

1968

Visual Information Coding by Nerve Impulse Patterns

D R. T. Walker

N. R. Carlson

S. S. Fox

Copyright © Copyright 1968 by the Iowa Academy of Science, Inc.

Follow this and additional works at: <http://scholarworks.uni.edu/pias>

Recommended Citation

Walker, D R. T.; Carlson, N. R.; and Fox, S. S. (1968) "Visual Information Coding by Nerve Impulse Patterns," *Proceedings of the Iowa Academy of Science*: Vol. 75: No. 1 , Article 42.

Available at: <http://scholarworks.uni.edu/pias/vol75/iss1/42>

This Research is brought to you for free and open access by UNI ScholarWorks. It has been accepted for inclusion in Proceedings of the Iowa Academy of Science by an authorized editor of UNI ScholarWorks. For more information, please contact scholarworks@uni.edu.

Visual Information Coding by Nerve Impulse Patterns¹

D. R. T. WALKER, N. R. CARLSON and S. S. FOX

Abstract. Microelectrode recordings of single cells were obtained from the visual cortices of twenty acutely prepared curarized cats. A 500 msec light stimulus was presented for 150 trials at interflash intervals of 1.3, 2.0, 2.5, 3.2 and 4.0 seconds. The poststimulus time histograms of cells responding with an accelerated firing to stimulus onset encoded the interstimulus interval by an increased firing during the second of three 166 msec periods during the stimulus. The firing at light offset and after did not encode interstimulus intervals.

The question of the manner in which information about the environment is encoded by nerve impulses within the central and peripheral nervous systems has occupied the attention of many investigators. The earliest workers laid the foundation for the development of two different approaches to this problem.

Mathews (1931), recording from single afferent nerves, showed that the frequency of firing in stretch receptors was related to the logarithm of the stimulus intensity and thus demonstrated a physiological coding of information. von Frey (1896), extending the Doctrine of Specific Nerve Energies, presented evidence which suggested that specific sensations were associated with specific receptors in the skin and thus supported an anatomical form of coding.

The Doctrine of Specific Nerve Energies as modified by von Frey has been decimated by the finding that the cornea, which possesses only one kind of receptor, is capable of recognizing pain, touch, and thermal stimuli (Lele and Weddell, 1956). Anatomically oriented approaches to coding are, however, still very much alive today. Mountcastle (1957, 1959) working in the somatosensory system has demonstrated that in the ventrobasal complex of the thalamus and in postcruciate cortex there are cells uniquely responsive to joint rotation, touch, or pressure. The joint receptors are exquisitely sensitive, being responsive, in some cases, only to certain directions of movement.

Anatomical coding in the visual system has been elaborated by Hubel and Wiesel (1959, 1965). These investigators have found cells which are sensitive to the direction, rate, orientation, and extent of a moving stimulus. Thus a given cell in the postlateral gyrus of the cat may respond with a burst of impulses to a slit of light $\frac{1}{8}^\circ$ wide by 2° long, oriented from two o'clock to eight o'clock, moving downward at 2° per second but not to one which has been altered only slightly in either length, width, orientation, or direction of movement.

¹This research by USPHS Grant MH11834 to S. S. Fox.

Physiological coding, that is, a code utilizing the temporal pattern of nerve impulses, like a Morse code, has been overshadowed by the spectacular researches of Hubel, Mountcastle, and others. Temporal patterning is, however, a possibility to be seriously explored within the framework of an anatomical code which has been so clearly demonstrated by the previously mentioned workers.

A code utilizing the temporal pattern of nerve impulses is intuitively appealing, since it is parsimonious of neurons if a single cell can handle different pieces of information at different times by means of an altered pattern of firing. A further consideration favoring this form of coding is that it would seem to be the only way in which visual, auditory, and somesthetic information could be integrated by a polysensory cell.

Regardless of whether one subscribes to an anatomical or physiological code one realizes that the nervous system is not wired with the security of a telephone exchange and that a particular cell does not always respond in the same way each time an identical stimulus is presented. This is viewed as a statistical process: that is, for a given stimulus a small population of cells is activated and in any instant within 50 to 100 milliseconds after the first response to the stimulus the firing of this population is roughly the same. The behavior of any given cell in that population may, however, alter radically from not firing at all to firing maximally. Obviously this aspect of nervous system behavior presents a problem to the study of response patterns. This problem is quite readily solved by constructing the average firing pattern of the single cell. This average firing pattern is referred to as a poststimulus histogram (PSH) and is collected using electronic equipment designed as follows.

If a signal (the response to the stimulus) is embedded in noise (the spontaneous nonstimulus related behavior of nerve cells) then summing responses on top of each other will result in any regularly occurring process emerging above a baseline of random processes. As a means of lining up the records so that the stimulus related responses fall on top of one another, the time of stimulus onset is employed.

The light stimulus used in the present experiment triggers one second of sampling of incoming action potentials by a Computer of Average Transients (CAT). The memory of the CAT contains 400 bins and thus with a one thousand millisecond analysis period each bin is open for 2.5 msec. Any nerve impulse occurring while one of the 400 sequential bins is open is registered as a count in that bin. Thus, if on eight of ten trials a response occurs 25 msec after the stimulus then there will be eight counts in the tenth bin which is the bin open at 25 msec. By repeatedly presenting stimuli and sweeping across these 400 bins where each bin bears a unique temporal relationship to the stimulus, regularly occurring stimulus related events are highlighted

while random or rarely occurring processes tend to level out. In this way the average pattern of firing is reconstructed.

In the introductory work on the problem of temporal coding a simple question was asked. Namely, is the degree of retinal dark adaptation encoded in the pattern of impulses? This was most easily accomplished with the materials available by holding the intensity of a 500 msec light stimulus constant and varying the interval between flashes. In the preliminary work reported here the light source was a glow modulator tube and the intervals used were 1.3, 2.0, 2.5, 3.2, and 4.0 seconds. These intervals were chosen since data from both Hecht and Shlaer (1938) and Wald (1959) indicate that dark adaptation is very rapid during the initial period of darkness.

METHOD

Under ether anesthesia the trachea and radial vein were cannulated in 20 cats. The animals were then secured in a stereotaxic instrument and routine surgical procedures (Fox and Norman, 1968) were employed for exposing visual cortex prior to microelectrode recording with 3M KCl filled glass pipettes, the DC resistance of which was 50-100 megohms. Wound margins and pressure points were treated with procaine. The animals were maintained on the paralyzing drug d-tubocurarine chloride and were artificially respiration. Body temperature was maintained at 36-38° C. with the aid of a hair dryer. Spike impulses were led from the micropipette to a conventional cathode follower preamplifier system, the output of which passed to a loud-speaker; a dual beam oscilloscope; and a Scmitt trigger. Scmitt trigger output entered the CAT and was monitored on the oscilloscope. The light stimulus and interstimulus intervals were electronically timed by a series of pulse and waveform generators which also initiated the sweep of the CAT.

After preparation and superficial placement of the electrode the pupil was dilated with atropine and the eyelid retracted with a wound clip. One hour was allowed for pupil dilation and recovery from ether. Electrode advancement was made with a micromanipulator and was generally at a rate of about 100 micra per minute. Upon isolation of a cell whose firing pattern could be influenced by the light stimulus, which was presented through a lucite tube, the experiment began and recordings of 150 stimulus presentations were made. The order of administration of the different intervals was varied according to a previously arranged random schedule.

After the completion of 150 sweeps the display of the CAT was photographed and the stimulus programmer was switched to the next interval and stimuli were administered at the new rate for two minutes prior to recording. In this way it was hoped that the degree of dark adaptation at stimulus onset had stabilized to a new value.

The 35 mm. negatives of the averaged displays were enlarged by a projector and traced on coded paper. In this preliminary investigation the 500 msec stimulus period was divided into three equal time blocks of 166 msec each and the areas under each were measured with a planimeter. The poststimulus period was divided into two blocks of 166 msec each and was similarly measured. These integrals form the principal data analyzed in this study.

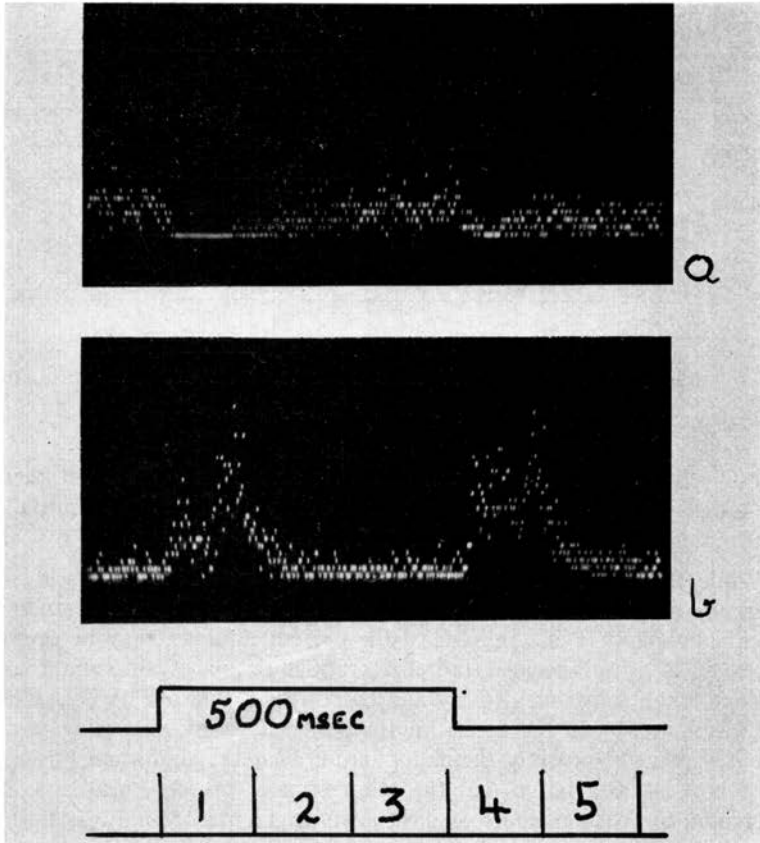


Figure 1. 1a depicts a cell inhibited at both stimulus onset and offset. In 1b a cell showing increased firing to the stimulus is shown. Total sweep time is one second and the ordinate is number of impulses. The upper line shows the onset duration and offset of the stimulus and the lower line indicates the division of the poststimulus histogram into the five periods.

RESULTS AND DISCUSSION

Two representative response patterns and the five 166 msec periods are presented in Figure 1. In Figure 1b it can be seen that there is a

Furthermore, the phasic firing at stimulus onset and offset is much stronger than the tonic firing throughout the stimulus. In Figure 1a the cell is initially inhibited by the stimulus with a gradual recovery of firing to the prestimulus level during the stimulus, followed by a weaker inhibition at stimulus offset. From Table 1 it can be seen that the area of Period 2 increases as the interstimulus interval is lengthened. This trend is significant at the 0.001 percent level on the Krushal Wallis H test.

Table 1

Mean Area of Poststimulus Histograms at the Five Stimulus Periods for the Five Interstimulus Intervals					
Intervals (sec.)	Stimulus Periods				
	1	2	3	4	5
1.3	24.2	17.2	20.0	29.5	29.5
2.0	27.0	26.4	31.1	28.5	30.4
2.5	33.5	32.3	23.0	27.8	31.0
3.2	27.4	34.8	25.0	27.8	26.2
4.0	37.0	35.0	35.5	33.5	28.2

In the first stimulus period there is a generally increasing trend marred by an inflection at 3.2 seconds. This trend is, however, not significant. No significant trend is observed in the highly variable areas of Period 3.

For cells which show a decreased firing at the stimulus onset there are no significant trends. For both initially inhibited and initially accelerated cells the poststimulus periods are not remarkable.

While the above results do not fill one with unbounded optimism there are some aspects of the data which indicate that further studies, modified somewhat on the basis of the present findings, may be profitable. It is a well-verified fact that phasic responses to stimuli are stronger than tonic ones (Gray and Sato, 1953; Fuortes, 1959). This may explain why in the first stimulus period a strong increasing trend is not observed: possibly the manipulation of dark adaptation was not as potent as anticipated and the strong phasic response was able to overcome the weaker effect of dark adaptation. Accordingly in future work, much shorter and longer interstimulus intervals will be employed. The fact that the second stimulus period shows a significant increasing trend as a function of interstimulus interval is in keeping with the notion that there is some residual effect of the state of the retina which is manifested during this period of tonic firing.

The firing during the two poststimulus periods was unaltered as a result of the interstimulus interval which indicates that a 500 msec stimulus of the intensity employed is quite adequate for these studies since it presumably brings the retina to the same level of light adaptation each time it is presented regardless of the interstimulus interval.

Should the results of later studies parallel the present findings, it will be concluded that the state of retinal dark adaptation is encoded by the number of impulses emitted by certain cortical units during certain periods of their firing. Since the stimulus intensity in all sensory systems is encoded by number of impulses (Mountcastle, 1957) the present results offer a physiological correlate to the psychophysical finding that the sensitivity of the eye increases as a function of time spent in the dark.

Literature Cited

- Fox, S. S., and R. J. Norman. 1968. Functional congruence: an index of neural homogeneity and a new measure of brain activity. *Science*, 159:1257-1259.
- Fuortes, M. G. F. 1959. Initiation of impulses in visual cells of *Limulus*. *J. Physiol.*, 148:14-28.
- Gray, J. A. B., and M. Sato. 1953. Properties of the receptor potential in Pacinian corpuscles. *J. Physiol.*, 122:610-636.
- Hect, S., and S. Shlaer. 1938. An adaptometer for measuring human dark adaptation. *J. Opt. Soc. Amer.*, 28:269-275.
- Hubel, D. H., and T. N. Wiesel. 1959. Single unit activity in striate cortex of unrestrained cats. *J. Physiol.*, 147:226-238.
- . 1965. Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *J. Neurophysiol.*, 28:229-289.
- Lele, P. P., and G. Weddell. 1956. The relation between neurohistology and corneal sensibility. *Brain*, 79:119-154.
- Matthews, B. H. C. 1931. The response of a muscle spindle during active contraction of a muscle. *J. Physiol.*, 72:153-174.
- Mountcastle, V. B. 1957. Modality and topographic properties of single neurons of cat's somatic sensory cortex. *J. Neurophysiol.*, 20:408-434.
- Mountcastle, V. B., and T. P. S. Powell. 1959. Central nervous mechanisms subserving position sense and kinesthesia. *Johns Hopk. Hosp. Bull.*, 105:173-200.
- von Frey, M., *Abh. Sachs. Gesellsch. Wis.* 1896. 40:175 cited by Rose, J. E., and V. B. Mountcastle, Touch and Kinesthesia. Ch. XVII *Handbook of Physiology*. Section I, Vol. I, J. Field (Ed.) Baltimore; Williams and Wilkins, 1959.
- Wald, G. 1959. The photoreceptor process in vision. Ch. XXVIII *Handbook of Physiology*. Section I, Vol. I, J. Field (Ed.) Baltimore; Williams and Wilkins.