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The Shift-Effect in Retinal Ganglion Cells of the Rhesus Monkey*

J. Krüger, B. Fischer and R. Barth
Neurologische Universitätsklinik mit Abteilung für Neurophysiologie, Freiburg i. Br. (FRG)

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McIlwain's periphery effect [7, 1, 5, 6] and the shift-effect of Krüger and Fischer [2, 4, 6] are elicited by moving patterns, projected outside and at a long distance from the receptive field of retinal ganglion cells. The shift effects studied in the cat's retinal ganglion cells [4, 6] and lateral geniculate neurons [2] point to a visual information processing which is different from that performed by the classical receptive field mechanism and requires long range neuronal connections in the retina. So far, these effects were reported for cats only. This research report gives the first description of the shift effect in the monkey's retinal neurons.

In the present experiments the monkeys faced a projection screen. Artificial pupils 5 mm in diameter and contact lenses checked by retinoscopy were used. During the recordings both eyes were open. Extracellular spikes from axons of retinal ganglion cells have been recorded in the optic tract using the same surgical preparation, anesthetics, muscle relaxation and optical stimulation as in cats (for detailed description see [4]).

79 optic tract fibres have been recorded from two adult rhesus monkeys and in 63 of these the receptive fields could be located and classified as 40 on-center and 23 off-center neurons: In all these 63 neurons we observed phasic discharges following grating shifts in the periphery. These responses were elicited by eac displacement of a grating well outside the receptive field. An example is shown in Fig. 1a. The receptive field of this on-center neuron was adequately illuminated by a steady bright spot of 1.8 deg. in diameter separated by a large dark surround from the moving grating as indicated at the right of Fig. 1a. (Stationary area 40 deg. in diameter; amplitude of displacement, 2 deg.; velocity of displacement, 400 deg./sec). Under these conditions the response latencies were about 50 ms.

In most neurons an adequate steady visual stimulus was necessary to obtain the shift-effect, i.e. bright spots of suitably chosen size against a dark surround for on-center neurons, dark spots against a bright surround for off-center neurons, provided a steady background activation on which the shift response appears. In a homogeneous field of brightness or darkness the shift-effect was almost absent or at least weak. Reversing brightness and darkness in the stationary field illumination ("inadequate illumination") abolished the shift-effect in all units tested and in two neurons we observed a weak inhibitory shift-effect. Thirteen neurons whose receptive fields could not be located and which therefore could not be activated showed no shift-effect under homogeneous illumination. This does not prove, however, that they had no shift-effect.

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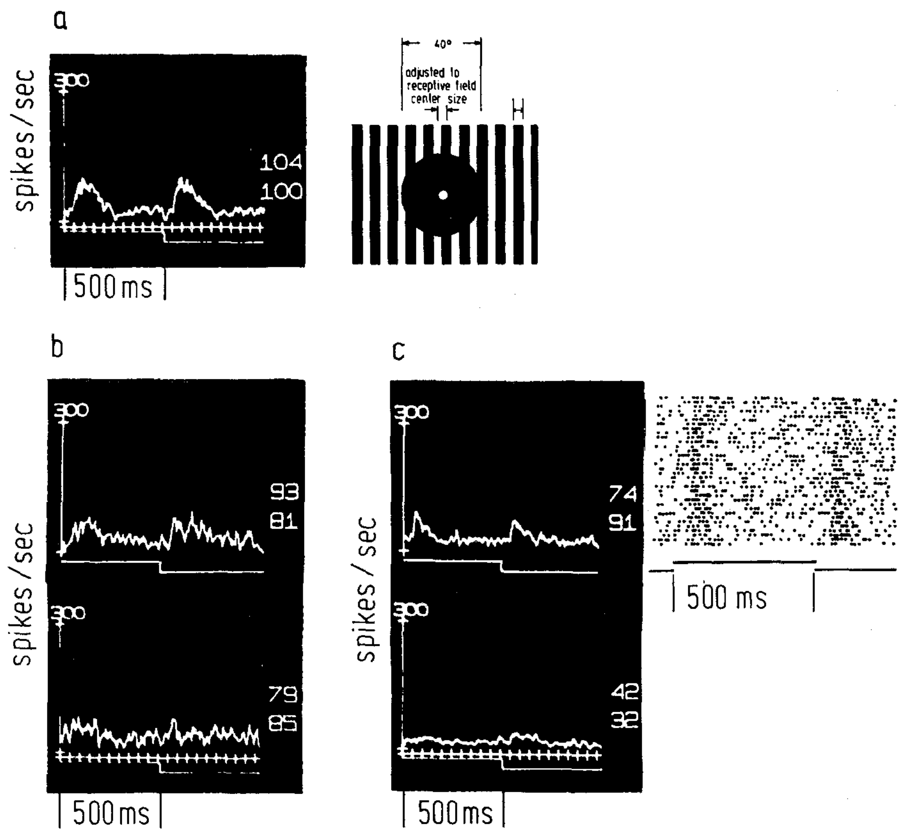

Fig. 1. Shift-effect in retinal neurons of rhesus monkey. (a) Shift responses of an on-center retinal ganglion cell and stimulus configuration. The grating is shifted to and fro in about 20° distance from the receptive field center. Blank area diameter 40 degrees; grating bar width and shift amplitude 2 degrees (arrows); stationary spot diameter 1.8 degrees: total pattern covering 100×100 deg. of the visual field. (b) Shift response of an off-center retinal ganglion cell after the introduction of a dark stationary center spot. Top: during the first 10 seconds, bottom: during the 50th—60th sec. (c) Shift response of the same neuron as in b. Top: A grating covered the total 100 deg. field including the receptive field (Bar width and shift amplitude 0.6 deg.). A slow drift of about 0.1 deg./sec was superposed on the grating shifts in order to exclude a stimulus configuration fortuitously symmetrical to the receptive field center. The dot display shows the similarity of all single responses. Bottom: Same grating restricted to the receptive field center. Other stimulus parameters unchanged. The ordinate in the post-stimulus time histograms is spike frequency, the numbers at right are peak frequencies in the two halves of the histogram (in spikes/second). A grating shift occurs each 500 ms (step trace below all frames). Ten to 60 stimulus presentations were averaged depending on the clarity of the response

Adaptation of the shift effect to the receptive field illumination was observed and studied in detail in five neurons. The upper record of Fig. 1b shows the shift-effect obtained during the first 10 sec after the introduction of the adequate stimulus (black spot in field center) for an off-center neuron. The lower record shows a diminution of the average response of the same neuron about 1 min later. When the grating shifts occuring each 500 ms were continued while the adequate center illumination was removed the shift response could be completely restored when the center spot reappeared after some time, and then the response gradually decreased again. Therefore the shift-effect adapted to the adequate receptive field illumination bud did not habituate to prolonged stimulations by displacements of the peripheral grating.

In the same off-center neuron of Fig. 1b, we also used a fine grating (stripes of 0.6 deg. width, Fig. 1c) which covered the total 100 deg. field including the receptive field. Sudden displacement of one bar width superimposed on a slow drift of about 0.1 deg./sec yielded the responses shown in the upper record of Fig. 1c. They are similar to those obtained under adequate illumination and have also a long latency. The dot display shows the similarity of the single responses. Finally, the grating covered only the receptive field and was moved again in the same way. The corresponding responses are shown at the bottom of Fig. 1c.

These results suggest that the shift-effect apparently is not restricted to regions beyond the limits of the receptive field or the peripheral retina but can be obtained from any part of the retina. As discussed by Fischer *et al.* [4] it is, however, difficult to ascertain that the shift effect can be elicited in the receptive field center alone, for the center mechanism might respond to gratings too fine to elicit a shift effect so that with coarser gratings a strong center response cannot be avoided, which may obscure the pure shift-effect. This may be the reason why the shift-effect is easily seen after moving stimuli in the peripheral retina but is less apparent in many neurons when the receptive field is included in the shifts of the grating.

In comparison to the cat the monkey's retinal shift-effect is of smaller amplitude and is more sensitive to the stationary spatial pattern stimulus in the receptive field. Similar to the cat the monkey's retinal shift-effect is excitatory in on- as well as in off-center neurons. In all cases where the shift-effect can be elicited also under homogeneous illumination simultaneous excitations occur in both subsystems. These responses are clearly distinguished from the reciprocal antagonistic responses after receptive field stimulation of the on- and off-center neurons.

The shift-effect points to lateral connections over very large distances between the receptors and the ganglion cells in the rhesus monkey retina. These long distance connections, possibly via amacrine cells, may serve as the basis for an extra processing of afferent visual information in combination with eye-movements as discussed earlier [3, 4].

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Dr. J. Krüger
Dr. R. Barth
Neurologische Univ.-Klinik mit Abt. für Neurophysiologie
D – 7800 Freiburg i. Br.
Hansastr. 9
Federal Republic of Germany

Doz. Dr. B. Fischer
Physiology Dept. Johns Hopkins University
735 N. Wolfe Street
Baltimore, Maryland 21205
USA