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Visual Adaptation*

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Abstract. 1) The eye may be regarded as an automatic camera that keeps the average sensitivity near the middle of the working range.

2) Nerve signals are contrast-coded, and hence are not changed by changes in general illumination.

3) Rod thresholds can be raised three-fold by a background from which only 1% of the rods have caught one quantum.

4) Adaptation is of two kinds a) to backgrounds (the Weber-Fechner relation) and b) to bleachings which is entirely different.

5) After bleaching the threshold is raised as though a bright background were present. The positive after-image following bleaching has quantitatively the properties of that bright background.

6) The visual incapacity after bleaching seems a pointless visual disaster.

Key words: Backgrounds — Bleachings — Threshold — Organisation — Automatic camera.

Adaptation is one of the cardinal properties of living organs and tissues. It is the way that living things respond to impressed conditions so that life and activity is maintained.

Visual adaptation is in many ways similar to the action of an automatic photographic camera that adjusts the light falling on the film to give the correct exposure i.e. so that the average light intensity is brought near to the middle of the response-range of the film.

The vertebrate eye paints upon the retina with bleached photopigments a picture of the luminous world outside. The most familiar aspect of visual adaptation is that which secures that this picture maintains its contrast over a great range of illumination.

I. Adaptation to Backgrounds

This has long been studied as the Weber-Fechner relation. When a flash ΔI is superimposed upon a steady background I, the threshold for its detection is found to be

$$\Delta I = KI \quad \text{(Weber's Law)} \qquad (1)$$

approximately, over a great range of I. If ΔI represents not threshold, but many other simple criteria of detection, Weber's Law still holds. So it appears that the nerve signals

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from the receptors to the brain are all scaled down by a fixed fraction which is proportional to I.

This means that the retinal picture is encoded in terms of *contrast* i.e. the ratio of the illumination of each point to the average illumination of the picture. Now contrast is not changed by changing the intensity of general illumination, consequently the variation in sunlight by the interposition of cloud etc. makes little difference to the encoded signals by which the outside world is perceived.

Background Adaptation therefore is the scaling of nerve signals so that in most conditions the average signal is of fixed size. This has two advantages. (a) The encoded information about the world outside does not depend on illumination. (b) The signals keep their discrimination over an enormous range of external luminance.

For rods and for cones this adaptation mechanism must operate somewhat as follows. A steady background stimulates the exposed photoreceptors and these scale down the signals arising from the same kind of receptor in proportion to the background luminance. We may ask for human rod vision "How many quanta must be caught per rod to raise the threshold three times?" This is easily answered by experiment.

Allow the background to shine for 2 s and during the last part of this period apply a superimposed flash. Adjust the background so that the threshold for seeing the flash is 3 times the threshold with zero background. Now measure the luminance of this critical background and the diameter of the subject's pupil. Then, making the reasonable estimate that 10% of the quanta entering the pupil are absorbed by rhodopsin in the rods, we find how many quanta were caught per rod during the whole 2 s when that background shone. It turns out to be 1 quantum per 100 rods! Thus 99% of the rods did not 'see' that there was a background there, for they did not catch a single quantum from it. But these are the rods whose threshold was raised three-fold. They must have been 'told' that the background was there by the 1% who saw it. How did this information spread from the 1 to the 99?

This is the fundamental problem of adaptation in the vertebrate eye. It might happen by lateral feed back (e.g. via the horizontal cells) though feed forward seems more straight-forward. In that case the answer to the question "What is the effect of background adaptation upon the receptor cell?" is "Nothing. It affects not the cell but the transmission of its nerve message."

We may now return to the definition of Adaptation. The automatic camera responds to a sudden increase in light, as does the eye, by a change that may be called adaptation since it secures that the camera continues to operate in its efficient range. On the other hand a sudden hammer-blow upon the lens that shatters it is not "adaptation to percussion" since fragmentation of a lens does not improve it.

So in considering the changes called "light adaptation" produced in the tissues of the eye, we must consider whether the eye can be shown to function more efficiently as a result of these changes. Might they be simply non-adaptive causal consequences like the shattering of the camera lens?

II. Adaptation after Bleaching

There is an entirely different kind of retinal adaptation which certainly involves the receptors themselves. This follows a strong light exposure that has bleached away a fraction of the visual pigment. In the subsequent period in the dark the pigment is regenerated, and at all stages of regeneration the threshold ΔI is given by

$$\log\left(\frac{\Delta I}{\Delta I_0}\right) = aB \,, \tag{2}$$

where ΔI_0 is the fully dark adapted threshold, B is the fraction of pigment in the bleached state at the time, and a is a constant that has the value 12 for human rods.

The rod threshold consequently is raised a million times by bleaching away half the rhodopsin; it recovers to full sensitivity as regeneration proceeds. This, then, may properly be called 'Dark Adaptation'.

The term 'light adaptation' commonly used for the effect of very strong light exposure is improper. The change resulting does not improve vision: it goes far to abolish it.

Now, visual thresholds depend upon the parameters of the test stimulus (e.g. the aria of the test flash), thus equation (2) will depend upon these parameters. Crawford (1947) removed this complication by showing that the threshold in background adaptation, Equation (1), depends on them in exactly the same way. Thus at each stage, bleaching raises the threshold (whatever the test parameters) in just the same way as does a particular background called the "equivalent background" (with the same test parameters). Consequently bleaching acts as though it generates a corresponding luminous background.

But it is well known that bleaching does generate a luminous after-image — a kind of persistance of the sensation of the bleaching light. This is not simply a *memory* in the brain, for if the eye is blinded by pressing upon it throughout the whole bleaching period so that the bleaching light was in fact never seen, the after-image of it will still appear when, later, the pressure is removed.

So long as some visual pigment remains in the bleached state, its photoreceptors generate a signal similar to that generated by light. Is this after-image Crawford's equivalent background?

Barlow and Sparrock (1964) measured the brightness of the after-image by matching it with a stabilized image of real light. Their results, in conjunction with our objective measurements by retinal densitometry of pigment bleaching in man, lead to the following conclusions.

(a) The log matched luminance of the after-image is proportional to the fraction of visual pigment in the bleached state, and hence fades exponentially with time since pigment regeneration is exponential.

(b) At all stages of recovery, when the after-image is matched in brightness by a stabilized patch of real light, the threshold for a flash falling on each of these matched areas is the same. Now, the flash falling upon the background of real light is the familiar Weber-Fechner situation. When the test falls upon the after-image it is the familiar dark adaptation threshold. This gives quantitative support to the statement "Bleaching" raises the threshold because it generates a luminous after-image which acts like a luminous background in the Weber-Fechner situation.

What is the photoreceptor mechanism that generates an after-image which continues so long as some photopigment remains in the bleached state? Why is its brightness linear with the *logarithm* of the fraction bleached? And above all, what is the purpose or necessity of this persistent and paralysing phenomenon? To me it seems simply a visual disaster!

References

Barlow, H. B., Sparrock, J. M. B.: The role of after-images in dark adaptation. Science **144**, 1309–1314 (1964)

Crawford, B. H.: Visual adaptation in relation to brief conditioning stimuli. Proc. Roy. Soc. B **134**, 283–302 (1947)

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