Visual Motion Detection in the Cat

Abstract. *Responses of some cells in the cat cortex to moving stimulation depend on direction of motion. These cells give neither "on" nor "off" responses to uniform illumination. Response can be elicited over a wide region of the retina in either eye, and the discharge pattern does not follow the temporal variations in luminance on the retina which accompany the movement of the stimulus.*

Afterimage effects of a moving stimulus, the phi phenomenon, and other phenomena (*1*), suggest that the sensory mechanism of vision may include a subsystem uniquely suited for motion perception. Evidence is accumulating for neural elements which respond specifically to movement in such species as the frog (*2*), the pigeon (*3*), the rabbit (*4*), and the cat (*5*). With moving stimuli, we have found variations in neural response in the cat with changes in luminance, stimulus pattern, direction of stimulus motion, and with binocular as compared with monocular stimulation.

Animals were prepared under ether anesthesia and maintained under a long-acting local anesthesia (*6*). They were immobilized by bulbo-spinal section and the administration of *d*-tubocurarine chloride. Eyes were held open and the corneas maintained moist with a regular flow of isotonic saline solution. The head of the animal was fixed in relation to a hood which excluded all light from the eyes except that coming from a 32°-diameter opal glass screen (0.5 millilambert). The eyes could be individually occluded.

In searching for active cells, a glass microelectrode filled with KCl was lowered into the brain through a 5-mm, open hole in the skull, while the shadow of a striated pattern of parallel lines and spaces of equal width (1° 26′) oscillated back and forth (2.5-seconds period) across the screen. The lines, vertical in mid-position, rotated through an angle of 36.4° during motion from one side to the other. Thus, during search, the stimulus moved with changes in angular orientation, direction, and rate. Maximum rate in terms of visual angle was 13.5° per second. Patterns were moved along a straight line during direction testing. Responses were displayed on a cathode ray oscilloscope and photographed along with synchronized displays of stimulus variation and the electroencephalogram.

A total of 140 units was studied in 25 animals. A characteristic "on" response to uniform illumination of the 32° field was obtained from 62 units, 38 gave a clear "off" response, 3 showed inhibition with both "on" and "off", and 37 gave either no response at all or none that could be consistently classified as "on" or "off."

Responses of "on" and "off" units correlated with variations in luminance at some fixed point as the moving pattern scanned past (Fig. 1). Response was independent of direction of motion. High discharge frequency, gradual adaptation, and a monophasic potential with a fast rising phase (<0.3 msec) suggested that some of these responses came from geniculo-striate fibers. Binocular sensitivity and a biphasic potential with a constant prepotential and a slower rising phase (>0.3 msec) suggested that other responses originated in cells within the cortex (*7*).

Some of the units which gave neither an "on" nor an "off" response to uniform illumination gave a nonrhythmic burst of activity to pattern motion independent of direction. Twenty-seven of these units responded nonrhythmically to movement only in certain directions and otherwise gave no response distinguishable from the resting level (Fig. 2). These units continued to respond when the direction was changed by as much as ±45° around the optimum. Stimulation seemed to require a component of motion in a specific direction, but it was not dependent on a precise setting of the direction. Movement in the appropriate direction of a single edge between a dark and a lighter region served as an effective stimulus of these cells quite independent of whether the dark region led or trailed the light region. They did not respond to a single light flash illuminating either a large uniform field, a small spot, or a stationary line pattern in any orientation. Spike discharge frequency of these units was increased by an intermittent light which flashed at some regular rate

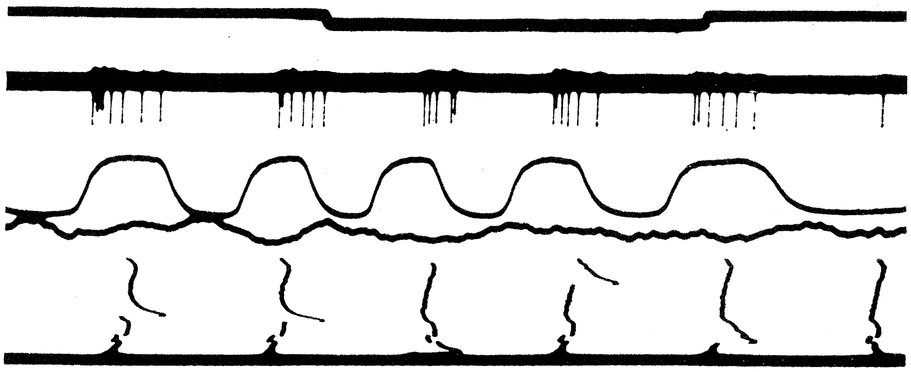

Fig. 1. Record of response of an "on" neuron to stimulation by a moving grid pattern. The top trace is a coded indication of direction of motion; the second trace represents neuronal discharge; the third trace is a photocell indication of variation in luminance at a fixed point as the pattern scans past; the fourth trace is the electroencephalogram; vertical records are spikes on an expanded time base. Responses of this type were never found to depend on direction of motion.

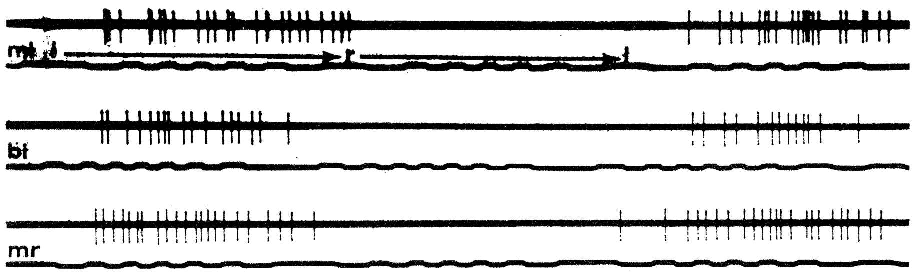

Fig. 2. Responses of a cell which depended upon direction of stimulus motion. Neuronal discharge is represented by the top and photocell response by the bottom of each pair of traces. Stimulus direction is left-to-right on the left, right-to-left in the middle, and left-to-right again on the right. Upper records were obtained with monocular stimulation of the left eye, middle records with binocular stimulation, and bottom records with monocular stimulation of the right eye.

between 5 and 10 per second, but the spikes showed no grouping in synchrony with the flashes. In general, these cells responded with either eye, although usually not equally. In ten cases the response to binocular stimulation was stronger, and in ten cases weaker, than the stronger response to stimulation of the eyes individually. Weaker responses may have resulted from the slight divergence which occurs when muscle relaxants are used and the consequent noncorrespondence of stimulation in the two eyes.

Responses of some cells to stimulation of one eye by movement in any direction were also reduced when both eyes were stimulated. Three cells, stimulated by movement in any direction, gave a nonrhythmic response which was much stronger for binocular than for monocular stimulation. These binocular effects again suggest that the responses originated in cells within the cortex.

A circular field stop, movable within the limits of the larger field, was used to determine whether responses of the various cells were specific to any region. In general, the rhythmic responses of on- and off-cells were strongly localized, while nonrhythmic responses showed much less localization and continued when the 5° field was displaced as much as 15° or 20°.

Luminance thresholds for response to the moving-line pattern, obtained with the use of neutral density filters, were found to fall between 0.001 and 0.01 mlam for all types of cells. Three units (one "on," one "off," one directional) stopped responding at luminances of from 5 to 14 mlam and resumed when luminance was again reduced. One neuron began to respond at 0.001 mlam for movement of the stimulus pattern from left to right. Response to both directions began at 0.004 mlam. For all units there was little change in response strength with change in luminance over the range in which any response occurred.

The effect on response of width of lines in the stimulus pattern was studied at a luminance of 0.5 mlam. The diffusing screen was located behind the pattern in order to achieve a sharper definition of the stimulus. Patterns were available with widths of 1°26′, 1°, 36′, 22′, 11′, and 5.5′. In no case could response be related to stimulus movement with certainty for patterns narrower than 22′. Usually, directional neurons did not respond to patterns narrower than 1°. All "on" and "off" neurons responded clearly to movement of the 1° pattern, and most to the 36′ pattern also. One unit responded clearly to movements of the 1° pattern in both directions but only from left to right with the 36′ pattern. These results probably were not limited by temporal resolution of the eye because pattern speed varied around zero. They do not afford a good measure of spatial resolution because sharpness of the retinal image was not controlled, but they do provide additional qualitative evidence as to the nature of the coding of information in cortical cells.

In the cat, neural elements which are excited specifically and uniquely by stimulus motion are apparently not found peripheral to the cortex (see *5*). Motion specificity is accompanied by response to retinal stimulation over a wide region and an accompanying reduction in the fidelity of response to temporal variations in stimulation at specific locations. These results must stem from convergence of many retinal cells on single cortical cells, but they do not fit any simple scheme. Restriction of "movement" cells to the higher visual centers, in contrast to the situation found in the frog, pigeon, and rabbit, may have some relation to the binocular vision of the cat, a capacity which frogs, pigeons, and rabbits lack.

GÜNTER BAUMGARTNER*
JOHN LOTT BROWN
Department of Physiology,
School of Medicine,
University of Pennsylvania,
Philadelphia 19104
ARNOLD SCHULZ
Department of Clinical
Neurophysiology, University of
Freiburg, West Germany

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6. Preliminary experiments indicate that the responses of certain cortical cells are altered qualitatively by general anesthesia. For this reason animals were maintained on a long acting local anesthesia, Depot-Novanaest in oily solution, which was injected subcutaneously and intramuscularly all around the head and at the point of exit of medial and lateral branches of the trigeminal nerve on both sides. We have found this drug to afford complete anesthesia of from 12 to 24 hours when used with human patients. Additional descriptions of the preparation are presented elsewhere: G. Baumgartner and P. Hakas, *Pflügers Arch.* **274**, 489 (1962); G. Baumgartner, J. L. Brown, A. Schulz, *J. Neurophysiol.*, in press.
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* Permanent address: Department of Clinical Neurophysiology, University of Freiburg, West Germany.

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Separation of the Salivary and Motor Responses in Instrumental Conditioning

Abstract. *If an instrumental conditioning schedule is arranged so that a dog must repeatedly perform a movement in response to one stimulus in order to secure the presentation of another stimulus, which is then followed by food, a virtually total separation of motor and salivary responses is observed. The first stimulus elicits the trained movement without salivation, and the second stimulus elicits salivation without instrumental responding. These experiments show a relative independence between classical and instrumental conditioned responses and clarify the rather complex relations between the two in the usual experimental procedure.*

In early papers by Konorski and Miller (*1*) a method was described for studying the relations between the salivary and the motor responses in instrumental conditioning. According to the views then held by these authors, the instrumental response produced its proprioceptive feedback which became a classical conditioned stimulus signaling the presentation of food. In consequence it was predicted that salivation should closely follow the instrumental response.

However, their own experimental data (*2*), as well as those of later workers (*3*), showed that although in many cases the predicted relation is in fact observed, in others large discrepancies exist between the two responses: the motor response may be either preceded by the salivary response, or the two responses may not even coincide at all. The origins of these discrepancies have been poorly understood, and the causal relation between the salivary and instrumental responses has remained obscure. The experiments reported here were designed to clarify this situation.

The subjects were four mongrel dogs trained in the following manner: first a classical conditioned response (for