7 Contrast Sensitivity and Light Adaptation in Photoreceptors or in the Retinal Network

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Sensitivity to contrast is one of the most important attributes of the visual system of humans and other animals. This chapter is about some of the reasons for the dependence of visual responses on contrast and about the neural machinery in the retina that makes it possible.

One of the questions that has recurred in this field is this: to what extent does light adaptation depend on processes that take place within single photoreceptors, and to what extent does spatial interaction within the retinal network contribute to visual adaptation? In this chapter, in honor of Christina Enroth-Cugell's Helmerich Award, we consider old and new evidence about receptoral adaptation, in particular the evidence about light adaptation in primate cone photoreceptors. This has recently become an area of intense interest because of apparently conflicting evidence about this fundamental issue. Our goal in this paper is not to resolve the conflicts definitively—that will require sharper experiments—but to present the points of disagreement and to suggest possible means of reaching a definitive answer.

Before delving into the receptor adaptation issue, we review classic evidence about the function of adaptation, recapitulating some of the ideas in the massive review that Christina Enroth-Cugell and one of us composed (Shapley and Enroth-Cugell, 1984). Visual adaptation has been one of Christina Enroth-Cugell's lasting research interests, and she and her colleagues have made many contributions to our understanding of retinal adaptation in the retina of the cat. The question regarding the role of photoreceptors in adaptation remains to vex us all.

Visual adaptation is inextricably linked to the perception of brightness. Although it seems that perception of the brightness of objects is effortless, visual scientists know that complex neuronal computations are required to perform the task. The perception of brightness is not simply a matter of counting photons. The primary determinant of brightness perception is local contrast, the local difference between luminances on either side of a boundary normalized by the (local) average luminance (Heinemann 1955, 1972; Shapley and Enroth-Cugell 1984).

CONTRAST, CONTRAST SENSITIVITY, AND CONTRAST GAIN

Contrast is a physical property of the visual stimulus. When studying the visibility of aperiodic objects such as uniform disks or bars or rectangles on a background, an investigator would naturally define contrast as

$$C = (L_0 - L_B)/(L_B) \tag{7.1a}$$

where L_0 is the luminance of the object and L_B the luminance of the background. $L_0 - L_B$ is usually called ΔL, and so equation 7.1a is usually written as

$$C = \Delta L/L_B \tag{7.1b}$$

At high mean luminance, and for test stimuli of large area and long duration, psychophysical sensitivity follows Weber's Law, as shown empirically below. Then we can write

$$\Delta L_T/L_B = k \tag{7.2a}$$

$$C_T = k \tag{7.2b}$$

where k is a constant, the threshold contrast. The threshold contrast C_T is also referred to in the psychophysical literature as the *Weber fraction*. Equation 7.2 says, in words, that, when Weber's law is obeyed, the visual system's criterion for detection is that the stimulus contrast must equal a fixed value, k, the threshold contrast.

There is a second definition of contrast that is used for periodic spatial patterns like sine gratings.

$$C_R = (L_{max} - L_{min})/(L_{max} + L_{min}) \tag{7.3}$$

The two different definitions, equations (7.2) and (7.3) are related because they refer to a single physical quantity: the relative variation of a modulated component referred to (or normalized by) a steady-state component.

Contrast sensitivity is the reciprocal of the psychophysical threshold contrast. Contrast gain (Shapley and Enroth-Cugell 1984) is neural response divided by stimulus contrast in the limit as contrast approaches zero, and will be expressed in units of mV/unit contrast or (impulses/sec)/unit contrast. Contrast gain and contrast sensitivity depend directly on the process of light adaptation, as shown below.

BRIGHTNESS, CONTRAST SENSITIVITY, AND ADAPTATION

Animals evolved in a world of reflecting surfaces. What characterizes a reflecting surface visually is its reflectance. The reflectance is determined by the physical properties of the surface of the object. Reflectance is therefore invariant with respect to illumination. The luminance of an object is proportional to the product of the object's reflectance and illumination. Over a wide range of illumination, the brightness of a reflecting object is constant even though its luminance may vary widely. Land and McCann (1971) explained

the purpose of brightness constancy by asserting that the visual system was designed to calculate reflectance. We know now that this is not correct, but it is on the right track.

The early stages of vision compute contrast, not reflectance. One can view contrast as *relative reflectance*, the comparison of the reflectance of an object with its background. The response of retinal, geniculate, and some primary cortical neurons is dependent on contrast. Constancy of neuronal response with contrast may be achieved for stimuli that activate only the center mechanism of the receptive field (Enroth-Cugell and Robson 1966; Shapley and Enroth-Cugell 1984). This means that the responsiveness of the visual system to contrast is not simply a result of center-surround interaction or of lateral inhibition (as in the standard textbook accounts, e.g., Cornsweet 1970). Rather, contrast dependence is primarily a result of the automatic gain control that produces light adaptation (Whittle and Challands 1969; Shapley and Enroth-Cugell 1984). The automatic gain control that regulates the contrast sensitivity of a receptive field center is localized to the center, and thus contrast is computed only locally (Shapley and Enroth-Cugell, 1984).

CONTRAST VS. REFLECTANCE: SIMULTANEOUS CONTRAST

An example of the power of contrast to determine perception is the elaboration of the classic picture of equally luminant circles on a nonuniform background, as in figure 7.1. The figure shows sixteen equally luminant circles placed on six rectangular strips that vary in luminance. This could be interpreted as a scene with sixteen equally reflective disks placed on a cloth with six different rectangular regions of reflectance. If the visual system is computing local contrast, then the disks should all appear different in brightness because their contrasts are not all the same. If the visual system were computing reflectance as Land and McCann (1971) suggested, then all sixteen disks should look the same shade of grey. It is obvious to every observer that they look different and so, at least qualitatively, the quantity computed by the visual system must be closer to contrast than to reflectance.

Land and McCann (1971) anticipated this refutation of their theory (the 1971 Retinex) in a footnote to their 1971 paper in which they asserted that pictures such as those in figure 7.1 were unnatural because the objects were completely surrounded by their backgrounds. This is a weak argument, since in nature isolated objects on backgrounds are the rule rather than the exception. But, accepting the Land and McCann argument as valid for the moment, we can put it to the test by constructing a "Mondrian"-like pattern (which Land and McCann considered more natural) and then looking again at equally reflective objects on nonuniform backgrounds. This is shown in figure 7.2, which I have reproduced from an earlier paper (Shapley 1986). It can be seen that the circle and square, though equally luminant, are not equally bright. An explanation is that neurons are computing local contrast and the visual system is basing its estimate of brightness on contrast-dependent neural responses. Reid and Shapley (1988) measured the magnitude of such brightness induction

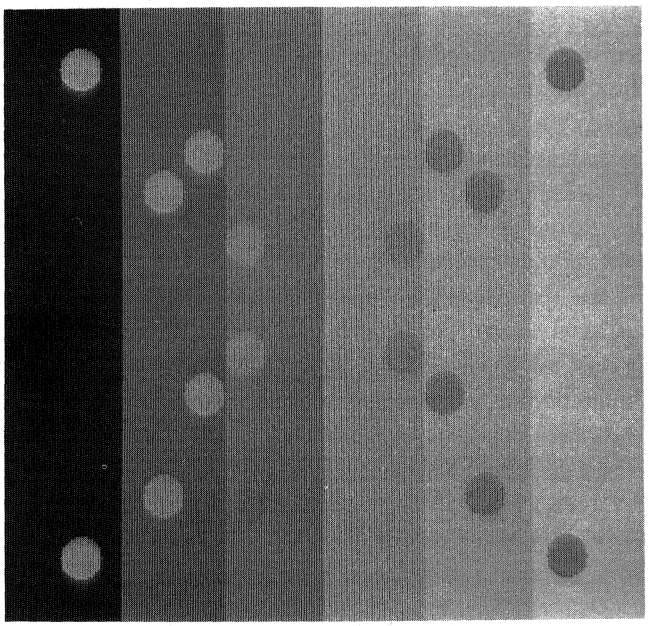

Figure 7.1 Sixteen equiluminant circles on a luminance staircase. This pattern was created on a CRT display with a computer-controlled instrument. Each rectangular area in the staircase is of a fixed uniform luminance. The luminance of the circles—all of which have the same luminance—is the same as the mean luminance of the staircase.

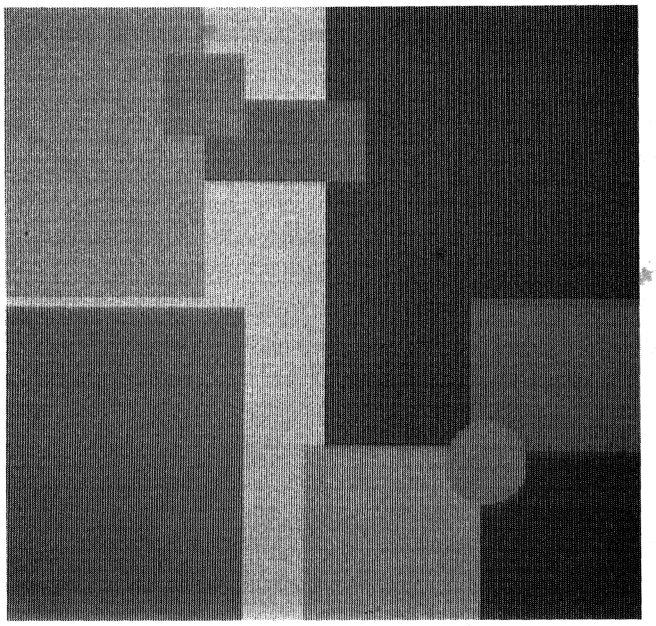

Figure 7.2 "Mondrian"-like pattern with an equally luminant square and circle. The local areas of contrast around the square and circle are different and opposite in sign, so the square appears dark while the circle appears light.

in Mondrian-like patterns like that in figure 7.2, and it was virtually identical to that seen in more conventional displays, such as that in figure 7.1.

Psychophysical Evidence

Constant contrast sensitivity is the ideal toward which retinal light adaptation must strive if it is to achieve its main goal: perceptual invariance of reflecting surfaces with changes in background illumination. To the extent that psychophysics approaches Weber's law, this major goal has been met. A graph of threshold contrast versus background retinal illumination shows a clear break between rod and cone function (for example, see Blackwell 1946). The minimal contrast threshold for the rods, at the high end of the scotopic range of backgrounds, is about 0.08, which approximately corresponds to a contrast sensitivity of 12. There is a clear jump in performance when the cones come in, with contrast thresholds declining asymptotically to 0.005 in the high photopic range.

In the regime of Weber's law, contrast sensitivity is constant as in equation (7.2); a graph of contrast sensitivity vs. mean illumination would be a flat line. In fact, human contrast sensitivity increases as the square root of mean luminance over most of the scotopic range, though it is beginning to level off toward behavior described by Weber's law for the largest targets at the high end of the scotopic range (Blackwell 1946).

THE REGULATION OF PHOTOPIC CONTRAST SENSITIVITY

The cone system (photopic system) is like the rod system in yielding results in line with Weber's law under some circumstances and in line with the square root law under others. In human vision the cones take over at threshold from the rods above 0.1 to 1 troland (td) in background retinal illumination (Wyzecki and Stiles 1982). The increment threshold curves in the literature tend to show a cone plateau from 0.1 up to about 10 td. Above 10 td one usually observes results in line with Weber's law for a bipartite field or a moderate-sized test spot (diameter $> 0.5°$). For most targets, and in particular for moderate-sized spots with sharp edges, on a large background, Weber's law holds from 10 td to 10^5 td, i.e., throughout the photopic range of backgrounds (Whittle and Challands 1969). The mechanisms that cause Weber's law to apply in human photopic vision are therefore also achieving the goal of brightness constancy, i.e., illumination-invariant appearance by making responses proportional to contrast.

The concept of light adaptation in photoreceptors comes from psychophysical investigations of color vision. For example, the success of the two-color method of Stiles for isolating chromatic mechanisms provides some support for the independent adaptation of different photoreceptors (Wyszecki and Stiles 1982). More recently, the extensive investigations of chromatic detection by Stromeyer and colleagues have been framed in terms of the Weber contrast in each cone type (for example, see Stromeyer et al. 1985).

The coherence of the account of chromatic detection in terms of cone contrast supports the concept of cone adaptation in the human visual retina. For instance, Stromeyer and colleagues found that chromatic detection thresholds fell on a straight line in Weberian cone contrast coordinates, indicating that signals proportional to L cone contrast are simply subtracted from signals proportional to M cone contrast in the detection of chromatic targets.

However, recent experiments by Krauskopf and Gegenfurtner (1992) on color discrimination seem to suggest that cone adaptation is not required to account for their results at retinal illuminations of 500 td or below. They found that the chromatic modulation threshold, on different chromatic backgrounds that were fixed in luminance, did not depend upon the color of the background, but only on background luminance. The predictions of independent cone adaptation were not confirmed. These experimental findings thus raise again the question of whether there is light adaptation in human cones. In our view the crucial findings in this area concern the link between dynamics and gain control in light adaptation, which we will present now.

THE DYNAMICS OF PSYCHOPHYSICAL LIGHT ADAPTATION

A clue to the mechanisms of adaptation, and a crucial adumbration of later physiological work on photoreceptor light adaptation, was provided by the psychophysical study of the dynamics of light adaptation. The temporal frequency of a stimulus influences the dependence of sensitivity on mean level. This has been shown in psychophysical experiments, mainly by Kelly (1972). At low spatial frequency and low to intermediate temporal frequency, he obtained results described by Weber's law. At high spatial frequency and low to intermediate temporal frequencies he observed results described by the square root law. At very high temporal frequencies he discovered that sensitivity was more or less independent of mean level. This is what Kelly called the "linear" region of temporal frequencies, because the visual system appears to be behaving in a linear manner in that the sensitivity for a modulated stimulus is not affected by the presence of different steady levels.

An explanation for Kelly's results has emerged from recent work on the dynamics of light adaptation in photoreceptors and retinal ganglion cells, though there are some contradictory results that require consideration. We will refer back to Kelly's findings when considering the dynamics of retinal adaptation. In the context of our previous discussion of contrast and brightness constancy, it is interesting to note that brightness induction and the stable estimation of brightness fail at moderate temporal frequencies (DeValois et al. 1986). Thus, stable brightness perception seems to work only in the low temporal frequency region within which Weber's law holds.

CONTRAST GAIN IN PRIMATE RETINAL GANGLION CELLS

There are several types of retinal ganglion cells in the retinas of macaque monkeys, close evolutionary relatives of man. Two different types of ganglion

cells project to the lateral geniculate nucleus (LGN) of the thalamus. These types, called P cells and M cells (Shapley and Perry 1986), resemble human ganglion cells in morphology (Rodieck 1988), and therefore it is reasonable to suppose that they might also resemble human ganglion cells physiologically. Quite a lot is now known about the contrast gain of these neurons. The P cells have low contrast gain (Kaplan and Shapley 1986) like their parvocellular targets (Shapley et al. 1981; Kaplan and Shapley 1982; Hicks et al. 1983; Derrington and Lennie 1984) within the macaque's LGN. P cells are color-opponent neurons and probably constitute the front end for chromatic perception. M cells project to the magnocellular layers of the LGN. Like magnocellular neurons, M cells have high contrast gain (Shapley et al. 1981; Kaplan and Shapley 1982; Hicks et al. 1983; Derrington and Lennie 1984; Kaplan and Shapley 1986). M cells have a broad-band spectral sensitivity and may be the neural basis for "luminance" perception.

The dependence of contrast gain on mean level is always informative, so we have studied this function in macaque ganglion cells (Purpura et al. 1988). Some of our results are shown in figure 7.3 as contrast gain vs. mean illumination. There it can be seen that M cell contrast gain is higher than P cell contrast gain at all light levels. Furthermore, many P cells have an unmeasurably small contrast gain when the mean illumination is lowered into the scotopic range where rods determine neural responses. This suggests that scotopic pattern vision depends on the responses of M cells that are relayed

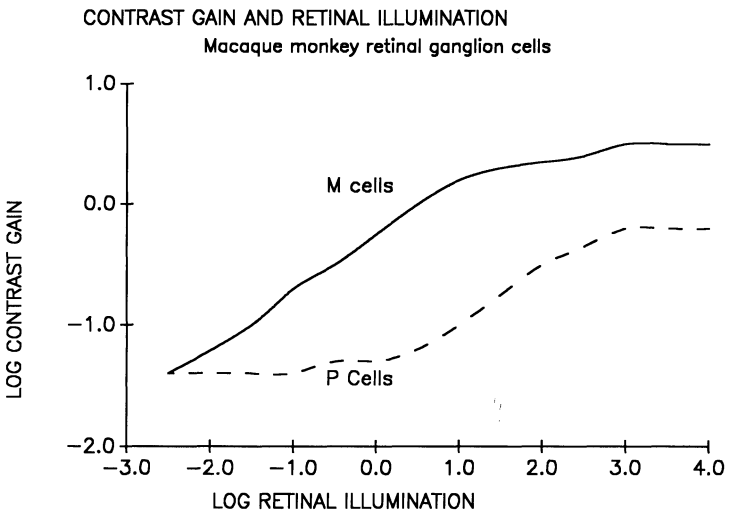

Figure 7.3 Contrast gain of macaque monkey retinal ganglion cells. These are averages of the contrast gains of the data presented by Purpura et al. (1990). The stimuli were drifting sine gratings at around 3 c/deg spatial frequency and 4 Hz temporal frequency. The stimuli were achromatic patterns on a "white" screen. Contrast gain is the slope of the response vs. contrast function and has units of (impulses/sec)/percent contrast. Mean retinal illumination is in macaque trolands (td). One macaque troland is equivalent to a retinal illumination of 200 quanta/cone sec incident on the retina, and about 50 quanta/cone sec absorbed by the cone and effective in transduction (estimated).

through the LGN to the visual cortex. Finally one can see that the contrast gain of macaque ganglion cells does not reach the flat line of Weber's law until the cells are exposed to medium to high photopic levels of illumination, as in human observers. It is interesting that in the cat, a nocturnal animal, many retinal ganglion cells reach the flat, Weber-law asymptote under scotopic conditions (Shapley and Enroth-Cugell 1984; Shapley 1991).

There is a close correspondence between the contrast gain functions of retinal ganglion cells and the contrast sensitivity of human observers. This suggests that the basic mechanisms of contrast sensitivity are located in the retinal network. These basic mechanisms include the local gain controls of light adaptation, spatial and temporal filtering by the photoreceptors and interneurons that provide input to the ganglion cells, and amplification of receptor signals.

The Dynamics of Retinal Adaptation

The site of light adaptation in the retina and the mechanisms of retinal adaptation have been studied extensively. It is beyond the scope of this paper to discuss the subject fully. In an earlier article (Shapley and Enroth-Cugell 1984), Christina Enroth-Cugell and one of us reviewed the already large body of literature on the subject and concluded that there were multiple, hierarchically organized mechanisms for light adaptation. The multiplicity of retinal mechanisms is a consequence, we think, of the multiple neural channels that are set up by the functional connections of the retinal network. For instance, in the macaque monkey retina there are P and M ganglion cells and they have different numbers of functional connections to photoreceptors (Rodieck 1988). More cones make functional connections with M cells than with P cells, and the cone connections to P cells may be quite specific. Therefore, gain controls for preventing response saturation and for making responses invariant with levels of illumination may have to exist in single cone photoreceptors and also in retinal interneurons within which cone signals are pooled.

The characteristic "signature" of cone photoreceptor adaptation is the differential effect of mean illumination on cone dynamics, as illustrated in figure 7.4. This is redrawn from figure 2 in Sneyd and Tranchina (1989) and illustrates the temporal frequency response of a cone photoreceptor from the retina of a turtle. These data on cones resemble quantitatively the earlier results obtained by Tranchina et al. (1984) on turtle horizontal cells and by Naka et al. (1987) in their study of turtle cones, and they are qualitatively very much like the psychophysical results reported for human observers by Kelly (1972), cited above. Weber's law is observed for low temporal frequencies only. At intermediate temporal frequencies, the dependence of gain on mean illumination has a shallower slope on log-log coordinates, and so the contrast gain vs. mean illumination will also have a slope between 0 and 1. At high temporal frequency there is no dependence of gain on mean illumination, so contrast gain at high frequencies grows proportionally with mean light level in these photoreceptors.

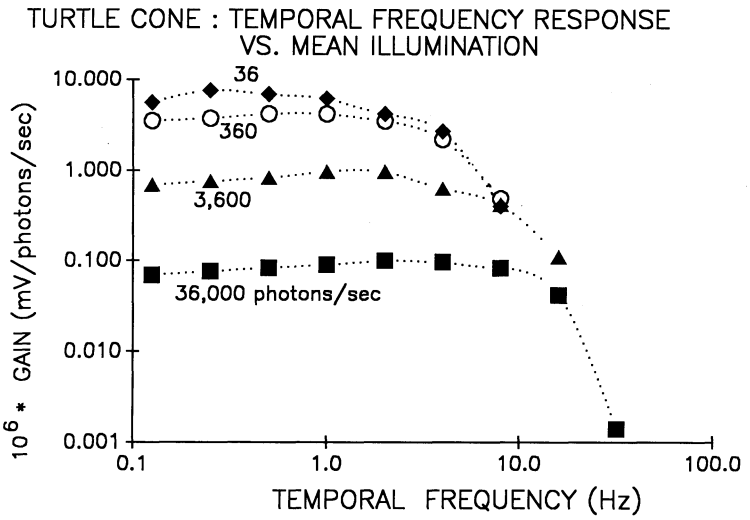

Figure 7.4 Temporal frequency responses of a turtle cone at different background illuminations, redrawn from Sneyd and Tranchina (1989). Retinal illumination of the background for each data set is written next to the curves. These are not theoretical curves but merely splines through the data.

It is surprising and significant that monkey ganglion cells of the P variety reveal the same sort of dynamic dependence on mean illumination as do turtle cones. This seems to us to indicate that photoreceptor adaptation is the predominant influence on these neurons. Figure 7.5 shows some of the data on this point, redrawn from Purpura et al. (1990). It is also significant that, at higher mean illumination levels, a similar link between gain and dynamics is seen in M ganglion cells, as demonstrated in figure 7.6. The background illuminations for the monkey ganglion cell data are given in terms of quanta/cone sec. This is done to facilitate comparison with the turtle cone adaptation data in figure 7.4. It is remarkable that the dynamic changes in the temporal frequency responses and the corresponding vertical shifts, indicative of corresponding gain changes, are very similar between these two different data sets.

The peculiar and highly structured dynamic dependence of temporal frequency response on mean illumination constrains theoretical models of photoreceptor function. The earliest mathematical models of photoreceptor adaptation were designed to explain the link between gain and dynamics in a transducer with an automatic gain control (e.g., Fuortes and Hodgkin 1964). However, there were no satisfactory phenomenological models of photoreceptor function prior to the theory advanced by Tranchina et al. (1984), in part because the dynamic dependence of frequency responses on mean illumination had not previously been measured. In the admittedly black-box theory advanced in Tranchina et al. (1984), the cone's temporal frequency response is written as

$$\mathrm{R(f)} = \frac{A(f)}{1 + I_0 B(f)} \tag{7.4}$$

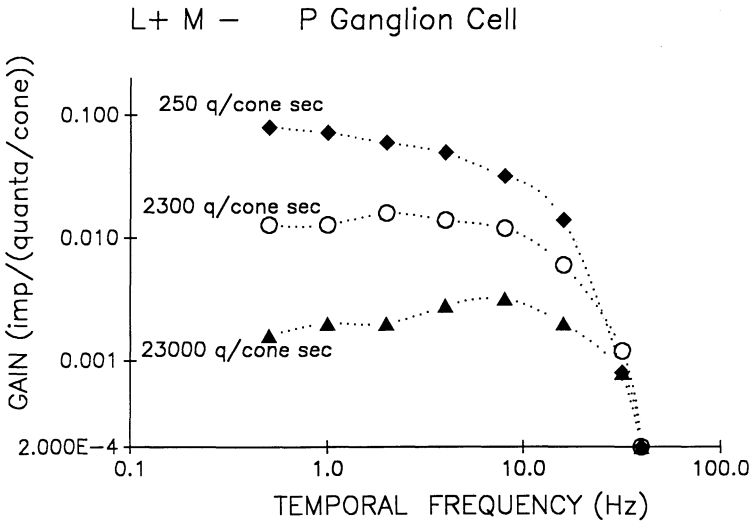

Figure 7.5 Temporal frequency responses at different mean illuminations for a P retinal ganglion cell from macaque monkey, redrawn from Purpura et al. (1990). Achromatic sine gratings were used as stimuli. Spatial frequency was 3 c/deg. Gain is given in impulses/(quanta/cone). Mean retinal illumination in quanta/cone sec is given alongside the data sets.

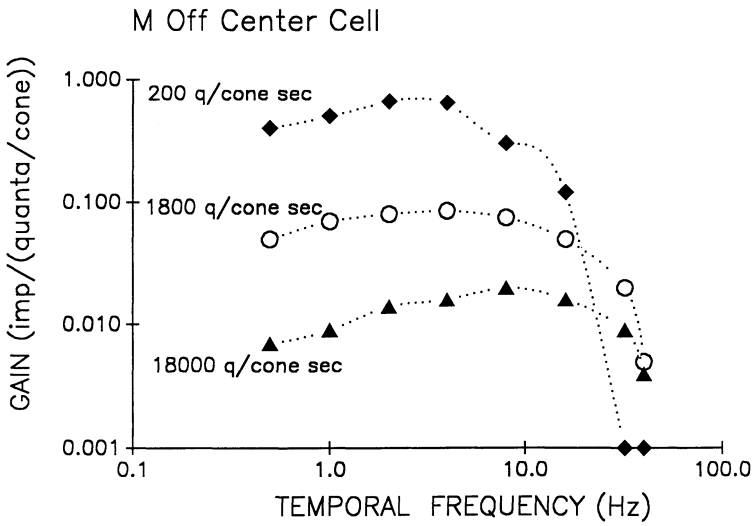

Figure 7.6 Temporal frequency responses at different mean illuminations for an M retinal ganglion cell from macaque monkey, redrawn from Purpura et al. (1990). Achromatic sine gratings were used as stimuli. Spatial frequency was 3 c/deg. Gain was derived from the response vs. contrast function. Gain is given in impulses/(quanta/cone). Mean retinal illumination in quanta/cone sec is given alongside the data set.

where R is the frequency response of the cone, A and B are the frequency responses of (low-pass) stages of neural transduction and temporal integration, and I_0 is the mean illumination level. One could criticize this formula as being no more than a formal description of the data, because there is no valid mechanistic theory to explain the functional form. Tranchina and Peskin (1989) elaborated this model and made it plausible in terms of possible mechanisms. However, a conceptual advance has recently been made by Sneyd and Tranchina (1989) in their article on a kinetic theory of cone photoreceptor transduction, which is based on the known biochemistry of photoreceptors. These authors show that the characteristic frequency response data of figure 7.4 can be accounted for very well using a model that includes calcium-dependent feedback in the biochemical cascade from activated rhodopsin to channel closing in the photoreceptor. Therefore, the ganglion cell data in figures 7.5 and 7.6 also presumably can be explained with similar biochemical kinetic mechanisms at work in the cones of the monkey retina. There is ample physiological evidence of the role of calcium in photoreceptor light adaptation (Lamb and Pugh 1990). Tranchina et al. (1991) present the most elaborate version of the model. The heart of the adaptation mechanism is the (highly nonlinear) regulation by calcium of the production of cyclic GMP, the internal transmitter in photoreceptors, by an enzyme called guanylate cyclase.

It would seem that the physiological evidence is all on the side of cone light adaptation, and the psychophysical results of Krauskopf and Gegenfurtner (1992) must be accounted for in terms of some postreceptoral mechanism. However, the recently reported results of Schnapf et al. (1990) on light adaptation in primate cones suggest that the picture is darker. Their results on the photocurrent of isolated monkey cones recorded with suction electrodes indicated that gain was not reduced until the retinal illumination was about 3×10^5 quanta/cone sec. This is about 300 times more illumination than one expects based on the monkey ganglion cell recordings, and much higher than is expected from human psychophysics. Previous work on photoreceptor mass responses in the monkey retina is equivocal. Valeton and Van Norren (1983) found light adaptation in primate foveal ERG to begin at a mean illumination between the high level reported by Schnapf et al. and the lower level implied by the data of Purpura et al.

One striking difference between the responses of monkey ganglion cells and cone responses concerns the dynamics of dark-adapted cones. Human psychophysics, monkey ganglion cells, and turtle cones were all low-pass in temporal frequency tuning when dark-adapted. However, Schnapf et al. (1990) reported the remarkable result that the temporal impulse response of dark-adapted cones was biphasic, implying by linearity that the temporal frequency response of these cones would be band-pass in temporal frequency tuning. It is possible that a low-pass filter between cones and ganglion cells could reshape the cones' temporal frequency response to resemble that of the ganglion cells. However, the existence of such a filter would imply that the retina would be attenuating most of the signal strength of the cones under dark-adapted conditions. This seems implausible on functional grounds. Further-

more, according to this hypothesis the dynamic changes with light adaptation in ganglion cell responses observed by Purpura et al. would have to be produced by postreceptoral circuits.

The state of the field at this point is confusing and contradictory on a fundamental functional point—whether cone photoreceptors of the primate retina adapt to light at the beginning or only at the high end of the photopic range of vision. Future experiments on the basis of visual perception must address this fundamental issue. One could imagine further experiments on light adaptation in retinal ganglion cells and in retinal interneurons as techniques improve for recording from primate retinas in vitro. Better studies of the role of second-site adaptation within the retina will also clarify the nature of the processes that control gain downstream from the photoreceptors. It seems that cone adaptation will have to be investigated again using extracellular and intracellular recording techniques in order to resolve the contradictions in the present data. This further research is needed because the perception of brightness and color depends upon the regulation of contrast sensitivity within the retina. It is surprising and humbling that such a basic issue remains unsettled. But it is also encouraging that there is important work yet to be done!

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