in their natural surroundings. Considerable experience with *P. potto* does not substantiate the reputation for ferocity that the species has apparently gained.

U. M. COWGILL
Osborn Memorial Laboratory,
Yale University,
New Haven, Connecticut

Note

Supported by NSF grant [B473]. The animals were provided by Prof. John Buettner-Janusch of Yale University. Intellectual and other forms of support were offered by Prof. G. E. Hutchinson of Yale University and Dr. Alison Jolly of the New York Zoological Society.

19 October 1964

Responses of Single Cells in Visual System to Shifts in the Wavelength of Light

Abstract. *Spectrally opponent cells of the macaque lateral geniculate are very sensitive to shifts from one wavelength to another, independent of the relative intensities of the different wavelengths. Shifts in opposite spectral directions from the adaptation wavelength produce opposite changes in firing rate, regardless of the particular wavelengths involved; however, any given cell is more sensitive to shifts in some spectral regions than in others.*

A person with normal vision can distinguish between two different lights on the basis of differences in intensity or wavelength. We are attempting to determine the neural organization underlying this ability by examining in the monkey the responses of single cells in the lateral geniculate nucleus (LGN), the relay station between the retina and the visual cortex.

We reported previously that two classes of cells can be distinguished in the primate LGN on the basis of their responses to stimulation of the eye by flashes of diffuse light of different wavelengths: (i) spectrally non-opponent cells, which are inhibited by light of all wavelengths, or excited by all wavelengths; and (ii) spectrally opponent cells, which are excited by some wavelengths and inhibited by others. These response differences have led us to hypothesize that the opponent cells constitute the system for analyzing and conveying information about color vision, and that the non-opponent cells constitute the brightness signalling system. Furthermore, it was predicted on the basis of certain assumptions (*1*) that the opponent cells should not only be able by their responses to distinguish between different wavelengths, but should do so better in some parts of the spectrum than in others, exhibiting the same differential sensitivity that is seen in the psychophysical hue discrimination function. In the experiments reported here, we tested these theories by examining directly the responses of LGN cells to momentary shifts in the intensity or wavelength of light presented to the eye.

The recordings were made from macaque monkeys, animals which our behavioral tests indicate have the same relative spectral sensitivity and the same color vision as normal human observers. Single cells in the LGN were isolated with microelectrodes. The oscilloscopic display of the nerve discharge was photographed on moving film and the number of spikes in the various stimulus intervals counted.

The optical system had two beams of light, one from a monochromator and the other from a tungsten source, brought to a common focus at right angles. A mirror located on a shutter arm at this focal point allowed us to reflect one or the other beam to the animal's eye. The eye was adapted to a standard light of a certain wavelength and intensity. Then the mirror was repeatedly switched to present alternately the standard light and a test light of a different wavelength or intensity. The ability of the cells to detect a change in the wavelength of the light was tested around eight spectral points: 464, 490, 528, 555, 570, 593, 622, 656 mμ. At each spectral point the responses to wavelength shifts of various amounts in both spectral directions were recorded. For instance, the responses to a shift back and forth between 593 and 580 mμ would be recorded, then between 593 and 600 mμ, 593 and 570, 593 and 590, 593 and 620 mμ, and so on. The responses of the same cell to wavelength shifts around 490 mμ might then be studied. We have examined the responses of a total of 58 LGN cells to shifts in wavelength.

Lights of different wavelengths differ in hue and brightness; if one is concerned with investigating hue discrimination, the lights should be equated for brightness—that is, adjusted on the basis of the photopic luminosity curve, as was done in these studies. The luminance of the various lights was 6.2 candela per square meter; this is well within the photopic range. In addition to the equal-brightness shifts, we have investigated shifts to wavelengths which are brighter than the standard wavelength, and to those which are dimmer. It should also be noted that with the exception of the 464-, 622-, and 656-mμ filters, the points studied were on the relatively flat part of the luminosity curve and very little correction for luminosity was required over the spectral range studied for any filter. In the intensity-shift experiments the wavelength of the light was kept constant, or more commonly, white light was used.

Non-opponent cells are extremely sensitive to shifts in intensity, increments and decrements in intensity from the adaptation level producing symmetrical changes in firing rate in opposite directions (*2*). Such cells, however, are quite insensitive to shifts in wavelength when the standard and test wavelengths are of equal brightness.

Opponent cells, on the other hand, are in general very sensitive to a shift in the wavelength, while being relatively insensitive to a change in the intensity of the light. When adapted to a light of any wavelength these cells have a maintained firing rate which is only slightly related to the wavelength. They respond with an increase in firing rate to a wavelength shift in one spectral direction from the adaptation wavelength, and with a decrease in firing to a shift in the opposite spectral direction. The red-excitatory, green-inhibitory (+R−G) cells and the yellow-excitatory, blue-inhibitory (+Y−B) cells show an increase in firing in response to a shift toward the longer wavelengths, and a decrease in firing in response to a shift toward the shorter wavelengths. The +G−R and +B−Y cells do just the opposite. An example of this can be seen in the records in Fig. 1.

This +G−R cell can be seen to discriminate clearly the 20- to 30-mμ shifts from 593 to 570, or from 593 to 620; even the 7- to 8-mμ shifts from 593 to 585 and 593 to 600 produce easily discernable changes in firing rate. When the 570- and 593-mμ lights are being alternated, the cell is fired by the 570- and inhibited by the 593-mμ light; when the shift is between 593 and 620 the cell is fired by the 593- and inhibited by the 620-mμ light. It is apparent that shifts in opposite spectral directions produce

opposite changes in firing rate, and that the main determinant of the firing rate is the relation between the wavelengths involved, rather than the absolute wavelengths.

That these changes in response produced by shifting the wavelength are not a function of intensity differences is shown in Fig. 2. These records are from the same cell as in Fig. 1. The middle record in Fig. 2*a* is of a shift between 593 and 570 mμ when the intensities are equated for photopic brightness. In the top record, the 570-mμ wavelength is 0.5 $\log_{10}$ unit brighter than the 593; in the bottom the 570-mμ wavelength is 0.5 log unit dimmer. These differences in intensity make very little difference in the firing rate; the response is almost entirely determined by the change in wavelength. In other words, this cell is fired by yellow and inhibited by orange light regardless of whether it is a bright yellow and a dim orange, or a dim yellow and a bright orange: it is signalling a shift in the color of the light, not in its brightness. The same response to changes in wavelength independent of intensity differences can be seen in the 593- to 620-mμ shifts in Fig. 2*b*.

The responses of opponent cells to shifts in wavelength are not, however, completely independent of intensity: in some parts of the spectrum the cells become very intensity-dependent in their responses to wavelength shifts. There is a roughly reciprocal relationship between their sensitivity to wavelength shifts and their intensity dependency. The relative intensities of the different spectral lights makes little difference in those parts of the spectrum where the cells are very sensitive, as in Fig. 2. In other parts of the spectrum, for example, the very long and very short wavelengths, the cells are very intensity-dependent while at the same time being rather insensitive to shifts in wavelength. These relationships are probably reflected in the Bezold-Brücke effect.

Although the opponent cells are sensitive to shifts in wavelength over a wide spectral range, a given cell is much more sensitive to shifts in some spectral regions than in others. The +R−G and +G−R cells are extremely sensitive to shifts in the region from about 560 to 610 mμ, and distinctly less so at other wavelengths. Figure 3 shows the average responses of ten +G −R cells to shifts in wavelength about

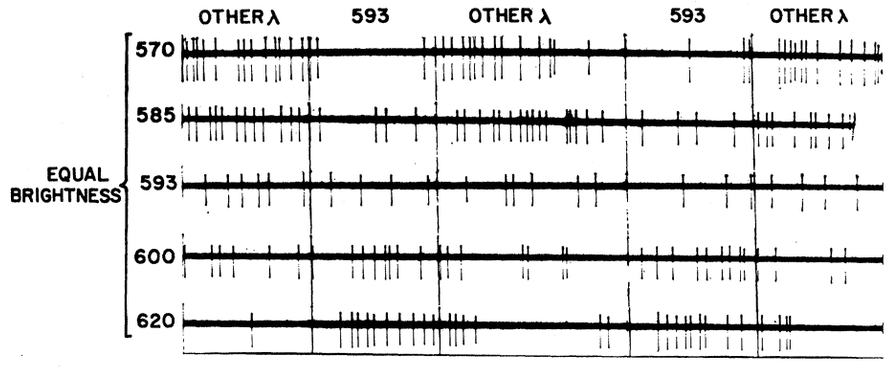

Fig. 1. Superimposed records of the responses of a single cell to various shifts in wavelength around 593 mμ (duration of 593: 1 second). The other wavelength in each case is indicated on the left.

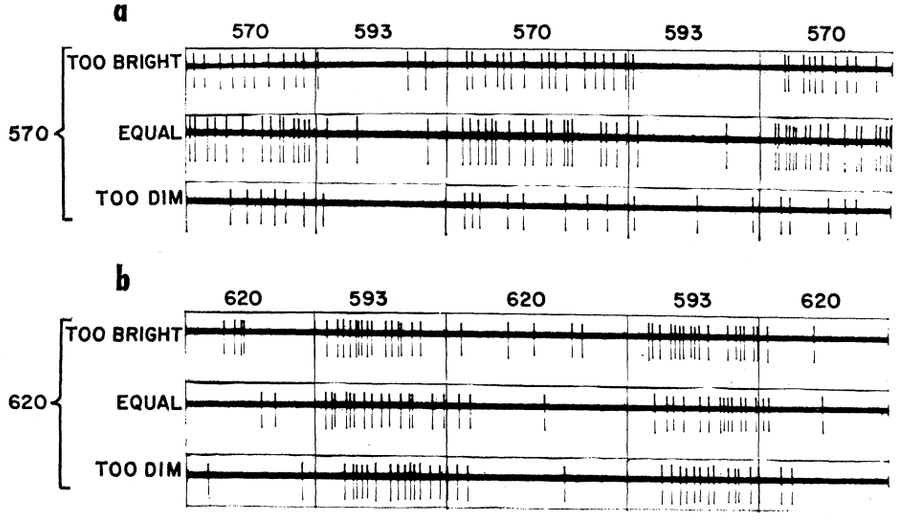

Fig. 2. Records from the same cell as in Fig. 1. In (*a*) the 593-mμ wavelength is at the same intensity in each case, but the 570-mμ wavelength is 0.5 $\log_{10}$ unit brighter, equal to, and 0.5 $\log_{10}$ unit dimmer than the 593-mμ wavelength, respectively, in each record. In (*b*) the same relationships hold for the shift between 593 and 620 mμ.

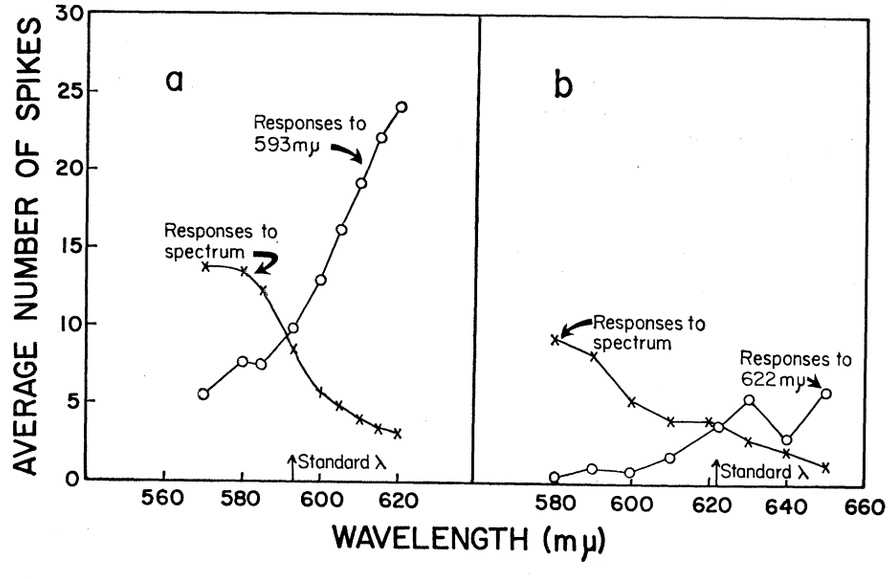

Fig. 3. A plot of the average number of spikes fired by a number of green-excitatory, red-inhibitory (+G−R) cells in response to shifts in wavelength at two different spectral loci.

593 mμ, and of four cells to shifts around 622 mμ. In each case the open circles indicate the response to the standard wavelength and the crosses the responses to various other wavelengths.

For instance, in the shift back and forth between 570 and 593 mμ, the cells averaged 5.5 spikes to the 593-mμ wavelength and 13.8 spikes to the 570-mμ wavelength. These cells distinguish very well between 593 mμ and other wavelengths, but only quite poorly between 622 mμ and the other wavelengths, particularly ones of still longer wavelength. One might also note that the ability of the cells to discriminate between two wavelengths is just a continuous function of the wavelength difference. There is no evidence for a threshold in the sense of a region around the match point within which there is no discrimination.

The +B−Y and +Y−B cells in some cases are quite sensitive to the 550- through 600-mμ range, but in addition are very sensitive to wavelength shifts in the region of 470 to 500 mμ. The combined sensitivity of all of the opponent cells to wavelength shifts in different spectral regions agrees well with the hue-discrimination function of the macaque and human.

Previous experiments with intense chromatic adaptation (*1*) indicate that each LGN cell has inputs from several different types of receptors, each of which responds to changes in intensity with changes in amount of output. The non-opponent cells have two or more such systems feeding in the same direction—that is, all having excitatory or all inhibitory effects; whereas the opponent cells have an excitatory input from one system and an inhibitory input from another system.

The non-opponent cells are very sensitive to changes in intensity, since their responses reflect the changes in receptor output. Such a system is very insensitive to shifts in wavelength, however, since a shift from one part of the spectrum to another would merely lead to a shift from one excitatory input to another, or from one inhibitory input to another.

The opponent cell system is rather insensitive to changes in intensity because increasing the intensity of light simultaneously increases the amount of excitation from one system and the amount of inhibition from the other; the effects thus largely cancel each other out. This would occur, however, only in those spectral regions to which both of the underlying cone systems are sensitive.

For instance, since only the red system is very sensitive to the long wavelengths, the +R−G and +G−R cells become intensity-dependent rather than wavelength-dependent in this part of the spectrum. The opponent cells are very sensitive to wavelength shifts in parts of the spectrum which affect both underlying systems. In the case of the +G−R cell illustrated in Figs. 1 and 2, for instance, a shift toward the shorter wavelengths simultaneously increased the excitatory input from the G system and decreased the inhibitory input from the R system, thus producing a large increment in firing rate. A shift toward the longer wavelengths has just the opposite effect on such a cell.

RUSSELL L. DE VALOIS
GERALD H. JACOBS
ISRAEL ABRAMOV
Psychology Department,
Indiana University, Bloomington

References and Notes

1. R. L. De Valois, G. H. Jacobs, A. E. Jones, *Optik* **20**, 87 (1963).
2. ———, *Science* **136**, 986 (1962).
3. This research has been supported by USPHS grant No. NB-02274.

5 October 1964

Computer Analysis of the Nuclear Test Ban Treaty

Abstract. *Experiments were undertaken to determine the applicability of a computer program for automatic syntactic analysis to the systematic discovery of ambiguities in textual material. Specific application of this program was made to portions of the Nuclear Test Ban Treaty. Results, though promising, indicate that such applications are not now economically feasible for large volumes of text.*

Syntactic analyzers, originally developed for the automatic translation of languages (*1*), may one day be used as automatic "ambiguity detectors" in our law courts and legislative assemblies. In automatic language translation, the syntactic analyzer determines the structure of each input sentence in terms of its constituent phrases and clauses. It makes no semantic discriminations. Consequently, it uncovers ambiguities in our everyday communication that may escape the human analyst who knows what a document is "supposed to say."

Would not such a syntactic analyzer, systematically determining the several interpretations of a sentence, have substantial application in fields remote from automatic language translation? (2).

Much of the litigation filling our court calendars arises directly from procedural or substantive ambiguities in the law. In drafting legislation or in drawing up contracts, legal advisers often identify, and sometimes remove, language that may be later subject to dispute. Treaties, which may at times retain somewhat ambiguous provisions, should perhaps be drafted with the fullest possible knowledge of precisely what these ambiguities are. Would not a syntactic analysis of such documents sometimes prove revealing?

It seemed worth while to attempt to answer this last question, particularly since a mechanized syntactic analyzer is essentially free from bias with respect to subject matter. Thus, it may discover ambiguities that are easily overlooked, since the review of documents is often approached with a particular "set" of mind, or attitude.

The opportunity to test automatic syntactic analysis as a technique for the systematic detection of ambiguities in legal and other documents was recently enhanced by the availability of the dictionary, grammar, and operational program for the Multiple-Path Syntactic Analyzer (*3*). This analyzer, which operates on the IBM 7090/94 computer, is believed to be unique in its capability to provide multiple analyses of syntactically ambiguous sentences in an effective and efficient fashion.

Since it was readily available, the analyzer was used to process selected portions of the recent Nuclear Test Ban Treaty. In this paper we present the results of the analysis of six of the more significant sentences from that treaty.

The actual text of the treaty, and the text as run through the analyzer, are given in Fig. 1. The minor differences between the two texts were necessitated by several considerations: (i) the analyzer will not at present