The response criteria were based on regularity of cell discharge: more than one consistent failure to fire or the development of erratic latencies constituting a graphical boundary.

One-hundred-six wavelength responses were recorded from 51 lateral geniculate cells. Eighty-nine of these were classified as one of seven types; the sensitivity curve for a representative member of each type is shown in Fig. 1. Two of these types were inhibitory, spike discharge occurring only when the stimulus was removed. One of these, the most common response observed, had its maximum spectral sensitivity between 500 and 510 mμ (38 cases). The other inhibitory response, much rarer, was most sensitive to wavelengths of 440 to 450 mμ (five cases).

Five excitatory types were seen, spike discharge occurring only when the stimulus was presented. The most common and well-defined response of this group had a maximum sensitivity at 505 to 515 mμ (10 cases). A less well-defined type had its maximum sensitivity at 430 to 440 mμ (18 cases). Three other distinctive excitatory responses were suggested with sensitivity maxima at the following wavelengths: 455 to 465 mμ (five cases), 575 to 585 mμ (two cases), and

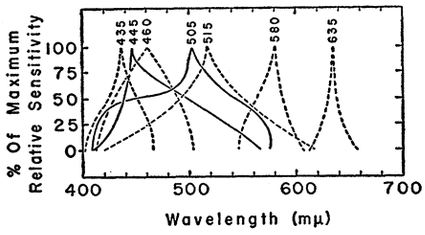

Fig. 1. Sensitivity curves of representative members of each of the seven response types. The broken lines represent the excitatory responses; the solid lines, the inhibitory ones.

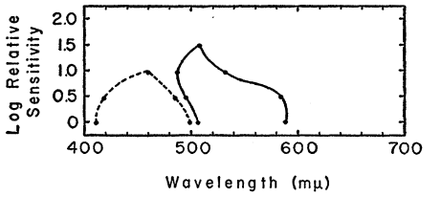

Fig. 2. Plot of the response of a single lateral geniculate cell showing the distortion of excitatory (dashed line) and inhibitory (solid line) responses to wavelength-intensity changes. The enclosed regions delineate the stimulus conditions producing a criterion response (see text).

635 mμ (one case). Nearly all the units studied developed some inconsistent spontaneous discharge at low stimulus intensities, causing the balance of the responses from these 51 cells to be too erratic to classify.

The seven response types described occurred in several combinations; the most common was one inhibitory with one or more of the excitatory responses from a single geniculate cell. Frequently the sensitivity curves for these responses would appear distorted as in Fig. 2, the graphical record of a unit having an excitatory response (460 mμ) bounded by the dashed line, together with an inhibitory response (510 mμ) bounded by the solid line. The noninfringement of inhibitory and excitatory responses, to the degree that one of them continues to develop over a greater spectral range on the decline of the other at reduced intensities, may be the reflection of information funneling from different retinal sources into common lateral geniculate cell pathways.

One additional unit was recorded which differed from the others by maintaining a regular spontaneous rate of discharge (about 30 spikes per second) during uninterrupted stimulus periods. Intermittent stimulation, however, had the effect of arresting this activity during the on or off phases of light, depending on its special composition.

The responses described here frequently had a well-defined spike prepotential. This was thought by Frank and Fortes (*4*) to be due to the soma of the recorded cell and therefore the sign of a postsynaptic discharge.

Certain characteristics of this study resemble earlier findings of other investigators. Dodt and Elenius (*1*), recording from retina of the rabbit under photopic conditions, reported two sensitivity maxima, 460 mμ and 510 mμ, resembling two of the excitatory responses reported here.

De Valois (*5*) observed a number of on responses distributed across the spectrum when recording from single cells of the monkey's lateral geniculate nucleus. Single cells were found in this animal also which produced on or off discharge depending on wavelength. Combinations of excitatory and inhibitory responses from single cells have been reported as well by Wagner *et al.* (*6*), who found that the output of ganglion cells from the goldfish retina could be governed by the spectral composition of the stimulus.

The recording of differential wavelength responses from the lateral geniculate nucleus of the rabbit does not, of course, permit direct conclusions about the animal's perception of color. It is of interest, however, that the responses observed were restricted largely to the blue and green regions of the spectrum, a finding which agrees with earlier behavioral work (*7*) and Laue's (*8*) results obtained by use of the gross electrode (*9*).

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Licking Behavior of Rats on a Schedule of Food Reinforcement

Abstract. Rats were trained on a variable-interval food reinforcement schedule. Lever presses and licks at the milk reinforcement were recorded independently. A dose of *d*-amphetamine which increased lever-pressing rates failed to affect licking rates. Licking rates increased as the duration between reinforcements on the variable-interval schedule increased.

The use of a touch-sensitive relay ("drinkometer") to measure rates and temporal characteristics of licking behavior in rats is now well established (*1*). I have added a drinkometer to the dipper mechanism of a Skinner box in order to correlate food-reinforced lever pressing with licking behavior.

Four rats were trained to press a lever in a standard (*2*) Skinner box on a variable interval (VI) schedule of reinforcement. Four successive repeating intervals (0, 30, 60, and 120 sec-

Table 1. Means rates of licking at milk reinforcements received after different intervals on a variable-interval schedule of reinforcement. Entries are mean licks per second (with standard errors) for individual rats.

Rat	Approximate interval between reinforcements (seconds)			
	0	30	60	120
AM-43	5.054 (± .054)	5.073 (± .058)	5.143 (± .058)	5.490 (± .053)
AM-44	4.889 (± .133)	5.270 (± .041)	5.367 (± .048)	5.549 (± 0.54)
AM-39	5.270 (± .042)	5.314 (± .031)	5.354 (± .039)	5.556 (± .037)
AM-47	4.825 (± .070)	4.889 (± .080)	5.444 (± .040)	5.346 (± .049)

onds) were employed during the 2-hour session; the first response after each of these intervals elapsed was reinforced. For reinforcement, rats were given access to a large dipper of sweetened milk for 4.5 seconds. They could not consume the entire contents of the dipper within the time allotted.

The Skinner box was modified as follows: (i) the floor grids were wired in parallel: (ii) the dipper was isolated electrically; (iii) when presented, the dipper was made accessible to the rat's tongue only; and (iv) a drinkometer (*3*) was connected to the floor and the dipper in order that individual licks at the dipper could be recorded.

Figure 1*A* illustrates behavior under this schedule. Lever pressing (top curve) was stable and moderate in rate. Reinforcements (bottom line) were accompanied by rapid licking (middle line) at the mean rate of about five licks per second.

The program is amenable to the investigation of certain drugs possessing alleged stimulant and anorexigenic properties. Figure 1*B* illustrates the effect of 1 mg/kg of *d*-amphetamine sulfate in aqueous solution which was administered intraperitoneally. The time course of the stimulation of the rate of lever pressing is apparent. Licking rates, on the other hand, were evidently not affected. Increased rates of lever pressing were shown by all four rats at doses of *d*-amphetamine which failed to reduce licking rates.

Controversial views have been expressed concerning the reputed anorexigenic effect of *d*-amphetamine in humans: Is the anorexia a truly specific pharmacologic action or is it secondary to the central stimulant properties of *d*-amphetamine (*4*)? The present studies shed no light on whether the anorexigenic and central stimulating properties of *d*-amphetamine (here manifested as increases in response rate) are mediated by separate mechanisms. Clearly, however, an observable stimulant action of *d*-amphetamine arises at a lower dose than does any reduction in lever-pressing and licking behavior (Fig. 1*B*). To the extent that this finding can be extrapolated to humans, it suggests that "therapeutic" doses of *d*-amphetamine which produce anorexia would most likely also elicit central stimulant effects.

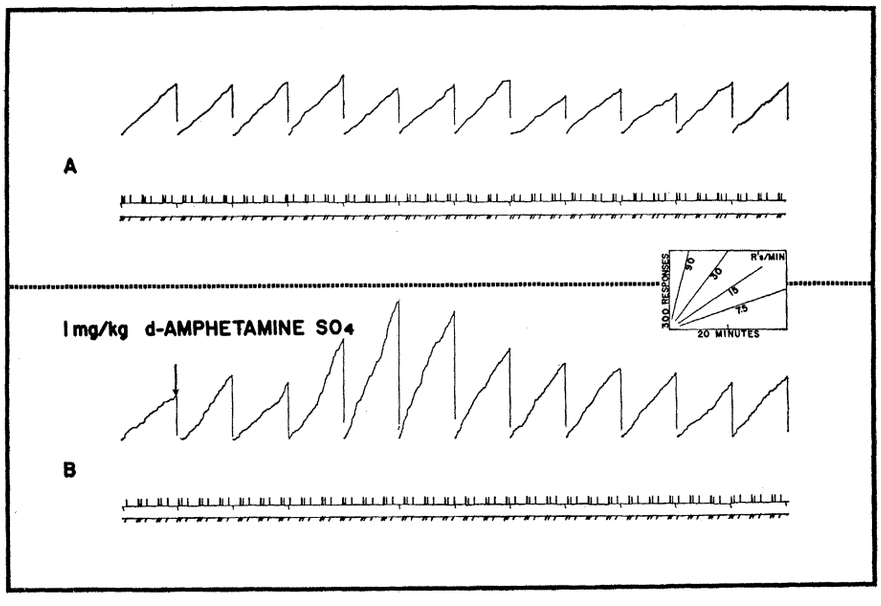

Fig. 1. Cumulative curves for lever pressing and licking from rat AM-44. *A*, control record; *B*, 1 mg/kg of *d*-amphetamine sulfate, as shown. Top curves: lever pressing; middle curves: licking; bottom curves: reinforcements. The reset lines in the top curve and the signal (downward) deflections in the middle curve were made simultaneously every 10 minutes.

After a series of doses of 2 and 4 mg/kg of *d*-amphetamine the rats stopped responding for long periods after drug administration. When response rates recovered, licking also resumed. Over the range of doses studied (0.25 to 4 mg/kg) the examination of cumulative curves revealed no instance where reinforced lever presses were not followed immediately by rapid licking behavior (*5*).

The parameters of the schedule also affected licking rates on the reinforcement dipper. The four rats were exposed to five successive 2-hour sessions on the VI schedule without drugs. Licks and reinforcements from the four interval values comprising the schedule were cumulated individually during the fifth session and expressed as mean licks per second.

Table 1 relates mean licking rates to the four intervals between programed reinforcements. Latencies of responding after a reinforcement was programed were invariably on the order of a few seconds. They are not taken into account in the column headings. Mean licking rates consistently increased (with one exception) as the interval between reinforcements was increased, but there was no consistent form to the functions among the different rats.

It is difficult to isolate any single variable as a determinant of the increased licking rates at longer intervals. "Drive," as it is usually defined (in terms of deprivation), is probably not an important factor, since each mean entry in the table is comprised of many values from throughout the session. Drive conditions varied at different times during the session, and this would serve to negate their influence upon the different mean values. A more plausible explanation revolves around the concept of chaining (*6*) or "set." The probability, immediately after a reinforcement, that a lever press would be reinforced was only one in four. As

time elapsed, however, the probability increased until, following the elapse of 2 minutes after a reinforcement, the first lever press was always reinforced. The strength of the response chain which began with a reinforced lever press and terminated with licking behavior may thereby have increased as time elapsed after a reinforcement. It is also conceivable that responses which compete with dipper approach and rapid licking behavior (that is, grooming or swallowing behavior) were strongest just after a reinforcement. In any case, it is evident that identical reinforcing stimuli may evoke licking behavior which varies in relation to subtle environmental parameters (*7*).

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4 October 1961

Quantum Efficiency of Cytochrome Oxidation in a Photosynthetic Bacterium

Abstract. Illumination of *Chromatium* with light absorbed by bacteriochlorophyll causes the oxidation of intracellular cytochrome. The quantum efficiency of this reaction approaches one electron per photon at 589 millimicrons and at wavelengths between 862 and 908 millimicrons. The efficiency of converting excitation energy to chemical energy is estimated to be about 30 percent.

The oxidation of intracellular cytochrome pigments when photosynthetic bacteria are illuminated with light absorbed by chlorophyll appears to be a general phenomenon (*1*). This observation, coupled with the fact that these pigments are present in all the photosynthetic bacteria investigated so far (*2*), has led to the supposition that cytochromes are involved in electron transfer even in bacteria which have no respiratory capability.

If a cytochrome is directly involved in photosynthetic electron transfer, the light-induced oxidation reaction must proceed with an efficiency comparable to that for overall photosynthesis. For the purple sulfur bacterium *Chromatium* the quantum efficiency of cytochrome-423.5 oxidation has been estimated to be 0.5 electron per photon absorbed at 589 mμ (*3*). (Bacteriochlorophyll has a minor absorption band at 590 mμ in vivo.) This estimate was made on the assumption that the differential absorbancy index $\Delta\epsilon_{423} - \Delta\epsilon_{470}$ for cytochrome 423.5 was 100 cm^{-1}mmolar^{-1}.

The results of this earlier work have been recalculated in the light of the quantitative spectral data of Bartsch and Kamen (*4*) for *Chromatium* cytochrome *c* which appears to be identical to cytochrome 423.5 in the intact organism. In addition, the measurements of quantum efficiency have been extended to the far-red region where the main absorption peaks of bacteriochlorophyll are located, and the possibility of a drop in efficiency for wavelengths on the red side of the bacteriochlorophyll band at 890 mμ has been investigated.

The experimental methods have been described in detail previously (*3*). *Chromatium*, strain D, was grown in liquid inorganic medium and resuspended in fresh medium before examination. Fractional absorption of actinic light was determined by the integrating sphere method. Intracellular cytochrome oxidation was measured in terms of $\Delta D_{423} - \Delta D_{470}$ with a double-beam spectrophotometer. Actinic light was furnished by a 100-watt projector lamp and the following filters: 1 cm-H_2O, Wratten 88A, and Bausch and Lomb second order interference filter(s). Intensities up to 10^{-9} einstein cm^{-2}sec^{-1} were measured by means of a calibrated thermopile. For each wavelength of actinic light the initial rate of absorbancy change, $d(D_{423} - D_{470})/dt$ (see Fig. 1), was plotted versus the rate of absorption of actinic light, and the average slope was determined. The quantum efficiency was obtained by dividing the slope by the differential absorbancy index for *Chromatium* cytochrome *c*, 62.3 cm^{-1}mmolar^{-1} (*5*).

Some of the experimental data is

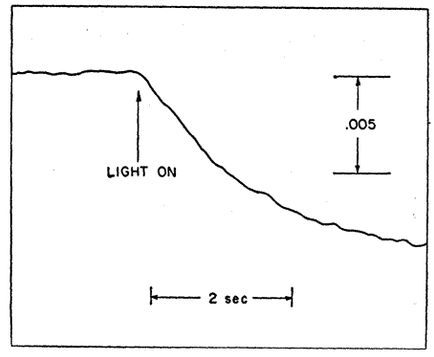

Fig. 1. Oscillographic recording of the absorbancy change $\Delta D_{423} - \Delta D_{470}$ caused by irradiation of bacteria with 892-mμ light of intensity 2×10^{-10} einstein cm^{-2}sec^{-1}.

summarized in Fig. 2. Nine efficiency determinations in the far red (862 to 908 mμ) gave an average value of 1.0 electron per photon. The average value for 589-mμ light (*3*) was recalculated on the basis of 62.3 cm^{-1}mmolar^{-1} and found to be 0.8. These two values are in good agreement in view of the different methods used to measure light intensity in the two cases. The efficiency approaches the theoretical maximum of one and appears to be essentially independent of wavelength. Although the value at 908 mμ is somewhat low, this is probably not significant in view of the fluctuation in the other values obtained in the far red.

Since each photon absorbed by bac-

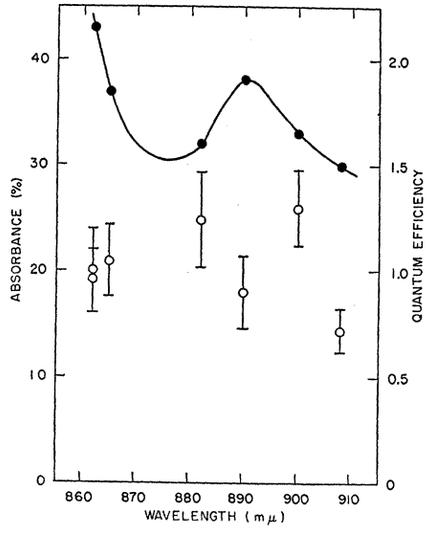

Fig. 2. Absorbance of actinic light (solid circles) and quantum efficiency of cytochrome oxidation (open circles) for wavelengths of 862, 865, 882, 890, 900, and 908 mμ. The horizontal bars indicate the r.m.s. deviation from the average efficiency value at each wavelength.