Receptive Field Organization of the S-Potential

Abstract. *The receptive fields of S-potentials have been studied in carp retinas. The relationship between the stimulus intensity and area of stimulation was examined for each component of three different types of S-potential. It appears that for each component there is full summation over a large portion of the retina, a type of organization different from that found in the ganglion cell.*

The S-potentials (*1*), which originate between the photoreceptor and ganglion cell layers of the retina, are characterized as slow, sustained, hyperpolarizing or depolarizing responses which are evoked upon illumination. What part they play in the transmission and organization of information concerning color and pattern vision is still not understood. Other investigators have examined the S-potential receptive fields in fish and found contributions to the evoked response over a large portion of the retina (*2*). We have studied the receptive field organization of the S-potential to ascertain how it might relate to the transmittal of information through the retina.

The method of preparation was similar to one described previously (*3*). Whole retinas were isolated from freshly enucleated eyes of the carp *Cyprinus carpio*. The retina was placed, receptor side up, in a water-cooled chamber through which the stimulus light could be projected. Under direct microscopic observation the micropipette was centered with respect to the stimulus field. As a penetration was made, the light spectrum was continuously being scanned from 400 to 750 nm by the optical stimulator.

Three types of S-potential were detected and studied—monophasic, biphasic, and triphasic (Fig. 1). The most commonly found biphasic responses show a hyperpolarizing component in the green part of the spectrum and a depolarizing component in the red, whereas the triphasic responses consist of a depolarizing green and hyperpolarizing blue and red components. Once a particular type of S-potential was isolated, the organization of its receptive field was studied by examining for each component the area-intensity relationship using a constant threshold criterion. In each case the stimulating wavelength was chosen which gave the largest response for each component, for example, 500 and 700 nm for biphasic type units (see Fig. 1b). The objective was to determine the dimensions of the field in which a reciprocal relationship persists between stimulus area and intensity (Ricco's law). If a distinctive field size does exist for each individual component, the largest stimulus area for which Ricco's law holds will be different for the red and green components of the biphasic unit. The results of a series of such experiments (Fig. 2b) reveal that this is not the case. Instead, the size of stimulus field for which Ricco's law holds appears to

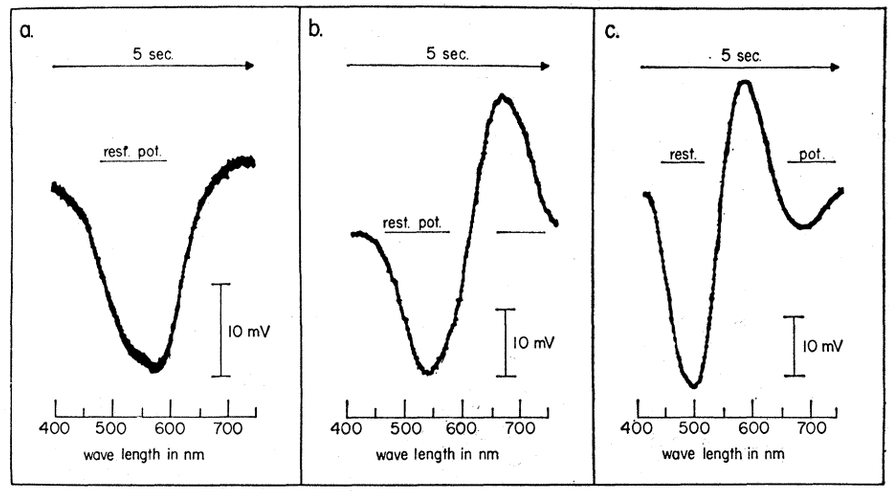

Fig. 1. Three common types of S-potentials: monophasic (a), biphasic (b), and triphasic (c). In all records a negative potential deflection (hyperpolarizing) at the recording electrode is downward. Horizontal traces—marked *rest*(ing) *pot*(ential)—indicate the potential level in the absence of a light stimulus. Direction and duration of the spectral scan for each record are indicated by arrow at top. Intensity of the stimulus at 650 nm is 9 μw/cm^2. For the energy spectrum of the light stimulus see (*3*). These records were made with a pen recorder.

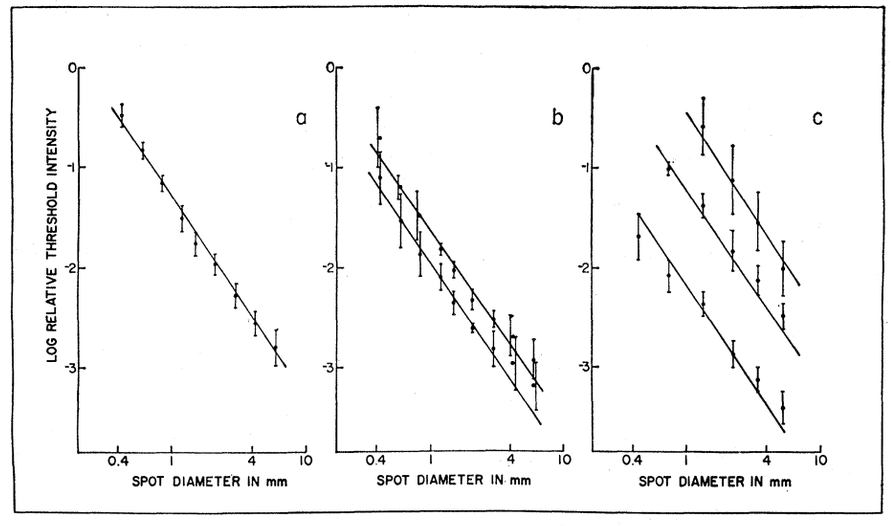

Fig. 2. Area-intensity relationship for constant threshold responses of S-potentials. The stimuli were circular and concentric with the micropipette tip. Zero (0) log intensity is approximately 55 μw/cm^2. Repetitive flashes, each with a duration of 0.5 second, were followed by dark intervals of 1.5 seconds. The horizontal axis gives the diameter of the spot focused on the retina. The straight lines of the three graphs represent the relationship, intensity $\times$ area $=$ constant (Ricco's law). The vertical bars are the standard deviation for each data point. (a) The results for 11 monophasic units; (b) results for eight biphasic units; (c) results for eight triphasic units. The data in (a) are obtained by stimulating with 625 nm; in (b) with 700 nm (upper data points) and 500 nm (lower data points); in (c), from top to bottom, with 680 nm, 580 nm, and 480 nm, respectively. The spot diameters in (c) are the outer diameter of an annulus minus the 0.75-nm diameter of a central stop.

be nearly equal to that of the entire retina. This demonstrates for each component that there is full summation over the receptive field. Similar results were obtained with monophasic units (Fig. 2a), as well as with triphasic ones.

To restrict the stimulus light to separate portions of the receptive field we examined the area-intensity relationship for each component of the triphasic unit with different size annuli (Fig. 2c). We found no significant differences from the results just described. To adapt out the contribution of one component from another we then combined background adapting lights of 430, 500, and 650 nm, respectively, with the annular stimulus fields. Again, the data confirmed the previous observations.

Our results support the conclusion that the S-potentials studied all have full summation over their entire receptive fields. This type of organization is in distinction to that described for ganglion cells in the closely related goldfish retina where the components have distinguishable field sizes (*3*). These results apply only to the types of S-potentials described in this study. Other types of S-potentials such as the reciprocals of those described, that is, triphasic units consisting of depolarizing blue and red and hyperpolarizing green processes, have been infrequently recorded in our laboratory, but there has been no opportunity to study them further and to ascertain their organization.

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1 March 1968

Archaeological Excavations in the Calico Mountains, California: Preliminary Report

Since 1964, excavations have been conducted at a site in the Calico Mountains near Yermo, in the Mojave Desert of southern California, under grants from the Research and Exploration Committee of the National Geographic Society, whose generous help is most gratefully acknowledged.

The site was selected by Dr. L. S. B. Leakey after he had undertaken preliminary investigations of the area in company with Miss Ruth Simpson. It is situated in an old alluvial fan which exhibits considerable erosion. The particular point of the fan where the excavations have been carried out was selected because specimens considered by Dr. Leakey to be human artifacts had been obtained nearby in a cut which had been made by a mechanical excavator.

Miss Simpson has been field director of the excavations ever since the inception of the work. She is assisted by a first-class crew, and we are deeply grateful to all members for the hard work and loyal support which they have given us throughout. Dr. Thomas Clements has been the geological adviser from the outset. Administration of the project has been under the general supervision of Dr. Gerald Smith, director of the San Bernardino County Museum.

The principal excavation [25 by 25 feet (7.5 m) and extending downward to an average depth of 13 feet into the undisturbed fan] has yielded more than 170 specimens in these undisturbed deposits. We consider them to be unquestionably the result of human activity. In addition, there are several hundred other specimens which, in view of their association with the first group, must also be regarded as possibly of human workmanship. The matrix of the fan itself, of course, contains a still larger number of pieces of stone which do not exhibit any suggestion of human activity.

Our view that the site has yielded very early humanly made artifacts is shared by a number of our colleagues who have visited the site and examined the material upon which we base our conclusions. Others, however, have found themselves unable to accept these specimens as being the result of human activity and regard them instead as having been produced naturally. The assemblage upon which we rely includes many examples of large flakes; some of them are very large, and all of them have well-defined bulbs of percussion. In a few cases the flakes also exhibit faceted striking platforms, while in some 30 specimens there is a well-defined *erailleure* across the bulbar face. In a few cases the bulb of percussion of a large flake has been subsequently trimmed away. In our view this trimming has been done carefully and by man.

The collection also includes more than 20 excellent concavo-convex flakes and some large hinge fracture flakes. There are a few specimens which we definitely regard as side and end scrapers and simple bifacially worked tools.

The whole assemblage has a very primitive appearance, but this is only to be expected in view of the probable age of the deposit from which it has been excavated. Geologists and geomorphologists who have examined the site are of the opinion that the age of the fan is over 40,000 years but probably less than 120,000 years, with a probable age of between 50,000 and 80,000 years.

In order to test the validity of a suggestion which had been made by some of those who disagree with us that what we call artifacts are no more than objects made by the natural action of movement of soil and rock within the fan, we excavated a large second pit, as well as a number of smaller test pits, at random points on the fan. The second large pit, situated somewhat higher on the fan than the first at a point indicated by those who disagreed with us, yielded no specimens which we would regard unquestionably as artifacts. Only a few artifacts were found in the smaller pits, especially those close to the main excavation.

Another factor which we consider to be of undoubted significance is that at our original site there appears to have been a very definite selectivity in respect of materials from which the flakes and other artifacts have been made. There is abundant chalcedonic material of less good quality in the fan, but the vast majority of the specimens which carry evidence of being artifacts were made from the better quality material. It seems improbable that nature would, or could, be thus selective.

In view of the great significance of the discovery, if our claims are valid, we cordially invite geologists and archaeologists who are interested to visit the site and also to make arrange-