

## THE ROLE OF SENSORY ADAPTATION IN THE RETINA

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### Summary

Adaptation, a change in response to a sustained stimulus, is a widespread property of sensory systems, occurring at many stages, from the most peripheral energy-gathering structures to neural networks. Adaptation is also implemented at many levels of biological organization, from the molecule to the organ. Despite adaptation's diversity, it is fruitful to extract some unifying principles by considering well-characterized components of the insect visual system.

A major function of adaptation is to increase the amount of sensory information an organism uses. The amount of information available to an organism is ultimately defined by its environment and its size. The amount of information collected depends upon the ways in which an organism samples and transduces signals. The amount of information that is used is further limited by internal losses during transmission and processing. Adaptation can increase information capture and reduce internal losses by minimizing the effects of physical and biophysical constraints.

Optical adaptation mechanisms in compound eyes illustrate a common trade-off between energy (quantum catch) and acuity (sensitivity to changes in the distribution of energy). This trade-off can be carefully regulated to maximize the information gathered (i.e. the number of pictures an eye can reconstruct). Similar trade-offs can be performed neurally by area summation mechanisms.

Light adaptation in photoreceptors introduces the roles played by cellular constraints in limiting the available information. Adaptation mechanisms prevent saturation and, by trading gain for temporal acuity, increase the rate of information uptake. By minimizing the constraint of nonlinear summation (imposed by membrane conductance mechanisms) a cell's sensitivity follows the Weber–Fechner law. Thus, a computationally advantageous transformation is generated in response to a cellular constraint.

The synaptic transfer of signals from photoreceptors to second-order neurones emphasizes that the cellular constraints of nonlinearity, noise and dynamic range limit the transmission of information from cell to cell. Synaptic amplification is increased to reduce the effects of noise but this resurrects the constraint of dynamic range. Adaptation mechanisms, both confined to single synapses and distributed in networks, remove spatially and temporally redundant signal components to help accommodate more information within a single cell. The net effect is a computationally advantageous removal of the background signal.

■ Key words: vision, light adaptation, retina, fly.

Again, the cellular constraints on information transfer have dictated a computationally advantageous operation.

### Introduction

Adaptation can be simply defined as a change in the relationship between stimulus and response that has been induced by the level of the stimulus. The following example illustrates that adaptation is a basic biological phenomenon (Koshland, 1983). Bacteria have chemosensory receptor molecules that act *via* intermediates to inhibit the reversals of flagellar rotation that cause them to tumble. Thus, when the receptors are active, the swimming bacteria tumble and change direction less often. However, the receptors adapt to the level of chemoattractant by being desensitized by a reversible methylation. As a result of adaptation, the bacteria are only inhibited from tumbling when the attractant concentration is continuously increasing. Thus bacteria tend to move up concentration gradients, towards attractants. Bacterial chemotaxis illustrates three points about adaptation. First, adaptation is a fundamental process, existing at many levels of biological organization. Second, adaptation derives, in the first instance, from a basic property of proteins, allosteric regulation (e.g. Stryer, 1988). Third, adaptation can be a critical component in the recognition of patterns. Given these observations on bacteria, it is not surprising that many components of sensory systems adapt. In other words, the relationship between a cell's response and the stimulus changes according to the prevailing level of stimulation. Insect compound eyes are no exception to this general rule, and they have the advantage that sensory processing has been extensively analysed at a number of levels, from optics to behaviour. With this detailed understanding of processing we are able to isolate a number of adaptation mechanisms and assess their function. In this review I have taken examples of adaptation phenomena from optics, phototransduction and synaptic transfer. In each case I examine the forms of adaptation involved, the underlying mechanisms, and the role played by adaptation in coding.

The adaptation processes that we will consider have counterparts in other sensory systems and illustrate general principles of adaptation. The examples have been chosen to illustrate three points. First, as in the vertebrate retina (Shapley & Enroth-Cugell, 1984), adaptation is found at many levels of processing and is executed by a correspondingly wide variety of mechanisms. Indeed, a comprehensive survey of adaptation mechanisms in insect compound eyes is beyond the scope of this article. Second, adaptation often involves trade-offs: sensitivity to one component of the stimulus is sacrificed for sensitivity to another. Third, adaptation reduces the effects of some fundamental limitations on sensory processing. These limits may be set by extrinsic constraints imposed upon the organism by the stimulus or by intrinsic constraints determined by the organism, such as the size, numbers of cells and the accuracy and signalling ability of receptors and neurones.

Many of the arguments presented here have been reviewed before (e.g. Werblin, 1973; Autrum, 1981; Laughlin, 1981a; Shapley & Enroth-Cugell, 1984;

Laughlin, 1987), but they are worth reconsidering, both to incorporate recent findings and for completeness. This latter consideration is important because each of the forms of adaptation that we consider will contribute to a re-assessment of retinal function. It will be shown that, by relating coding to measured biophysical limitations (Laughlin, 1989), one can conclude that adaptation minimizes the effects of extrinsic and cellular constraints. The welcome biproduct of this optimization is a highly desirable property for a visual system; a response to patterns of reflectance in the world that changes remarkably little over the wide intensity range encountered every day. In other words, by making the hardware work accurately, one generates an important constancy. This constancy is produced in the vertebrate retina by similar means (Shapley & Enroth-Cugell, 1984). Conveniently for the insect, retinal coding kills two birds with one stone. Coding both optimizes the performance of receptors and neurones, and provides higher centres with a computationally desirable neural image of the world.

### **Optical adaptation mechanisms**

An eye's optics collects light and generates an image on an array of photoreceptors. The optical factors determining image quality have been thoroughly analysed (Kirschfeld, 1976; Snyder, 1979; Land, 1981) and this enables us to assess the functions of optical adaptation mechanisms. In the apposition compound eyes of insects and crustaceans, the image is formed by a matrix of optical modules, the ommatidia. Each ommatidium contains a lens, focusing light onto a set number of photoreceptors (usually eight). As in rods and cones, a receptor's photopigment is contained in a densely packed membranous cylinder that holds light within it by virtue of its higher refractive index. This cylindrical waveguide is the fundamental spatial sampling element of the photoreceptor array. The apposition compound eye generates an image because each waveguide responds to light from a particular narrow cone of space (Fig. 1). The width of this cone or, more strictly speaking, a photoreceptor's angular sensitivity function, is defined by two optical factors, lens diffraction and the angle subtended by the waveguide. Only the light entering the waveguide contributes to vision and the remainder is absorbed by pigment cells. Note that, because every ommatidial lenslet admits light over a wide angle, the majority of rays entering the eye strike the screening pigment and are either absorbed, or reflected back into the world (Stavenga, 1979). If most of the light were not rejected, the apposition eye would not generate a reasonable image. By comparison, much more of the light entering the simple lens eyes of vertebrates and spiders strikes the photoreceptors and contributes to vision. Thus, the apposition eye is a decidedly inferior optical organ (Kirschfeld, 1976), using small lenses with poor resolving power and throwing away most of the incident light. The one recompense is that when one views the eye from any angle one sees coloured screening pigment over most of its surface, so allowing for camouflage and display (Stavenga, 1979). As far as I can see, this is the only advantage of an otherwise poor optical system.

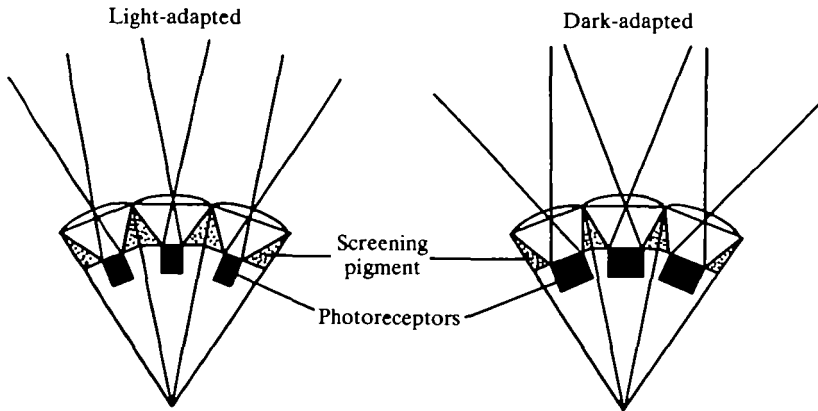


Fig. 1. Optical mechanisms trade off angular sensitivity for light capture during the dark adaptation of an apposition compound eye. In the light-adapted state the photoreceptors subtend a narrow angle of space, as indicated by their projection through the lens. In the dark-adapted state this angle is widened, the photoreceptors catch more light, and less is lost on screening pigment. There is now a considerable overlap between the fields of view of neighbouring ommatidia.

The loss of light in apposition eyes is a severe limitation to acuity, particularly at low light levels. Under dim conditions, fluctuations in photon catch make it impossible to discriminate the intensity levels received by adjacent ommatidia. These photon fluctuations are an extrinsic constraint, common to all optical signals, and imposed by the random nature of molecular absorption. The only way to reduce photon noise is to catch more light. An obvious strategy for an apposition eye is to reduce the losses in the screening pigments by expanding the window viewed by the photoreceptor waveguides. Indeed, arthropod compound eyes contain a variety of mechanisms, each of which trades angular sensitivity for photon catch (Walcott, 1975; Nilsson, 1989). Adaptation to low light levels usually involves a decrease in photoreceptor angular sensitivity, obtained by widening the angle subtended by the photoreceptive waveguides (Fig. 1). Widening mechanisms include growing fatter waveguides, moving the photoreceptors closer to the lens, and withdrawing pigment from around the photoreceptors (Walcott, 1975; Stavenga, 1979; Nilsson, 1989; Barlow *et al.* 1989). In each case, the extrinsic constraint of photon noise is reduced by sacrificing angular resolving power. The photon noise problem derives in part from low light levels and in part from an intrinsic constraint, the size and unfavourable geometry of the eye. It might be thought that any reduction in angular sensitivity would reduce the resolving power of the eye. However, at low light levels, photon noise reduces acuity by rendering signals in adjacent ommatidia indistinguishable. The gain in resolution that results from capturing more photons far outweighs the geometrical loss of angular sensitivity. Indeed, for every low light level, there is an optimum trade-off between angular sensitivity and photon catch (Snyder, 1979).

In summary, many apposition eyes adapt to a reduction in light intensity by

altering their optics. Adaptation is a graded process that trades angular sensitivity for photon catch (absolute sensitivity). This trade-off improves acuity at low light levels by reducing the effects of an extrinsic constraint, photon noise. The advantages of adaptation must be considerable because they involve a number of coordinated cellular processes, such as pigment migration and adjustments to cell shape and size. Such acuity/sensitivity trade-offs are not restricted to compound eyes. The opening of the pupil of a simple lens eye could execute the same trade-off by admitting more light, but creating a larger blur circle by increasing aberrations. Furthermore, the spatial summation of retinal signals in rod pools trades off spatial sampling density against photon catch and can, in principle, be adjusted over a wide range of light levels to maximize the quality of the resulting image (Snyder *et al.* 1977). Finally, it should be noted that many nocturnal insects and crustaceans use superposition eyes, in which arrays of lens cylinders (Exner, 1891) or mirrors (reviewed by Land, 1981; Nilsson, 1989) direct parallel rays entering many ommatidia to a small group of photoreceptors. Thus, as in many simple lens eyes, most of the light entering the eye contributes to the retinal image and losses in the screening pigment are greatly reduced.

### Adaptation in photoreceptors

#### *The basic unit of response is the bump*

An invertebrate photoreceptor's membrane potential codes the number of photons arriving over its angular acceptance by means that broadly resemble those of a rod or a cone. Visual pigment molecules in the photoreceptive membrane (reviewed by Vogt, 1989) absorb a high proportion of the light contained within the ommatidial waveguide. Each absorption triggers a conformational change in a single rhodopsin molecule. This photoisomerization is coupled to the opening of channels in the photoreceptor membrane by a second messenger (phosphoinositide) cascade (Fein *et al.* 1984; Fein & Payne, 1989). Thus the basic unit of phototransduction is the quantum bump – a discrete fluctuation in membrane potential, corresponding to the opening of a small group of channels in response to a single photoisomerization. Individual bumps are often visible in totally dark-adapted cells, viewing very dim lights (Fig. 2A). A comparison between the energy of a photon and the energy of one of the bumps shown in Fig. 2A (generated in a cell of 30 M $\Omega$  input resistance) suggests an amplification of almost 4000. Larger bumps and a higher amplification are observed in the larger photoreceptors of *Limulus* (Fein & Payne, 1989; Barlow *et al.* 1989). Most quantum bumps produced by a dark-adapted fly photoreceptor are large enough to produce a detectable response in postsynaptic cells. As in rods, amplified single-photon signals enable the visual system to approach the limits of acuity set by the photon catch (Reichardt, 1970; Dubs *et al.* 1981).

At higher light levels the quantum bumps fuse to generate a continuous but noisy response that increases in amplitude with intensity. The photoreceptor also adapts to light, as seen in the reduction in response to a maintained and constant

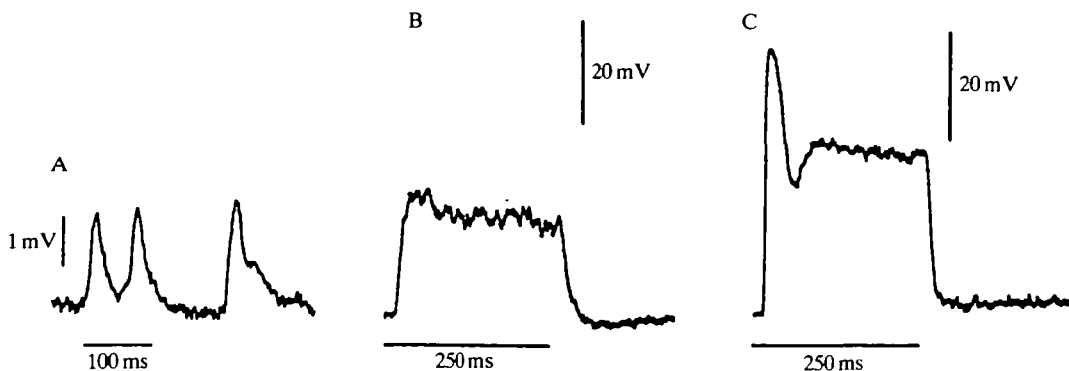


Fig. 2. (A) The photoresponse is composed of elementary events, quantum bumps, seen at low light levels in fully dark-adapted photoreceptors of the fly *Calliphora vicina*. (B) At intermediate intensities the bumps fuse to produce a sustained but noisy response. (C) Photoreceptors rapidly adapt to high-intensity stimuli, as demonstrated by the decline of the response to a steady light pulse delivered to an initially dark-adapted cell. The bumps in A were selected from a long train elicited by sustained dim illumination. In B and C the light pulse was presented for the 250 ms period indicated by the marker.

stimulus (Fig. 2C). Adaptation enables a single photoreceptor with a 70 mV dynamic range of response to cope with the huge intensity changes encountered from night to day. At the absolute threshold of the fly's optomotor response, a single photoreceptor registers 3 quantum bumps per second (Reichardt, 1970; Dubs *et al.* 1981). Under bright daylight conditions this flux increases to  $10^7 \text{ s}^{-1}$  (Howard *et al.* 1987). The adaptation effects required to encompass this range must substantially decrease the gain of the photoreceptor. The single dark-adapted bump is 1 mV or more in amplitude, but steady daylight depolarizes the cell by 35 mV (see Fig. 4B), implying microvolt bumps.

#### *Adaptation changes the rate, duration and amplitude of bumps*

Three adaptation mechanisms have been identified in fly photoreceptors. The first mechanism is an 'intracellular pupil' (Kirschfeld & Franceschini, 1969), which is also seen in many other apposition eyes (Stavenga, 1979; Nilsson, 1989). At high light levels, small pigment granules move up close to the photoreceptive waveguide and reduce the effective light flux within it (i.e. the bump rate) by as much as 100-fold (Franceschini, 1972; Howard *et al.* 1987). The second mechanism is a reduction in the gain of the transduction cascade. Voltage-clamp studies of *Limulus* photoreceptors (Wong *et al.* 1982) show that light adaptation reduces the number of channels opened by a single photon. In the fly this effect is most obvious as a reduction in the effective duration of quantum bumps from about 20 to 1.7 ms (Howard *et al.* 1987). Light adaptation also reduces the response latency and rise time (Fein & Payne, 1989). It is not known which particular stages of the phototransduction process are modified during adaptation. The third adaptation mechanism is a large voltage-sensitive potassium conductance that is activated by

depolarization of the photoreceptor membrane (Muijsers, 1979; M. Weckström, R. C. Hardie & S. B. Laughlin, in preparation). This conductance prevents the photoreceptor from saturating by generating a delayed current that repolarizes the cell. The conductance also decreases bump amplitude by reducing the receptor's input resistance from 30 to approximately 3 M $\Omega$ .

*A non-linear summation of response facilitates contrast coding*

The operating range of photoreceptors is extended by an additional factor, a non-linear summation of voltage response. For the vertebrate retina this phenomenon is also known as response compression (Shapley & Enroth-Cugell, 1984). In arthropod photoreceptors, non-linear summation results from the self-shunting of the receptor potential. The depolarization induced by light reduces the potential driving ions through the light-activated conductances. Thus, conductance channels generate progressively less current as the response amplitude increases, and this causes the curve relating the response to the number of channels to flatten. This self-shunting of response is a fundamental intrinsic constraint, stemming from the parallel arrangement of conductance channels in the membrane. Self-shunting was first analysed at the postsynaptic membrane of the neuromuscular junction (Martin, 1955), and shapes the response–intensity curves of a number of sensory receptors and interneurons (reviewed by Lipetz, 1971), including the Pacinian corpuscle (Loewenstein, 1958) and retinal horizontal cells (Naka & Rushton, 1966). The action of self-shunting is described by the familiar hyperbolic function:

$$V/V_m = G/(G + L), \quad (1)$$

where  $V$  is the response, measured relative to dark resting potential,  $V_m$  is the saturated response amplitude,  $G$  is the light-activated conductance generating the response, and  $L$  is a constant that equals both the load conductance of the cell and the value of  $G$  required to produce a response of half-maximal amplitude.

If we assume that, at intensity  $I$ ,  $eI$  photons each activate a conductance (averaged over the bump time course) of  $g$ , we obtain

$$V/V_m = eIg/(eIg + L). \quad (2)$$

Response–intensity curves of this form are plotted in Fig. 3. When the conductance change generated by a single photon,  $g$ , is much less than the load conductance,  $L$ , the bump amplitude is given by  $V_m g/L$ . This equals the initial slope of the curve and is, therefore, one possible measure of sensitivity.

Although non-linear summation progressively decreases the sensitivity of the cell to increments and decrements as intensity rises, it is not a form of adaptation. Irrespective of the adaptation state, non-linear summation is part of the relationship between response and intensity. Adaptation changes a cell's sensitivity to produce new response–intensity curves with different initial slopes. The action of each of the adaptation mechanisms discussed above can be identified in equation 2. The intracellular pupil changes the quantum capture efficiency,  $e$ . Bump adaptation modulates the conductance activated per photon,  $g$ . The voltage-

sensitive potassium conductance modifies the load conductance,  $L$ . In conclusion, non-linear summation results from a fundamental cellular constraint, the activation of parallel conductance channels, and defines the context within which adaptation operates. The intensity–response functions of vertebrate cones exhibit this same hyperbolic form of non-linear summation and similar adaptation effects (Normann & Perlman, 1979). Because light is closing channels, self-shunting is not responsible for this non-linearity (Baylor & Fuortes, 1970) and site saturation within the phototransductive cascade is the probable cause (Baylor *et al.* 1974).

For insect photoreceptors, self-shunting is an intrinsic cellular constraint which limits coding by reducing the slope of the response–intensity curve. The photoreceptor's sensitivity to small changes in intensity decreases as the response amplitude rises. This limitation to incremental sensitivity is, in some senses, beneficial because it helps extend the intensity range over which a receptor can operate. Self-shunting, and similar forms of non-linear summation, perform what amounts to a logarithmic transformation on the input, as illustrated by replotting equation 2 on semi-logarithmic coordinates (Fig. 3B). The result is a sigmoidal curve with the response approximately proportional to the logarithm of intensity in its mid-region. This log–linear region is commonly observed in the response–intensity curves of sensory receptors and is equivalent to Fechner's Law (Hartline & Graham, 1932; Granit, 1955). It is well known that the logarithmic transformation is particularly advantageous for vision because it scales signals according to their proportions (von Helmholtz, 1924). For example, an object that reflects twice as much light as its surroundings will generate a signal that is  $0.3 \log$  units larger, irrespective of the intensity of uniform illumination. This observation shows that the logarithmic transformation generates a set of photoreceptor responses to a set of reflecting objects in which the differences in amplitude among cells are identical at all light levels. The level of illumination simply determines the response level at which this invariant response profile sits. If we ignore (or remove) this average level, the logarithmic transform provides a representation of objects that is invariant with respect to illumination level. Thus, those photoreceptors that implement a logarithmic transform code the reflectance of uniformly illuminated objects. Reflectance is directly related to a common measure of relative intensity, contrast. Here we define contrast as  $\Delta I/I$ , where  $\Delta I$  is the difference in intensity between an object and the average level of illumination  $I$  (the Weber contrast of Shapley & Enroth-Cugell, 1984). For the object that reflected twice as much as its surroundings, the contrast is 1.0, irrespective of the mean intensity,  $I$ .

#### *Adaptation combines with non-linear summation to code contrast*

The responses of a photoreceptor of fixed sensitivity cannot cover the full range of daylight intensities. The sensitivity required to register a single photon is so great that the receptor would saturate in daylight. In addition, the functionally advantageous logarithmic region of a self-shunting cell only spans 1 of the 7 or more log units of intensity normally encountered (Fig. 3B). Photoreceptor adaptation mechanisms continuously adjust sensitivity to generate a new response–



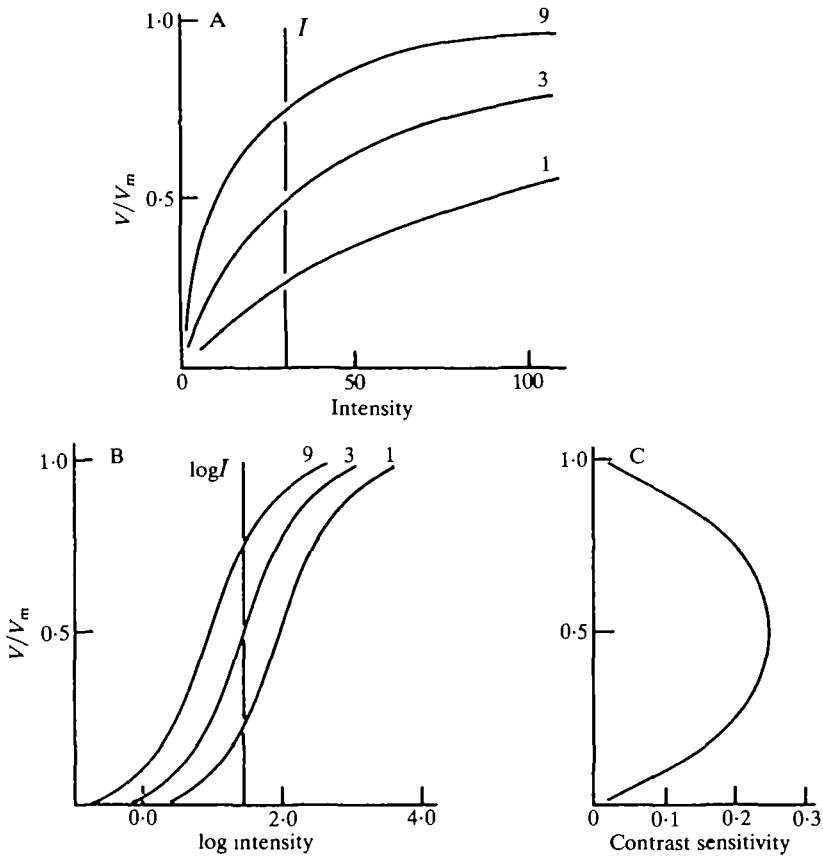


Fig. 3. The effects of non-linear summation and adaptation on the coding of intensity and contrast by photoreceptors. In all cases the response amplitude  $V$  is normalized to a fraction of the maximum (saturated) response  $V_m$ . (A) Linear plots of three response-intensity functions of the form determined by self-shunting (equation 2), with relative sensitivities (e.g. bump amplitudes) of 1, 3 and 9. The curve for sensitivity 3 codes changes of light intensity about the mean light level,  $I$ , with maximum slope. Sensitivity and intensity are in arbitrary linear units. (B) The same three functions plotted on semi-logarithmic coordinates, showing the shift in the log-linear region produced by changes in sensitivity. Again the middle curve passes through  $I$  with the highest slope. (C) The contrast sensitivity of a self-shunting photoreceptor depends on the response amplitude, with a broad maximum centred at  $V/V_m = 0.5$ . Contrast sensitivity was calculated from the slope of a response-intensity curve and is given as  $V/V_m$  per unit of Weber contrast.

intensity curve at each background (Fig. 3A). Adapting bumps and voltage-sensitive conductances are the two mechanisms of particular importance. These reduce the amplitude of quantum bumps, so lowering the initial slope of the response-intensity curve on a linear plot (Fig. 3A). On a semi-logarithmic plot their effect is to shift the curve to a higher intensity range (Fig. 3B). To avoid confusion in what follows, we should note that there are several definitions of

sensitivity (Laughlin & Hardie, 1978; Autrum, 1981; Shapley & Enroth-Cugell, 1984). Photoreceptor adaptation mechanisms alter the absolute sensitivity of the cell, defined as the reciprocal of the intensity required to give a response of constant absolute amplitude. This absolute amplitude is measured relative to a fixed point in the cell's response range (usually the resting potential in the dark). The absolute sensitivity can also be expressed in terms of the initial slope of the response–intensity curve, and this equals the amplitude of the response to a single photon.

To what extent should adaptation reduce a photoreceptor's absolute sensitivity as the level of illumination increases? For every light level there is an optimal response–intensity curve (Laughlin, 1981a). This is the curve that passes through a particular mean intensity with the highest slope, to give the largest responses to the intensity fluctuations set up by objects of low contrast. This optimum curve intersects the mean intensity at a response of half maximum (Fig. 3A,B). The slope of the response–intensity curve,  $dV/dI$ , is termed the increment sensitivity (Laughlin & Hardie, 1978) to distinguish it from the absolute sensitivity. The increment sensitivity determines the response per unit contrast (the 'contrast response' of Howard *et al.* 1987, or 'contrast sensitivity' of Shapley & Enroth-Cugell, 1984), and this, too, is maximal when the response is  $V_m/2$  (Fig. 3C). Inspection of Fig. 3A demonstrates that the optimum curve is a compromise between two factors. Too low an absolute sensitivity depresses the increment sensitivity over the entire curve, but too high an absolute sensitivity results in a loss of slope through non-linear summation. It follows (Laughlin, 1981a) that if a cell is to minimize the effects of non-linear summation on coding intensity changes about a background level, it should adjust its absolute sensitivity to operate at  $V_m/2$ . To implement this coding strategy, adaptation must continually reset the cell's sensitivity so as to maintain response at the same level. If this condition is fulfilled, the absolute sensitivity of the cell is inversely proportional to intensity. Under this condition, the contrast response and the absolute level of response are identical, irrespective of illumination levels. Consequently, objects of fixed reflectance and contrast generate identical signals at all light levels, a condition that is termed brightness constancy because it enables objects to appear equally bright to the animal over a wide range of illumination levels (Shapley & Enroth-Cugell, 1984).

To summarize, the biophysical constraint of non-linear summation (in this case self-shunting) necessitates the use of adaptation to optimize performance. Self-shunting and adaptation then work together to scale the signal in proportion to the mean intensity. The form of saturating behaviour exhibited by self-shunting and adaptation is often found in biological systems (e.g. Koshland *et al.* 1982). Consequently, the proportional scaling of signals may be a common phenomenon in transduction, communication and control systems. As examples, neurones and synapses are subject to self-shunting (Creutzfeld, 1972), and enzymatic site saturation generates a similar logarithmic transform in cones (Shapley & Enroth-Cugell, 1984).

The constraint of self-shunting is not the only factor influencing light adaptation

in the fly photoreceptor. To ensure that a self-shunting cell operates with the highest increment sensitivity, adaptation should not reduce sensitivity until the response reaches the level of half maximum. In a photoreceptor, this optimal level could be achieved at low intensities by having large bumps. The fly photoreceptor does not follow this pattern. Its dark-adapted quantum bumps are small (Fig. 2A), perhaps because they contribute to small neural summation pools (Laughlin, 1981a). In addition, light adaptation is initiated prematurely, when the response is well below half-maximal (Fig. 4). It is likely that increment sensitivity is being sacrificed for other advantages. First and foremost, the photoreceptors's adaptation state determines its temporal resolving power. During light adaptation, the response amplitude is reduced by shortening the duration and latency of quantum bumps. The reduction in response duration reduces the extent to which signals are blurred by being spread out over time. The resulting increase in temporal resolution is highly desirable because the fly is a rapidly moving and turning insect. With less temporal blurring, the eye generates a crisper and more detailed image. In more formal terms, the cell's information capacity is proportional to the highest frequency it transmits (Laughlin, 1981a; Howard & Snyder, 1983) and this favours the sacrifice of sensitivity for speed of response. The second reason for not maximizing the increment sensitivity at low intensities is that little is to be gained from this exercise. At low light levels, quantum fluctuations determine the signal

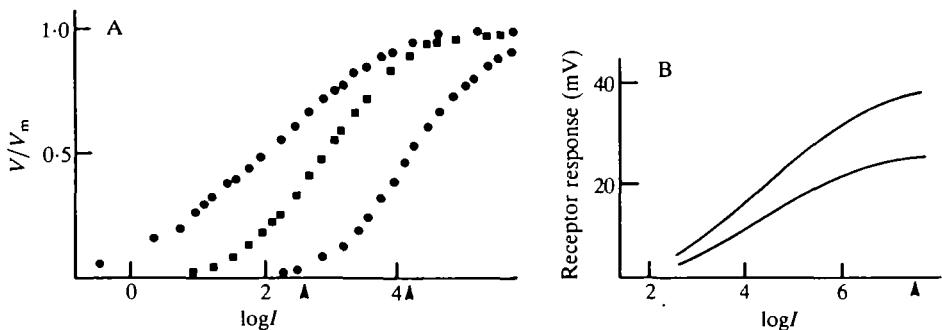


Fig. 4. Adaptation and the coding of intensity and contrast by photoreceptors of the blowfly *Calliphora*. (A) Light adaptation shifts curves relating response to log intensity to higher intensity levels. The left-hand curve is for a dark-adapted cell. The others are for cells adapted by prolonged exposure to the adapting intensities indicated by arrowheads. The slope of the dark-adapted curve is reduced by light adaptation occurring during the time taken for the response to develop to its full amplitude, an effect that has been described by a commonly employed modification to the self-shunting relationship (equation 2); raising the intensity term to a power less than 1 (Matic & Laughlin, 1981). (B) The upper and lower bounds of the response generated by a signal of average natural contrast over a wide range of mean intensities,  $I$ . The arrowhead indicates full daylight. The response is measured relative to the dark resting potential. Note that the contrast signal occupies a relatively narrow envelope which expands as the background elevates the level of response, so leading to an increased contrast sensitivity (Fig. 3C). Data taken from Howard *et al.* (1987) and Laughlin *et al.* (1987).

quality and changes in increment sensitivity do not improve the signal-to-noise ratio with respect to photon noise. The larger signal generated by a higher increment sensitivity is only advantageous when intrinsic noise, generated higher up in the nervous system, is restricting acuity.

At the highest intensities, corresponding to the daylight range, light adaptation maximizes increment sensitivity and minimizes the effects of non-linear summation. Sensitivity is regulated to maintain the steady-state response close to the optimal 50 % level (Fig. 3C) at daylight levels (Fig. 4B). Over the more restricted daylight range, the stimulus contrast is coded independently of mean intensity, resulting in brightness constancy. Two observations support the argument that the light-adapted cell is now responding to the dictates of self-shunting. First, a noise analysis (Howard *et al.* 1987) shows that, over a 3 log unit range of the highest intensities, the quantum bump duration is a constant 1.5 ms. Apparently, no further increase in temporal resolving power can be obtained by adapting bump duration. This minimum bump duration is sufficiently brief to suggest that the cell has hit the limits dictated by enzyme kinetics and by diffusion. Second, at high light levels, the intrinsic noise generated more centrally is more significant than noise generated during transduction (Laughlin *et al.* 1987). This shift in balance from quantum fluctuations to intrinsic noise favours the optimization of increment sensitivity because the larger the photoreceptor signal, the smaller the masking effects of intrinsic noise.

In conclusion, we see that a set of photoreceptor adaptation mechanisms is continuously adjusting sensitivity. At low light levels, adaptation trades off signal amplitude for temporal resolving power. At higher light levels, adaptation ensures that signals are coded in the region of the intensity–response curve where the slope is maximal. This latter strategy minimizes the biophysical constraint imposed upon the cell by the parallel organization of conductance channels in the membrane, and dictates an absolute sensitivity that is inversely proportional to background light level. Such a sensitivity produces brightness constancy. Vertebrate cones adapt in a similar manner to fly photoreceptors, and are subject to similar constraints. Cone light adaptation is associated with faster responses (Baylor & Hodgkin, 1974) and, as in Figs 3B and 4A, shifts  $V/\log I$  curves to maintain coding in the region of highest slope (Normann & Werblin, 1974; Normann & Perlman, 1979). The hair cells of the turtle ear are hyperpolarized by afferent inputs when strongly stimulated (Art *et al.* 1984). This effect is analogous to the activation of the voltage-sensitive potassium conductance in fly photoreceptors and could regulate the hair cell response–intensity curve to give a better increment sensitivity. The effect may also prevent saturation of the output synapses (Art *et al.* 1984).

### Synaptic adaptation

#### *Synaptic adaptation helps interface receptors to interneurones*

The most numerous photoreceptors in the fly eye, the class of cells R1–6,

terminate in the lamina. R1–6 cells have identical optical and electrical properties and synapse with several interneurons, the principal ones being the large monopolar cells (LMCs) L1–3. There is one set of lamina interneurons for every ommatidium, and its members receive their primary input only from those photoreceptors that look in the same direction (Kirschfeld, 1967; Braitenberg, 1967; van Hateren, 1987). Thus, the photoreceptor sampling stations map precisely and retinotopically onto neural modules, a fact that has greatly simplified the extensive anatomical and physiological analysis of this system (reviewed by Strausfeld, 1984; Shaw, 1984; Laughlin, 1989). Intracellular recordings can be made from LMCs (Autrum *et al.* 1970) in an intact preparation (Laughlin & Hardie, 1978). This allows one to study synaptic transfer from photoreceptors to LMCs (Järvilehto & Zettler, 1971; Laughlin & Hardie, 1978) and to relate mechanism to function (Hardie, 1987; Laughlin, 1987).

LMC responses are inverted, amplified and more transient versions of photoreceptor responses. Amplification occurs in the array of 1200 high-gain chemical synapses connecting photoreceptors to LMCs. The transience of LMC responses (Fig. 5) demonstrates that powerful neural adaptation mechanisms are at work. These mechanisms have not been identified, but a number of possibilities have recently been assessed (Weckström *et al.* 1989; Laughlin & Osorio, 1989). Voltage-sensitive conductances in LMCs, and synapses other than the direct photoreceptor input, play a secondary role in neural adaptation. The transient LMC waveform derives, in the main, from the transient activation of hyperpolarizing conductance channels at the receptor–LMC synapses. The synaptic transmitter is probably histamine, which directly activates chloride channels in the LMC membrane (Hardie, 1987, 1989; Zettler & Straka, 1987). When histamine is applied to LMCs *in situ* there is no sign of postsynaptic desensitization (Hardie, 1987). This observation suggests that neural adaptation is brought about by regulating the rate of histamine release. Step changes in presynaptic potential probably produce transient changes in histamine release rate. Because the photoreceptor synapses are tonically active both in the dark and in the light (Laughlin *et al.* 1987), such transient mechanisms can code both increments and decrements in light intensity, by modulating the release rate around a sustained level (Laughlin & Osorio, 1989). In this respect fly LMCs differ from their vertebrate analogues, the bipolar cells, which segregate the signal into ON (incremental) and OFF (decremental) components.

Adaptation, in the form of transient responses, allows photoreceptor synapses to combine a high gain with a wide operating range (Hayashi *et al.* 1985). In the fly, the photoreceptor–LMC synapses have a gain of 6 (Laughlin *et al.* 1987). The range of response amplitudes generated by an LMC is 60 mV. Consequently, without adaptation, the response of the postsynaptic cell would correspond to a 10 mV band of photoreceptor inputs. This band matches the envelope of photoreceptor signals generated by natural reflectances at one particular light level. However, diurnal changes in intensity increase the range of photoreceptor responses to over 40 mV (Fig. 4B). To cope with this range and maintain a high

gain, adaptation mechanisms continuously attempt to restore synaptic activity to a tonic level. This adjustment keeps the characteristic curve for synaptic transmission centred on the mean level of photoreceptor depolarization (Fig. 5B). The centring also ensures that small signals are transmitted using the mid-region of the synaptic characteristic curve, where the slope or increment sensitivity is highest (Fig. 5B). Thus, synaptic adaptation resembles photoreceptor adaptation because it prevents saturation and maintains coding in the region of highest increment sensitivity. Similar synaptic adaptation occurs at the histaminergic synapses of

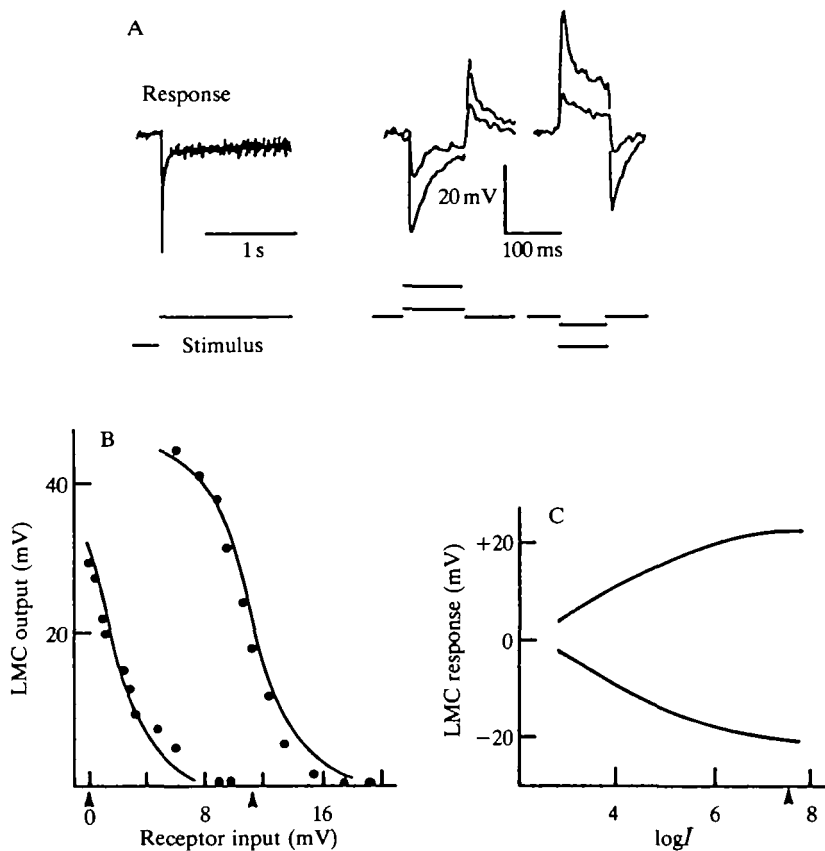


Fig. 5. Adaptation and contrast coding in the second-order large monopolar cells (LMCs) of the blowfly *Calliphora*. (A) Transient responses to a sustained stimulus and the high sensitivity to changes in intensity about that sustained level. (B) Curves relating the amplitude of postsynaptic LMC responses to the amplitude of the presynaptic photoreceptor signal determined when dark-adapted (left-hand curve), and when the photoreceptors were depolarized by a steady background light (right-hand curve). Both curves have the same steep slope indicative of a high-gain synapse, and are shifted by adaptation to keep them centred on the two levels of photoreceptor response, indicated by the arrowheads. (C) The envelope of the responses of an LMC to the same contrast signal presented to photoreceptors (Fig. 4B), over a similar range of background light levels. Note the larger amplitude of the envelope and the absence of background signal. Data from Laughlin *et al.* (1987).

barnacle and locust ocelli (Hayashi *et al.* 1985; Stuart & Callaway, 1988; Simmons, 1985; Simmons & Hardie, 1988). The cone-bipolar synapses of the mudpuppy retina also shift their operating range to forestall saturation and operate with a high gain (Werblin, 1977), but the locus of adaptation is less certain. Some auditory hair cells appear to have adapting synapses (Furukawa & Matsuura, 1978).

What mechanisms are responsible for adaptation at the output synapses of arthropod photoreceptors? The first, and most thorough, analysis of this phenomenon was made in the barnacle ocellus (Hayashi *et al.* 1985; Stuart *et al.* 1986). The mechanisms have not been resolved, but a plausible and attractive suggestion is that an interplay between voltage-sensitive calcium conductances and calcium-sensitive potassium conductances leads to a transient release of neurotransmitter (Hayashi *et al.* 1985). In the fly lamina, histamine release may also be regulated by changes in the extracellular potential (Laughlin, 1974; Shaw, 1975; reviewed by Shaw, 1984). According to this hypothesis, the light-induced depolarization of the photoreceptor terminal is accompanied by a slower depolarization of the surrounding extracellular space in the lamina. This extracellular depolarization subtracts from the intracellular signal at the presynaptic membrane, so shutting down transmitter release. Such extracellular potentials have often been reported and the appropriate resistance barriers are present. However, a definitive analysis is complicated by the tortuous nature of the extracellular spaces in the lamina cartridge (reviewed by Laughlin, 1981a; Shaw, 1984).

Whatever the mechanism, synaptic adaptation plays an important role in boosting the efficiency with which natural signals are transmitted from photoreceptors to interneurons (reviewed by Laughlin, 1987). Photoreceptors and LMCs combine to code signals from objects of constant reflectance (i.e. signals of constant contrast) with a high gain over a wide range of illumination levels (Fig. 5C). At any one level of illumination, the photoreceptors generate a narrow voltage band of signal which is susceptible to degradation by the intrinsic noise that must be encountered during subsequent transmission and processing. To complicate matters, this relatively narrow envelope of receptor signal is superimposed on a sustained depolarization of up to 30 mV (Fig. 4B). During the passage of the signal from photoreceptors to LMCs, synaptic adaptation first removes this sustained component. The remaining signal is then amplified to fill the dynamic response range of the second-order LMCs. Thus, adaptation allows the photoreceptor synapses to extract and amplify the contrast signals generated by differences in the reflectances of objects (Laughlin & Hardie, 1978).

The process of synaptic amplification promotes the accurate transmission of data from photoreceptors to higher-order cells by reducing the effects of intrinsic noise and making full use of the LMC response range (Laughlin & Hardie, 1978). Indeed, a detailed analysis of synaptic noise (Laughlin *et al.* 1987) suggests that amplification is a critical first step in the retinal processing of small signals. Amplification reduces the effects of the synaptic noise generated by the photoreceptors themselves. Photoreceptor synaptic noise is potentially damaging

because it affects contrast signals of low amplitude. Synaptic noise is introduced by the random processes of neurotransmitter release and postsynaptic channel activation. Amplification reduces the effects of these random processes by increasing the numbers of vesicles, histamine molecules and chloride channels carrying the signal. The improvement is considerable. Recordings from LMCs show that synaptic noise is equivalent to a contrast of approximately 1% (Laughlin *et al.* 1987) – a reasonable value for sampling at one spatial point or pixel. A simple theoretical analysis (Laughlin *et al.* 1987) suggests that the synaptic signal-to-noise ratio is proportional to the gain of amplification. Without amplification (a gain of 1) the synaptic noise would be equivalent to a contrast of 6%; a figure that is intolerable in an otherwise well-designed and acute visual system. A second method of reducing synaptic noise, a large array of parallel synapses, is used in the insect lamina (Laughlin, 1973) but is insufficient on its own. The signal-to-noise ratio is proportional to the square root of the number of synapses and, for the fly, a sixfold improvement would require the number to be increased from 1200 (Nicol & Meinertzhagen, 1982) to 43 000! These simple calculations demonstrate that the adapting and amplifying synapses of fly photoreceptors are an essential interface, designed to reduce a real and potentially damaging constraint, synaptic noise (Laughlin *et al.* 1987). Interfacing cells to reduce synaptic noise may be an important consideration in any neural network where a small signal meets a chemical synapse, and sensory systems such as the vertebrate retina are particularly likely sites (Laughlin, 1987).

*Adapting synapses reduce redundancy and improve coding efficiency*

The photoreceptor–LMC interface is well designed to reduce noise and transmit signals efficiently by maximizing amplification (Laughlin, 1987). Processing follows two principles: predictive coding (Srinivasan *et al.* 1982) and matched amplification (Laughlin, 1981*b*). Predictive coding is executed by the processes driving synaptic adaptation. Two classes of process are distinguishable, one spatial and the other temporal. The spatial process takes the form of an almost universal sensory interaction, lateral inhibition (Hartline, 1969). When one stimulates the ring of photoreceptors surrounding an LMC's central field of view, one can observe a response of opposite sign (Fig. 6) that opposes the signal from the centre (Zettler & Järvilehto, 1972; Dubs, 1982). It follows that the net LMC response is the difference between the signal generated in the centre of the receptive field and the average signal falling on the surround. The temporal process makes a larger contribution to synaptic adaptation. Its time course and action are illustrated by the decline in LMC response to a sustained light and by the biphasic response to a brief flash. In the latter, a brief hyperpolarization in response to light is followed by a longer period of depolarization. This depolarization is the temporal equivalent of lateral inhibition. It produces an LMC response which is the difference between the present signal and a weighted mean of earlier inputs. Both the spatial and the temporal processes attempt to restore synaptic transmitter release to the mean level. Consequently, the spatial and temporal processes are



subtracting an estimate of the background signal (Laughlin & Hardie, 1978; Srinivasan *et al.* 1982; Laughlin & Osorio, 1989).

This subtracted value has been derived by the spatial and temporal processes regulating the synapse. These processes are adjusted to execute predictive coding, a procedure first developed for compressing video and audio signals. Spatial and temporal antagonism formulate a statistical prediction of the signal expected at that LMC (Srinivasan *et al.* 1982) and then remove it. The dominant statistical parameter is photon noise. At low light levels the photoreceptor signals are heavily contaminated. To derive an accurate prediction, the spatial and temporal processes are weakened and extended to integrate over wider areas of space and time. At high light levels signals are reliable. Consequently, excellent prediction can be obtained from the nearest neighbours, and the spatial and temporal processes of adaptation contract and strengthen accordingly. In fly lamina, the properties of the temporal process are particularly well tuned to input noise levels so as to execute predictive coding (Srinivasan *et al.* 1982). The strengthening of antagonism with intensity is a general principle, observed in many visual processes, from the responses of retinal ganglion cells to behavioural discrimination. Note that it is generally beneficial to weaken and extend antagonism at low light levels, no matter what coding strategy is employed. One must avoid subtracting noisy signals, because the uncorrelated noise powers add, but the

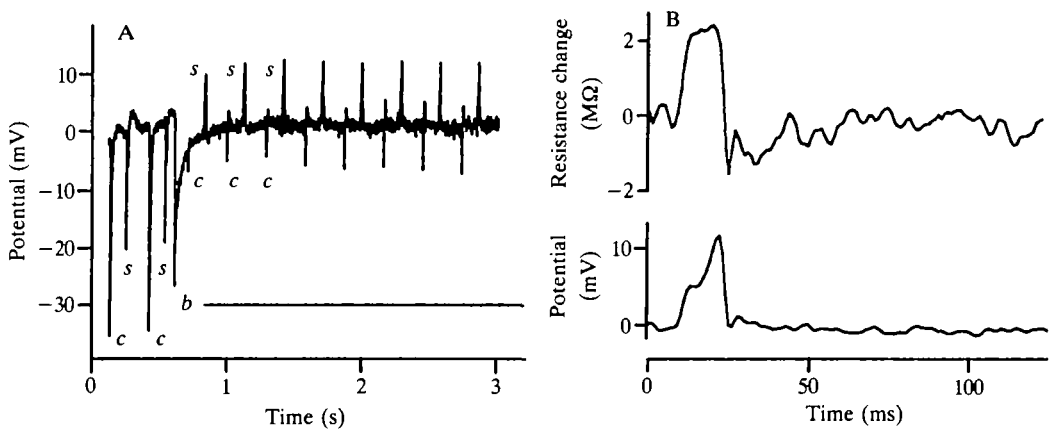


Fig. 6. Lateral inhibition in blowfly LMCs. (A) Light adaptation facilitates lateral inhibition. An LMC is stimulated by two types of test flash, one delivered to the centre of its receptive field (c) and the other to a surrounding ring (s). Initially the cell is totally dark-adapted and both types of test flash hyperpolarize it. At *b* a sustained and saturating background is applied to a large retinal area. Note that adaptation leads to a transient response to the background, releasing the cell from saturation and rapidly restoring sensitivity to the test flashes delivered to the centre of the receptive field. Light adaptation has facilitated lateral antagonism because surround stimulation now produces strong depolarizing responses. (B) The input resistance of an LMC increases during the depolarizing response to the surround, indicating that lateral inhibition acts presynaptically, to reduce the release of photoreceptor neurotransmitter. (Reproduced from Laughlin & Osorio, 1989.)

signal amplitude diminishes. The great advantage of predictive coding is that it removes signal components that are, by definition, redundant. Redundancy reduction improves the efficiency with which sensory signals can be coded, transmitted and processed at many levels of sensory processing (Attneave, 1954; Barlow, 1961, 1986). In the case of LMCs, signal amplitude is reduced without loss of information, to allow the remainder to be amplified with a higher gain. As we have seen, this high gain affords the signal greater immunity to noise.

Synaptic amplification is itself matched to signal statistics (Laughlin, 1981*b*, 1987). The curve relating an LMC's response amplitude to the contrast of the stimulus follows the statistical distribution of contrast in natural scenes. In other words, the gain is proportional to the probability of encountering a particular value of contrast in the retinal image. The slope of the curve (the contrast sensitivity) is maximal in the mid-region, where contrasts are low and common, and flattest at the extremities, where contrast is high and uncommon. By matching the incremental sensitivity to the input probability, the range of LMC response that is devoted to frequently encountered stimuli is expanded and the range used by the infrequent is compressed. This adjustment will tend to ensure that all the cell's levels of response are used equally often, so satisfying one of Shannon's criteria for efficient coding (Shannon & Weaver, 1949). Thus, matched amplification promotes the efficient utilization of the LMC's limited response range, a prerequisite for maximizing the cell's capacity to transmit information centrally. For this reason, matched amplification could be beneficial wherever a limited response range restricts information transfer.

In conclusion, synaptic adaptation enables information to be passed from photoreceptor to interneurone with high efficiency. This efficiency is achieved by minimizing a number of fundamental biophysical constraints. In particular, the signal is amplified to reduce the effects of intrinsic noise, and the synapse adapts to circumvent the constraint of dynamic range. Moreover, by restoring transmitter release to a set level, adaptation is effectively subtracting an estimate of the background signal, as suggested by the restoration of voltage to a near constant level (Laughlin & Hardie, 1978). This estimate is predicted from data entering the eye, so removing redundancy. The remaining information is then amplified according to signal statistics to make best use of the postsynaptic response range. Note that the processes involved in promoting coding efficiency are common in sensory systems, particularly in vision. A review related to principles of sensory processing could not overlook the contributions made to vision research by the analysis of lateral and self-inhibition in the *Limulus* compound eye (Hartline, 1969; Ratliff, 1965). In addition, retinal ganglion cells utilize the non-linear summation of responses in the peripheral retina, adaptation, amplification and lateral antagonism to generate a contrast signal over a wide range of background intensities (Creutzfeld, 1972; Shapley & Enroth-Cugell, 1984). Fly LMCs demonstrate more exactly the means by which these classical interactions promote the efficiency with which single cells code information. Note that redundancy reduction and a full usage of response range may be extremely important factors in

the vertebrate retina, because the optic nerve is a bottleneck for transmission to the brain (Barlow, 1981).

### **Adaptation and the purpose of retinal coding**

What is the purpose of retinal coding and how did it evolve to its present forms? Let us begin by restating the functional benefits of contrast coding by photoreceptors and LMCs. The photoreceptors scale the incoming signal, approximately logarithmically. Lateral and spatial processes act on the second-order neurone to remove the background component from the signal. The residual fluctuations are then amplified for transmission. The result is a signal that depends primarily upon contrast alone and this, in turn, depends upon the reflectance of objects (Laughlin, 1981a). This form of coding simplifies information processing at higher levels. One function of higher-order processing is to determine the properties of objects. The absolute light level is not usually a property of natural objects, but reflectance, and hence contrast, is. Thus, it is advantageous to reject information about the illuminant at an early stage of processing and code the object-related contrast signals. This filtering simplifies subsequent computations by allowing higher-order neurones to work on object parameters, regardless of light levels. A similar argument is presented by Shapley & Enroth-Cugell (1984) in their excellent review of adaptation in the vertebrate retina. They suggest that the invariant coding of the reflectance of objects, over a wide range of illumination, is the primary objective of retinal coding. Such a line of argument suggests that the similarities between retinal processes in insects and vertebrates come about through a convergent evolution, directed towards simplifying higher-order processing (Laughlin, 1981a). As an example of retinal properties tailored for central functions, one can cite the segregation of information on form and motion by different types of retinal ganglion cell with separate projection patterns.

Our experimental analysis of coding mechanisms in the insect retina establishes a second purpose for retinal coding, the minimization of cellular constraints. These constraints are imposed by the retinal receptors and neurones themselves. Thus, contrast coding could have evolved in response to purely retinal factors, without reference to higher advantages, such as object-based coding. Sensory adaptation plays an important role in this line of argument because it improves the basic measures of signal quality, such as signal-to-noise ratio, frequency response and channel capacity. These basic improvements take no account of the meaning that is to be extracted from information. The objective is to use the cells at one's disposal to bundle up as many bits as possible, and transmit them centrally. In the fly compound eye, these basic improvements to coding efficiency are achieved by reducing the effects of fundamental cellular constraints. For photoreceptors, the parallel arrangement of conductance channels in membranes produces self-shunting, and adaptation, acting within this constraint, leads to contrast coding. For photoreceptor synapses, the constraint of noise is reduced by increasing synaptic amplification. Synaptic adaptation is required to enable amplification to

act within a second constraint, a limited postsynaptic response range, and this, in turn, leads to redundancy reduction. Clearly, adaptation acts on transduction and synaptic transmission to maximize accuracy and, in doing so, it also generates the computationally advantageous property of brightness constancy. Thus, desirable transformations can be generated by minimizing biophysical constraints in the retina, without reference to higher-order goals. These cellular constraints are shared by the receptors and neurones of the vertebrate and the fly retina, hence the similarities in coding.

This second interpretation of the function and evolution of retinal coding is not incompatible with the first, and may well complement it. However, this wholly peripheral and cellular line of reasoning has a number of implications. The first is that the computationally desirable transformations of a higher order (contrast coding and brightness constancy) could have evolved by selecting for simpler improvements of a lower order. A second implication is that the adaptation mechanisms that might have evolved to improve basic signal quality also change the nature of processing. Adaptation requires new temporal and spatial interactions and these change the nature of coding. An adaptation process like lateral inhibition sets up connections which can then form the substrate for the development of new functions, such as edge detectors based upon more strongly oriented lateral interactions. The third implication is that adaptation occurs at a number of levels in the retina and lamina, optimizing processing wherever there is a constraint. Thus, adaptation mechanisms are potentially a rich source of changes, driven by constraints on accuracy to act at many sites in sensory systems. This raises the question of the general relevance of adaptation to the evolution of the brain as a whole. Can adaptation bring about useful changes at higher levels or does it only act at the periphery where the processing is simpler and the constraints more obvious?

A higher-order movement-detecting cell in the fly lobula plate, H1, demonstrates that adaptation of the type reviewed here is not necessarily restricted to photoreceptors and their synapses. H1 is a member of a population of unique identified cells in the third optic neuropile of the fly, the lobula plate. Each cell codes a particular direction of movement within its distinctive receptive field (Hausen, 1984). H1 codes stimulus velocity (in the preferred direction) as spike rate. When the retinal image is stationary, H1 has a high sensitivity to motion in its preferred direction. When exposed to continuous motion, H1 adapts in a manner that is remarkably similar to that of a photoreceptor (Maddess & Laughlin, 1985). H1's response to sustained motion declines to a steady level, but this drop in sensitivity releases it from saturation and enables it to code changes in velocity with a higher gain. The reduction in sensitivity is accompanied by a shortening of the response time constant (de Ruyter van Stevenink *et al.* 1986), reminiscent of the adapting quantum bump. Apparently, the common constraint of a limited response range has resulted in similar adaptation effects in photoreceptors and H1. Adaptation changes the nature of the information coded by H1. The cell responds to relative changes in velocity (velocity contrast) better than to absolute

velocity. In addition, adaptation acts locally within H1's receptive field and this property will enhance responses from those areas where the stimulus velocity changes (Maddess & Laughlin, 1985). This simple example demonstrates that adaptation can act more centrally and for purposes similar to those executed in the periphery. In doing so, adaptation generates new types of interaction.

In conclusion, sensory adaptation is a widespread process that, through the subtleties of molecular controls and patterns of cellular development, acts at many sites where information is transmitted or processed. We have seen that adaptation increases cellular information capacity by boosting the speed and accuracy of responses. In fulfilling this basic function, adaptation can have a profound effect upon coding because its actions take account of both the quality and the context of signals. The combination of a simple purpose, diverse sites of action and significant effects provides a powerful catalyst for evolutionary change. Thus sensory adaptation, and the adaptability of neural processes in general, may be a rich source of evolutionary pre-adaptations (Laughlin, 1989). Pre-adaptation helps resolve a familiar evolutionary problem. A complicated organ, such as a sensory system, is only beneficial when it works, but many organs have to reach a certain level of organization to function. An obvious resolution to this problem is for an organ to develop for one purpose and, in so doing, acquire properties that are useful for another. Sensory adaptation may provide both the simplicity of purpose and the profound effects that are required for this to occur.

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