ducible, or that large absolute differences are not required or necessarily desirable in the explant test. The cotton explant test we selected has been in use for several years (*1*), and the details were published in the proceedings of the 4th International Conference on Plant Growth Regulation (*2*).

A cursory survey of the literature clearly indicates that the specificity of explant tests for abscission activity varies greatly. It is correlated with size of explant, method and site of application of test substances, and other factors often peculiar to individual laboratories. With the techniques we used, in either beans or cotton, only a very few substances were found capable of accelerating abscission when applied to the petiole segment of the explant. Other compounds, including carbohydrates, various types of organic acids, a great many inorganic and organic substances, and toxic materials in general, delay abscission or are without effect. These results, collected over a period of 12 years, led to the conclusion that evidence for the acceleration of abscission in many instances is the result of secondary interactions rather than of a direct promotion. The cotton explant test was selected as the bioassay in part because of its specificity with respect to abscission-accelerating substances.

Evidence for the presence of an abscission accelerator in cotton fruit and for its probable role in abscission was presented at the 9th International Botanical Congress (*3*) and at various cotton defoliation and physiology conferences, with key references given in the bibliography of the report in question. To summarize these findings, the accelerator can be obtained by diffusion or extraction and can be identified either by its abscission-accelerating activity or by its inhibition of an indoleacetic acid–induced growth response. Peak production is correlated with the onset of fruit drop in cotton. Varieties with a higher percentage of fruit drop have been found to contain greater quantities of the accelerator than those with characteristically lower fruit drop. The presence of the accelerator in diffusates is indicative of its ability to move from the fruit (site of origin) to the abscission zone (site of action). Finally, the active factor is found to be concentrated in the fruit walls (the tissue which later makes up the bulk of the dried burs). Burs were selected as the material for extraction because of the need for a ready source of plant material and because preliminary tests demonstrated a similarity in the abscission and growth-inhibition responses in burs.

Thus, we agree with Addicott that ample correlative evidence exists to warrant the suggestion that this or similar substances play an active part in the abscission process. That abscisin is identical with the substance active in young fruit has not, of course, been established.

In the final analysis, the important fact is that abscisin is the first highly active compound isolated from a natural source which accelerates abscission.

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Responses of Retinal Ganglion Cells to Exponentially Increasing Light Stimuli

Abstract. Action potentials of ganglion cells were recorded extracellularly from opened cat eyes. It was found that inhibition, as judged by discharge frequency, may depend upon rate of change of light intensity. Apparently the balance between excitatory and inhibitory inputs at the ganglion cell level depends upon rate of change of illumination. Visual purple bleaching or sensory adaptation taking place during the stimulation does not explain the results.

A wealth of data concerning the discharge pattern of the vertebrate retinal ganglion cells has been obtained by use of square-wave stimuli of different intensities, durations, colors, and retinal distributions. In the present work stimuli of exponentially increasing intensity were used. We felt that a study of the discharge pattern in response to stimuli of known intensity variation with time might add to our knowledge about the transmission properties of the retinal network. One well-known characteristic of ganglion cell responses to a square wave of light is the decrease in rate of discharge that sometimes occurs during the stimulation. This inhibition by light may be noted as a complete cessation of firing as long as the stimulus lasts, or it may be observed as a temporary decrease in discharge frequency below the rate that prevailed before the stimulus was applied. The experiments reported here show that in some instances the degree of inhibition, as judged by discharge frequency of the ganglion cell, is determined not only by the level of intensity as such, but is also strongly dependent upon rate of change from one level of illumination to another.

Cats decerebrated under ether narcosis were used. Action potentials were recorded extracellularly from the opened eye with glass-insulated platinum electrodes (*1*). A lamp with a tungsten ribbon filament provided diffuse, even illumination of the eye. The light intensities were measured at the surface of the eye and, therefore, serve only as a rough estimate of the retinal illumination. In each experiment the eye was first adapted to a certain steady illumination (adapting light). The light intensity was then increased exponentially to a new steady level by rotating a neutral density filter in the beam ("ramp" stimuli). Square waves were also employed. They started from the same adapting level and reached the same maximum intensity as the ramp stimuli. The total rise time of the square waves varied from 50 to 75 msec.

Figure 1 (top) shows the response to an exponential "ramp" where the total rise time is slightly more than 2 seconds. The discharge frequency of the cell decreases well below the prestimulus level during the fastest portion of the ramp, only to increase again shortly after the maximum intensity has been reached. The inhibition that occurs when a step function is applied is much less pronounced (Fig. 1, bottom).

Figure 2 illustrates the same experiment in a more quantitative manner. On three records (the two shown in Fig. 1 and a third similar one) the number of spikes within each successive 200- or 100-msec period were counted, starting 5 seconds before onset of stimulus. Then the cumulative sum of impulses was plotted against time; the continuous lines at the bottom indicate

the three stimuli. In this type of plot the slope over any chosen time interval indicates the average impulse frequency for that interval. Hence, if there is some portion of the curve with less slope during the stimulation than before, inhibition occurs. Although the precise shape of the curves in Fig. 2 depends somewhat upon the time interval over which the spikes are counted, it is obvious that the degree of inhibition in this experiment depends not only on intensity level but also on the variation of the stimulus intensity with time.

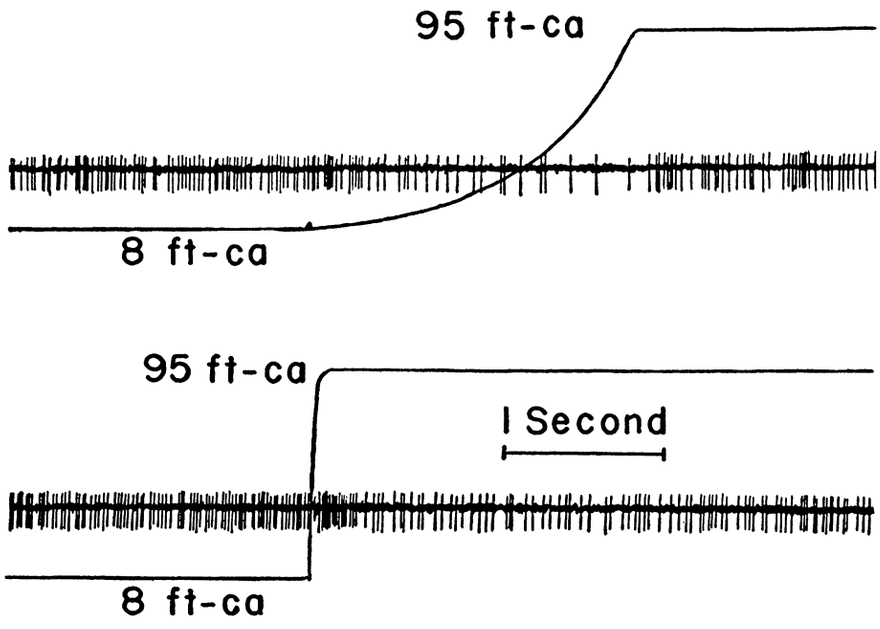

Fig. 1. Tracing of an experimental record showing action potentials from a single retinal ganglion cell in response to exponential (top) and square-wave (bottom) light stimuli.

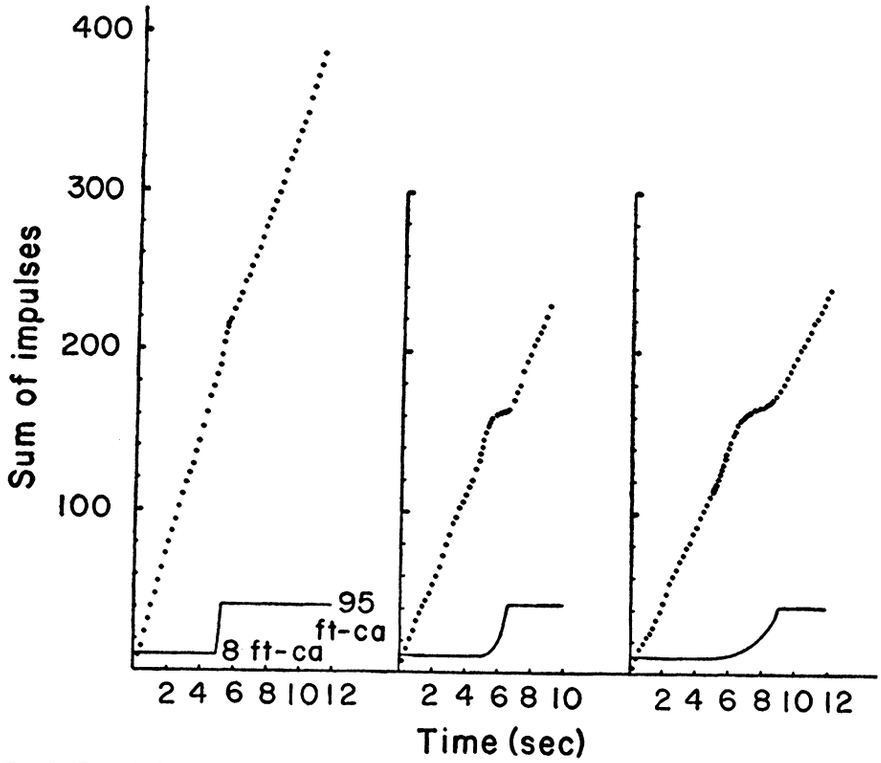

Fig. 2. Cumulative sum of action potentials versus time (dots) for three different stimuli as indicated by solid lines at the bottom. The data are from the same cell as in Fig. 1.

There is every reason to believe that the discharge frequency of a retinal ganglion cell is determined by the interplay between excitatory and inhibitory inputs which reach the ganglion cell from the receptors via inter-neurons (*2*). Our results indicate that for stimuli covering the entire receptive field of a ganglion cell, a change in the rate of increase of stimulus intensity can alter the balance between excitatory and inhibitory influences upon that cell. If the decrease in impulse frequency seen during the ramp stimulation were due to a visual purple bleaching effect or to sensory adaptation of the visual receptors, it would be difficult to explain why the spike frequency returns to the prestimulus level shortly after the stimulus has reached its maximum intensity (Fig. 1, upper tracing; Fig. 2, center and righthand plots). If the spike-frequency decrease were due to visual purple bleaching or sensory adaptation, one would also expect a decrease comparable to that observed during the fast part of the ramp stimulation during some period of the square-wave stimulation. But in several experiments a pronounced inhibition during a ramp could not be mimicked by exposing the eye to the same amount of radiant energy in the shape of a step function.

It is well known from work with square-wave stimuli that factors such as background illumination and state of adaptation, intensity and duration of stimulus, and extent and location of area stimulated within the receptive field modify the discharge pattern of vertebrate retinal ganglion cells (*2*, *3*). Our findings suggest that rate of change of stimulus intensity should be added to these parameters (*4*).

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