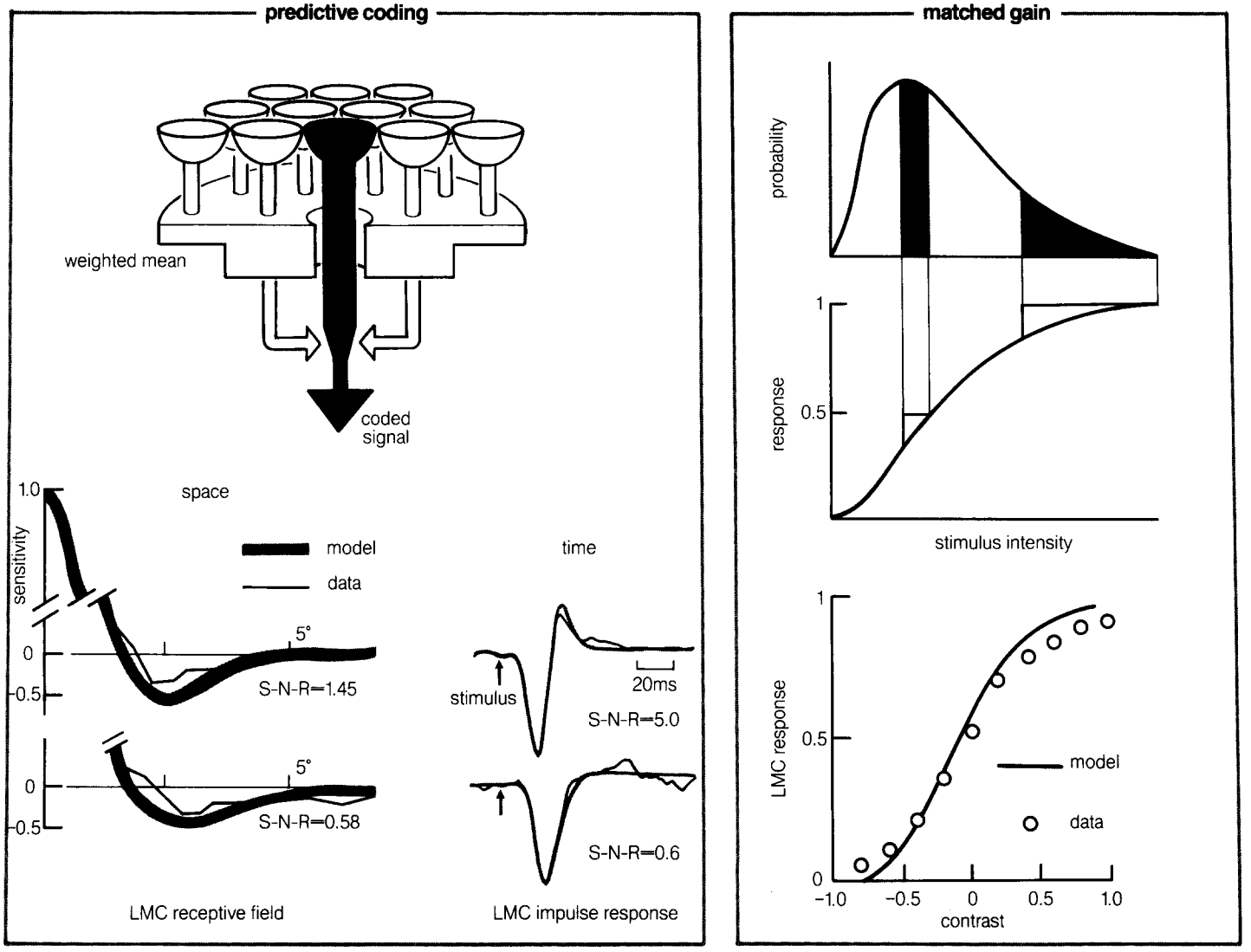

Fig. 3. *The experimental verification of the two coding strategies that match the form of the neural processing to its function: predictive coding and a matched gain of amplification. Predictive coding in space uses centre–surround antagonism in the receptive field (upper diagram). The surround takes a weighted mean of photoreceptor inputs, which is an estimate of the signal expected at the centre. This estimate, the prediction, is then subtracted from the signal found in the centre, and the residue – the coded signal – is transmitted to the next level of processing. Predictive coding in time requires a biphasic response to an instantaneous flash (impulse response). Modelling shows that the strength of antagonism should increase with the signal-to-noise ratio. Measurements of receptive fields and impulse responses at different signal-to-noise ratios (S-N-R, lower diagrams) are in good agreement with the model[24]. The matched amplification strategy requires a relationship between input intensity and response amplitude in which equal increments in response correspond to equal areas under the probability distribution of input levels (upper figures). Contrast coding in LMCs (lower figure) comes close to this expectation[26].*

narrower range, so increasing response probabilities. The net result is a uniform probability of response over the entire amplitude range. It is interesting to note that this same type of matching is routinely used in digital picture processing to ensure that the range of grey levels on a display monitor are fully utilized and is known as 'histogram equalization'[23].

How is the amplification of signals in the fly eye matched to the statistical distribution of contrast signals? Does the relationship between stimulus contrast and LMC response follow the cumulative probability distribution of signal, as suggested by information theory? The contrast levels encountered by flies in typical habitats were measured and compared with the electrophysiological measurements of the relationship between contrast and LMC response[26]. There was a close correspondence (Fig. 3), which means that the gain of amplification is matched to signal to make full use of the response range. The mechanisms responsible for this matching of the gain are being investigated. Matching requires a sigmoidal contrast–response curve (Fig. 3) with an appropriate slope in its mid-region. In the squid stellate ganglion, the relationship between pre- and post-synaptic voltages is sigmoidal[27]. An attractive hypothesis is that this characteristic of chemical synaptic transmission generates the sigmoidal shape, while the receptor–LMC synapses operate with the gain that is required to produce the correct slope[28].

Minimizing synaptic noise

Predictive coding and matched amplification act in concert to protect pictorial information from noise. Protection is achieved by maximizing the amplitude of the signal transmitted by the second-order LMCs. In principle, amplification will reduce the effects of any noise introduced during the neural processing of photoreceptor signals. A recent study[28] has identified a major noise source whose deleterious effects are reduced by amplification of the signal – the photorecep-

tor synapses. Noise levels and signal-to-noise ratios were measured in fly photoreceptors and LMCs. Two types of noise were identified: noise generated in the photoreceptors during phototransduction and intrinsic noise produced during the transmission of signal from photoreceptor to LMC. Under daylight conditions, the intrinsic noise is as significant a limitation to signal quality as the noise generated during phototransduction. Measurements of power spectra suggest that much of this intrinsic noise is generated at the photoreceptor–LMC synapse. This means that synaptic noise limits visual acuity at high intensities. The study extended a simple model of synaptic transmission, previously applied to retinal coding[29,30], to show that the signal-to-noise ratio of a chemical synapse increases with the sensitivity of the transmitter release mechanism. To maximize the signal-to-noise ratio, a chemical synapse should maximize the amount of transmitter released for a given change in input voltage, but avoid saturating the postsynaptic responses. Thus, synaptic noise provides a compelling reason for having a retina in which signal amplification is maximized at the first synapse. This suggestion could also explain the widespread occurrence of high-gain synapses in sensory receptors[18].

Implications and general conclusions

In the fly compound eye, the first step in visual processing interfaces receptors to interneurons in order to minimize the destructive effects of synaptic noise. Interfacing uses predictive coding and a matched gain of amplification to increase retinal coding efficiency. How does this conclusion compare with existing functional explanations for the form of retinal coding in vertebrates? It is remarkable that the fly retina uses the retinal gain control system deduced by Werblin and colleagues for the mudpuppy retina[31,32]. In addition, our understanding of coding in the fly draws upon three principles of visual processing, redundancy reduction, feature enhancement and the matching of coding to the structure of incoming data.

Barlow[33] argued from first principles that retinal coding is directed towards reducing redundancy by, as he succinctly put it, the neat packaging of information. In particular he suggested that lateral antagonism is an effective means of removing spatial redundancy. The fly retina demonstrates how the strategy of redundancy reduction can be implemented by predictive coding and how, to be effective, antagonism must be matched to the quality of the incoming signal (in this case its signal-to-noise ratio). It may be instructive to examine neurons of the vertebrate retina for similar relationships between receptive fields or impulse responses and signal-to-noise ratios. Predictive coding may be particularly relevant to bipolar cells[34] which are, like fly LMCs, second-order interneurons exhibiting lateral antagonism in their receptive fields. One can also explain the function of spectral opponency in human colour vision using a redundancy reduction argument that is similar to the one advanced for predictive coding[35]. The overlap between the spectral sensitivities of human blue, green and red cones introduces common signal components into their responses. The application of information theory[35] shows that this redundancy can be minimized by combining the cone outputs into three channels. One is a luminance channel, summing all three cone types. The other two are spectrally opponent channels in which weighted combinations of cone inputs antagonize each other. The opponent channels required to minimize redundancy are very similar to those deduced from classical behavioural studies of colour opponency[35].

The second general principle of visual processing, feature enhancement, is often proposed as a major function of the retina. For example, retinal antagonism and amplification emphasize the timing of intensity changes and the location of edges[34,36]. There need be no conflict between the principles of redundancy reduction and feature detection[24,34]. In the absence critical evidence, the coding efficiency argument embraces all feature enhancement arguments. Efficient coding will, by definition, emphasize every feature that carries information, including the location of edges and the timings of intensity change. To reject a coding efficiency argument in favour of feature enhancement, one must not only invoke the qualitative benefits of enhancement[36], one must consider and evaluate the information that is lost or channelled elsewhere. Such an analysis of information trade-offs could prove particularly important when considering the segregation of signals into parallel channels (e.g. the different types of retinal ganglion cell).

Consider now the third principle: matching of the form of coding to the structure of natural scenes[15]. In the case of LMCs, the matching of amplification to expected signal levels makes better use of neural signalling power. In this sense it is advantageous to build assumptions about natural objects into coding at the lowest level of neural processing. One might also expect matched amplification to improve the performance of those bipolar and ganglion cells of the vertebrate retina that, like fly LMCs, operate with high spatial resolution under bright light conditions. Nor is matching necessarily restricted to these lower levels of visual processing. The matched amplification strategy deduced for fly LMCs was independently derived in a theoretical study of human vision. Our judgement of the lightness of surfaces appears to use a scale that follows the cumulative probability distribution of surface intensities[37].

Finally, let us examine some of the more general questions that are raised by this analysis of the form and function of neural coding in the fly. The changes that take place as signals, transferred from fly photoreceptors to LMCs suggest a new solution to the problem posed by von Neumann in 1958[38]. How does the nervous system perform accurately when it is constructed of unreliable components? Unreliability arises because neural communication is particulate. Signals are generated by relatively small numbers of discrete events (e.g. channels opening and closing, quantal transmitter release) and these are subject to random variations. von Neumann suggested a simple solution to the reliability problem: the brain increases the number of particles carrying information by sending the same signal through several cells. The analysis of coding by fly LMCs suggests another solution – the circuitry is designed so that each neuron, and hence each particle, works most effectively. If this latter strategy is widespread, accuracy and efficiency will be important considerations for understanding the design of neural circuits. Furthermore, the precise characteristics of synaptic transfer can be a critical compo-

nent in determining efficiency. For the photoreceptor–LMC synapses of the fly, a particular sigmoidal non-linearity is combined with the appropriate gain to match synaptic amplification to input statistics. Are the exact characteristics of synaptic transmission critical to the performance of other neural circuits? If they are, what mechanisms determine these characteristics and how are they specified during development and maturation? The relationships between development, form and function can probably be addressed in the fly lamina. The development of the fly lamina has been extensively documented[5] and recent results suggest that both the performance and the wiring of lamina cartridges are influenced by early visual experience[39,40].

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books

Selective Neuronal Death *(Ciba Foundation Symposium 126)*

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This is based on a symposium on Selective Neuronal Death held at the Ciba Foundation, London, in April 1986. Neurons are known to die selectively in two quite different circumstances: physiologically, in development, when most brain regions lose about half their neurons during a sharply defined period; and pathologically, in neurodegenerative diseases, where particular cell groups are found to be vulnerable. These are both major phenomena that currently attract considerable research effort. It is widely suspected that shared mechanisms such as failure to obtain trophic molecules may contribute to them both, but the neuropathologists and developmental neurobiologists who study them tend to remain in two separate groups that rarely communicate. The unstated purpose of the symposium was apparently to bring these groups together, along with some specialists in neural transplants and the actions of neurotoxins, in the hope of fruitful cross-fertilization.

The resulting publication has the usual merits and defects of multi-author volumes. The authors all have good standing in their respective fields, and they provide 14 up-to-date summaries of their work, although most of it has already been published elsewhere.

No attempt has been made to cover the entire field, but the sample provided seems to me well-chosen and balanced. Eight of the 14 papers concern degenerative diseases of the CNS. Two (Agid and Blin; Price *et al.*) deal directly with neuronal dysfunction and death in such diseases, while a third treats the formation of amyloid in Alzheimer's disease and in unconventional virus diseases of the nervous system (Masters and Beyreuther). There are four neurotoxicological studies with implications for understanding neurodegenerative diseases: three (Coyle; Stone *et al.*; Spencer *et al.*) are on the effects of excitotoxins that act at glutamate receptors, and the fourth (Marsden and Jenner) deals with the production of persistent parkinsonism by the drug MPTP. The last of the eight papers (Doerung and Aguayo)