Spatio-Temporal Visual Receptive Fields as Revealed by Spatio-Temporal Random Noise

Eiki Hida and Ken-ichi Naka

National Institute for Basic Biology, Okazaki, 444, Japan

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A means was devised to visualize the retinal receptive fields in time and space using the noise on unused television channels as spatio-temporal inputs and performing correlation between the input and output photographically. The method was applied to characterize the receptive fields of catfish retinal ganglion cells. The results were 1) there were two major types of receptive fields, circular and elliptical, 2) shapes and sizes of the field components changed with time (latency), and 3) a field's surround was often localized as hot spots.

Neurons in the vertebrate retina process information on the incoming light stimulus which fluctuates in time and space. The basic functional units of the process are known as the receptive fields defined in terms of cell's spatial filtering characteristics. Hartline [1, 2] saw a cell's receptive field as an area on the retina a stimulus given anywhere within elicited a certain cellular response and Kuffler [3] discovered the concentric receptive field which has since been seen in the bipolar and ganglion cells [3–6].

We report here the results from a new approach to measure the receptive fields by cross-correlating spatio-temporal random inputs with the resulting response: The theory which underlies our approach has been described in details [7].

Spatio-temporal random light-input was the noise seen on unused television channel, TV-snow, which was random scintillation in space and time, and correlation between the input and output was made photographically. The experiments were performed on the ganglion cells of channel catfish, *Ictalurus punctatus*. Spatio-temporal stimulus. TV-snow stored on a video-tape recorder (VTR) was replayed and the image of TV snow was focused on the retinal surface (the spatial resolution of the grains of the TV snow was about 0.2 mm). Spike discharges from the ganglion cell evoked by the stimulus were recorded on the voice channel of the VTR. The VTR tape with stimulus (original TV snow) on the video channel and the response on the voice channel was played backward and the stimulus was displayed on a TV screen. It was so adjusted that the presence of a spike discharge in a 20-msec bin brightend the TV screen for 20 msec at a given latency, τ, *i.e.* TV frames which, in the real experiments, produced a spike discharge after a latency, τ, appeared on the screen for 20 msec. A camera took a long-exposure picture of the TV screen for the entire sequence of experiment (normally about 5 min) to accumulate, so to speak, those TV frames which gave rise to a spike discharge with a given latency. This (cross-correlation) process was repeated for several values of τ's which were from 20 to 200 msec. Each accumulated picture (or correlogram) was a cross section of the (linear) spatio-temporal receptive field [7] and the (imaginary) solid formed by the series of accumulated pictures was the spatio-temporal receptive field which revealed the spatio-temporal image that a particular ganglion cell 'sees' at a fixed latency before the cell produces a response. The methodology we developed here did not make any a priori assumption on the organization of the receptive fields; the stimulus explored the entire receptive field with uniform weighting function to make our results 'unbiased'.

Out of 115 ganglion cells examined 102 cells gave rise to clearly defined spatio-temporal receptive fields; when the reference was made at a delay of 20 to 60 msec, 84 cells were of the off-center and 18 were of the on-center type (Fig. 1). The results we have obtained revealed several interesting features; 1) Receptive field components changed their shape and size as well as their magnitude in time in reference to the on-set of stimulus. Often the components reversed their polarity. Here we have shown explicitly the time dependency of a receptive field organization. 2) The receptive field surrounds were rarely concentric but appeared often as hot spots localized around a field's center (Fig. 2). The hot spots could be as large as the center to make distinction between a field's center and surround not as clearly defined as in other cells. 3) A field's center was either circular or elliptical in shape. In the latter case the major axis was parellel to the fish's field of view with the dimension of 1 mm (major axis) by 0.5 mm (minor axis). A similar skewed field was

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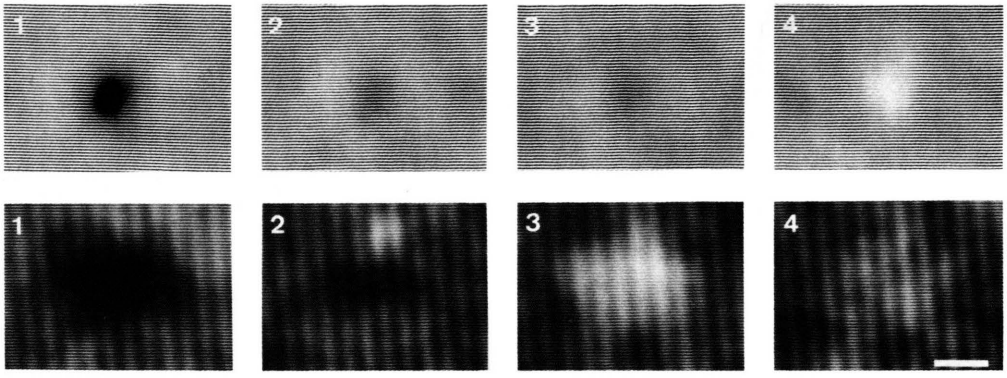

Fig. 1. Two spatio-temporal receptive fields (off-center type) shown as a series of two-dimensional (accumulated) stimulus patterns taken at different latencies; 60, 90, 120, and 150 msec for records '1' through '4'. The field in the upper row was a circular type and the one in the lower row an elliptical type. Dimming of the field's center was most likely to produce a spike discharge 60 msec later and brightening of the same area was most likely to produce a spike discharge 120 msec later. The changes in the fields' polarity took place sometime between 100- and 150-msec latencies. Note that in the lower record a small bright spot appeared with a delay of 90 msec on the ventral side of the field's dark center. In the figures, the ventral direction of the retina is for the upside of the frames. Calibration, 0.5 mm.

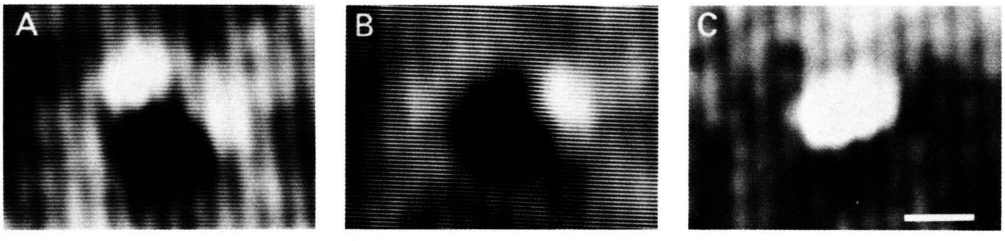

Fig. 2. Three examples of spatio-temporal receptive fields with localized surrounds or hot spots. A and B were off-center types and C was an on-center type. In the former fields their center appeared dark and their surround bright spots and in the latter field center is bright and its surround dark. Note that in all cases the localized surrounds were smaller in their dimensions than their field's center. All three patterns were the most efficient figures to produce a spike discharge 60 msec later. The regular vertical stripes were an artifact due to synchronization of TV frames. Calibration, 0.5 mm.

reported for the amacrine cells in the retina [8]. The organization of the circular and elliptical receptive fields changed with similar time course: the main difference was their spatial extent.

The results we reported here reflect only a field's linear component whereas the fields defined previously by such input as a flashing spot or an annulus of light included linear as well as nonlinear components. The fact that both measurements produced similar field configuration indicates that the basic organization of the catfish retinal receptive field was linear; a fact which should simplify our future attempt to unscramble the neural organization which produces a receptive field.

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