threshold so that the response was easily inhibited by any inhibitory stimulus.

An inhibitory area of a neuron which showed a phasic response and a nonmonotonic spike-count function is shown in Fig. 2. The inhibitory area greatly overlaps the response area. Inhibitory stimuli from the area outside the response area (for example, 0.6 khz) did not evoke a response from the neuron, but inhibited the response to the excitatory stimulus. Stimuli from the shaded portion within the response area were not only inhibitory but were themselves excitatory while suppressing the response to the second stimulus. Measurement of the recovery curve of the neuron showed an inhibitory period immediately following the discharge of impulses to the first stimulus. In other words, the phasic response pattern can be said to have resulted from an inhibitory bombardment immediately following an excitatory bombardment. The nonmonotonic spike-count function of the neuron is understandable in light of this inhibitory area overlapping the response area. A decrease in the number of impulses with increasing intensity of a single stimulus can be seen clearly in the inhibitory region overlapping the response area of the neuron. In the region of the nucleus magnocellularis dorsolis, the spike-count functions were usually monotonic when the intensity of the stimulus was below 100 db. The nonmonotonic spike-count function must be produced by an inhibitory effect from other neurons, as discussed for mammals (*13*).

In the medullary auditory neurons, the inhibitory area often covered most of the response area. Inhibitory areas tightly sandwiching a response area from both sides of the best frequency were found but were rare. Neurons with narrow response areas were not found in this sample. At this level in the auditory system, both the response and inhibitory areas of single neurons scarcely show indication of the funneling, or sharpening effect around the best frequency. But, as in the case of mammals, there was a general tendency for the response pattern to shift from tonic to phasic as higher centers became activated. This phasic response pattern might serve to code rapid changes in the stimulus.

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Receptive Fields in the Cat Retina: A New Type

Abstract. *A new type of receptive field of cat retinal ganglion cells is described and termed the "suppressed-by-contrast" type. The firing rate of these cells is suppressed by a variety of visual stimuli. However, it has not been possible to find a stimulus that increases the firing rate above the maintained level.*

The two common types of receptive field organization of cat retinal ganglion cells were first described by Kuffler (*1*). The "on"-center type increases its firing rate when there is an increase in the ratio of the luminance of a central region to that of a surround region of the visual field. The "off"-center type increases its firing rate when there is a decrease in this ratio. Thus both types have the same spatial form, but a stimulus that excites one inhibits the other, and vice versa.

Until recently no new types have been described in the cat retina, although other types of receptive field organization have been described in the cat lateral geniculate nucleus and striate cortex (*2*) and in the retinas of other animals (*3*). However, Stone and Fabian (*4*), by concentrating on the small ganglion cells of the area centralis, found 16 units whose organization was different from the center-surround type. Four of the units had receptive fields that produced an on-off response to a small spot of light anywhere in the receptive field. One of these four on-off units was direction-sensitive, two units had diffuse receptive fields, and the remaining ten did not appear to have a surround. More recently Spinelli (*5*) studied the response of ganglion cells to a flashing light in a sequence of positions in the visual field and interpreted his findings as new types of receptive field organization. However, Barlow *et al.* (*6*) have criticized this interpretation, arguing that spurious factors, such as the effect of stray light, are responsible for the response patterns obtained by Spinelli.

During a study of the maintained activity of retinal ganglion cells (*7*), two units were found that differed radically from those previously described. They both had the same response properties and were studied extensively with a variety of stimuli. They appear to represent a new type of receptive field organization here termed the suppressed-by-contrast type. The units were recorded extracellularly by the use of tungsten electrodes in the intact eye. One cat was decerebrate, the other anesthetized with nitrous oxide.

The location of each of these receptive fields was initially difficult to find. Yet when it was found and the effective visual stimuli discovered, the response was clear-cut and reproducible. Each unit had a receptive field estimated with small spots of light to be about 1.5° to 2.5° in diameter. Both were found medial to and above the area centralis. When a white disk (visual angle, 2°) before a gray background was moved into the center of the receptive field, the maintained firing was suppressed and remained so until the disk was removed. Upon removal of the disk there was no off-response characteristic of the off-center type of unit. The firing rate simply returned to the previous rate. When a black disk (visual angle, 2°) before the same gray background was moved into the receptive field, the firing rate was again suppressed and remained so until the disk was removed, at which time the firing rate returned to the previous value. Experiments with various edges, bars, annuli, parallel stripes, random patterns, and checkerboards at different contrasts and orientations all pointed to the same conclusion: The firing rate was suppressed by the presence of contrast in the receptive field. The nature of the contrast, the pattern, and the orientation of the pattern were not important in a qualitative sense. Perhaps the most dramatic response was observed with a large checkerboard pattern made up of black and white squares, 0.7° by 0.7°. This stimulus, presented to the second unit, completely suppressed the firing while it was over the receptive field. The pattern could be rotated and moved with velocities estimated to be up to 10°/sec yet the firing remained completely suppressed. Upon removal of the checkerboard pattern, the unit immediately returned to its previous firing rate. This stimulus, presented to units of the on-center or off-center type, invariably results in a strong activation.

Figure 1 illustrates the response of the first unit to moving black and white figures before a gray background. These figures moved, under servomechanical control (*8*), through the receptive field, first from left to right and then from right to left, at a constant velocity of 10°/sec. The graphs are histograms of averaged response and show the averaged firing rate of the unit to successive presentations of the stimulus. Response of center-surround units to this type of stimulus has been described (*8*).

The response of white figures before the gray background was much the same as for black figures before the same background (Fig. 1). The disks completely suppressed the firing as they passed through the receptive field. As the rectangles (5° by 10°) were larger than the receptive field, the leading and trailing edges suppressed the firing as they passed through this field, but the firing rate returned when the rectangle covered the receptive field.

Whereas a variety of stimuli suppressed the firing of the unit, no stimulus was found that produced an excitatory discharge. Only after a period of complete suppression (as in Fig. 1 for the 5° black rectangle) was the firing rate observed to rise above the prestimulus level. The gray screen could not be considered an excitatory stimulus because the firing rate in complete darkness was much the same.

Responses of both units to small flashing spots of light were similar. Every point on the receptive field gave the same type of response; but as the spot was moved to positions away from the center of the field the response became weaker. When the background luminance was low, turning the spot on suppressed the maintained firing; when the light was turned off the firing resumed. If the background luminance was increased to about 5 cd/m^2 (spot luminance 50 cd/m^2), there was a transient suppression when the light turned on or off. Immediately after increasing the background luminance to 5 cd/m^2, it was the flashing light turning off that produced the greatest transient suppression. After about half a minute it was the light turning on that produced the greatest suppression. Rapid (more than one per second) flashing of the light gave a complex response, but an increase in firing above the maintained rate was not observed. The units were therefore suppressed by a change in contrast as well as by the presence of contrast.

The second unit was antidromically invaded when the contralateral optic tract was electrically stimulated, thus demonstrating that it was in fact a retinal ganglion cell.

Two receptive fields are not many compared to the many that have been described as being of the center-surround type. If one assumes that the ganglion cells that I have studied are a representative sample of those present in the cat retina, then perhaps 400 out of the 86,000 present (*9*) belong to the suppressed-by-contrast type. Stone and Fabian (*4*) have commented on the difficulty of recording from the

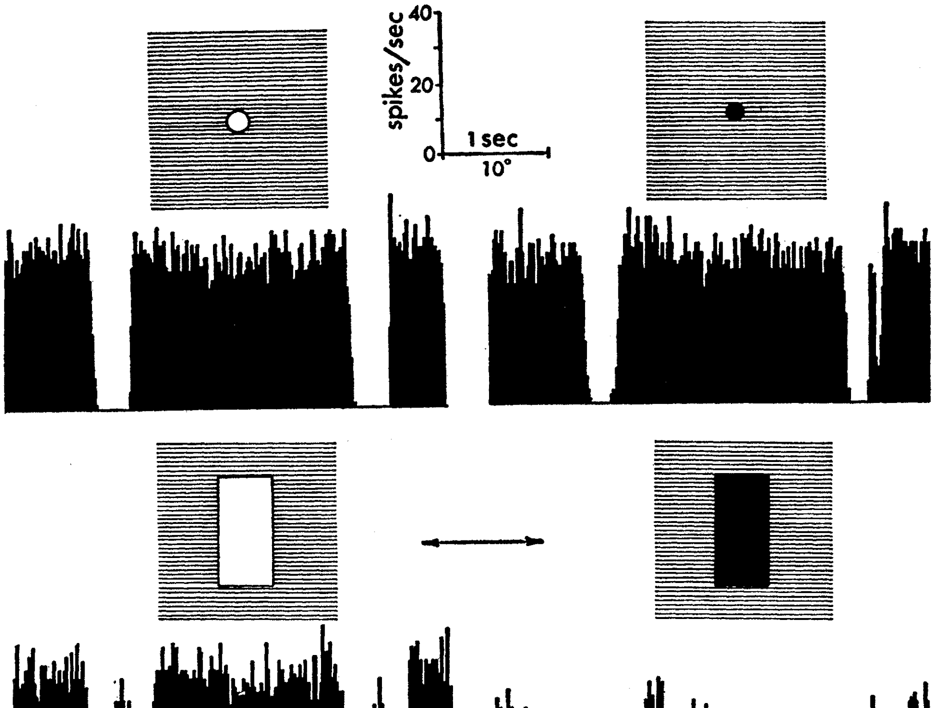

Fig. 1. Response of a suppressed-by-contrast unit to moving black and white paper figures before a gray paper background. The disks had a visual angle of 2°, and the rectangles were 5° by 10°. The figures moved at a velocity of 10°/sec through the receptive field, passing over the receptive field first from left to right and then from right to left; thus two responses are shown in each graph. The graphs are histograms of averaged response and show the averaged firing rate of the unit to 50 repetitions of the stimuli.

small ganglion cells of the area centralis (*10*), and I have experienced the same difficulty. If the tungsten electrodes preferentially recorded from larger ganglion cells and if most of the suppressed-by-contrast cells are small, it is possible that they are more abundant than the present sample of receptive field types would indicate.

Quantitative considerations aside, the suppressed-by-contrast type of receptive field is yet another to be explained in terms of retinal organization. This type of unit appears unique in sensory neurophysiology in that stimuli may suppress the firing but not increase it.

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The (±) Reference: Accuracy of Estimated Mean Components in Average Response Studies

Abstract. *The (±) reference is defined as the result of alternate addition and subtraction and division by* N *(the number of sample functions). Under suitable conditions both the (±) reference and the variable component (noise) of the usual average tend to be derived from the same Gaussian process, and the former can be used as a measure of the latter. This property is most easily applied when the noise is derived from a stationary process. Application of the (±) reference and the average of the square of the voltage in studies of evoked response is discussed.*

In recent years, biologists have begun to average random functions, particularly electrophysiological potentials, where the underlying mathematics is a combination of applied statistics and the theory of stochastic processes (random functions). Investigators using this technique have obtained new and important results but they generally have not applied measures of precision to their results. This could be due to the difficulty of the task. In this situation many investigators tend to distrust results obtained by averaging. For example, Perry (*1*) concluded a discussion of this question as follows: "Thus, disregard of noise in summation techniques weakens an otherwise impressive research tool."

It is the purpose of this report to clarify some of the problems attendant upon estimating the so-called "noise". A special kind of average is defined, called the (±) reference, which is computed by alternate addition and subtraction instead of by the usual addition. It is especially useful because its mean component is zero, while its statistical structure tends to be otherwise similar to that of the regular average. The computation of the (±) reference, whether for playback or on line, may be instrumented easily and inexpensively for a special-purpose averaging computer, either by manually or automatically alternating the "add" and "subtract" modes, or by alternating the polarity of the input.

The (±) reference, either alone or in conjunction with the average of squares, can be used in several ways (*2*): (i) for guiding the investigator in detecting and measuring mean evoked components; (ii) for indicating the nature of the variability of the evoked activity; (iii) for determining the size and structure of averaged ongoing background activity, including its frequency structure; and (iv) for revealing interaction between the stimulus and ongoing background activity.

Let v be the random function of time which is being studied. It will be assumed that v can be decomposed into the sum of two hypothetical components, u and x, where x is an oscillatory background component which is approximately stationary in the random process sense and is unaffected by the delivery of a stimulus, and u is taken to represent the activity evoked by the stimulus and is a nonstationary process. Neither u nor x nor their averages can be measured directly, but the decomposition hypothesis leads to interesting analytical results which can be tested empirically.

The following notation is used:

$\bar{v}$, $\bar{u}$, $\bar{x}$—the random functions obtained by averaging v, u, x, respectively, at each time point for N sample functions.

$\overline{\pm v}$, $\overline{\pm u}$, $\overline{\pm x}$—the special averages obtained by alternate addition and subtraction followed by division by N. The N is assumed to be even, and these special averages are called (±) references.

$\mu[\ ]$—the mean of the random variable in brackets.

$\sigma[\ ]$—the standard deviation of the random variable.

$\rho[\ ]$—the autocorrelation ratio for the random variable.

$\delta(\ )$—the deviation of the random function about its mean function (also a random function).

The functions μ, σ, and ρ are all deterministic functions of time; μ and σ, of one time point; and ρ, of two time points. The deviation from the mean, $\delta(\ )$, is frequently referred to here as the variable component of the random function. Mean as used here is called population mean by statisticians and mathematical expectation by mathematicians.

The following relations governing averages of random functions under independent sampling are readily derived from the mathematical definition of μ, σ, and ρ:

$$\mu[\bar{v}] = \mu[v]; \mu[\delta(\bar{v})] = \mu[\overline{\pm v}] = 0 \qquad (1)$$

$$\sigma[\bar{v}] = \sigma[\delta(\bar{v})] = \sigma[\overline{\pm v}] = N^{-\frac{1}{2}}\sigma[v] \qquad (2)$$

$$\rho[\bar{v}] = \rho[\delta(\bar{v})] = \rho[\pm v] = \rho[v] \qquad (3)$$

$\delta(\bar{v})$ *and* $\overline{\pm v}$ *both tend to be derived from the same Gaussian random process.* (4)

Equation 1 shows that the mean of the usual average, $\bar{v}$, is the same as that of the original function v. Equation 2 shows that the variability of $\bar{v}$ as well as that of $\overline{\pm v}$ has been reduced by a factor $N^{-1/2}$ as compared to the original random function, as measured by the standard deviation. This is the principal reason for averaging, and we call it the $N^{-1/2}$ principle.

Equation 4 is derived by application of the central limit theorem and is the fundamental mathematical rela-