



## Selective Sensitivity to Direction of Movement in Ganglion Cells of the Rabbit Retina

Horace B. Barlow; Richard M. Hill

*Science*, New Series, Vol. 139, No. 3553. (Feb. 1, 1963), pp. 412-414.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2819630201%293%3A139%3A3553%3C412%3ASSTDOM%3E2.0.CO%3B2-X>

*Science* is currently published by American Association for the Advancement of Science.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/aaas.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

orientation. In wide troughs, spreading is symmetrical, except for a bias at the edges, and the trough is demarcated by the selective accumulation of groups of cells.

In the case of substrata composed of stearic acid-barium stearate, the interaction between serum components, especially albumin fractions, skeletonizes the multilayers by the selective solubilization of stearic acid molecules residing in the upper five to ten layers. This "ripping off" reaction has been described by Sher and Sobotka (6). No such reaction occurs when behenic acid-barium behenate is used as the substratum. Consistent with the absence of this reaction for behenic acid is the observation that the minimum trough depth for alignment was 60 Å in behenic acid multilayers and 200 Å in stearic acid multilayers.

The experiments point to the change in physical thickness of the multimolecular films and concomitant alterations in the adhesivity and spreading rates as the principal factor underlying this phenomenon. Similar phenomena should be observed when cells contact any surface whose molecular composition in either a spatial or temporal sense provides regions of variegated cell adhesivity. Thus cells are trapped within troughs even on chrome-plated glass if the floor of the trough reaches down to the glass, to which cells adhere more readily.

The mechanism whereby cells sense alterations in their substrata as small as 60 Å remains obscure. Though the diameter of the cells studied was roughly 200,000 Å, many cell types are known to possess surface projections or "microfibrils" roughly 1000 Å in diameter (7). These or similar microprotrusions may serve as sensing elements capable of responding to small changes in the physical structure of molecular carpets in contact with cells. Additional experiments are necessary to determine their function. However, regardless of the mechanism underlying this highly sensitive interaction between cell and substratum, it has been demonstrated that the molecular composition of surfaces can play a salient role in directed cell contact, aggregation, and movement (8).

MURRAY D. ROSENBERG  
Rockefeller Institute, New York 21

#### References and Notes

1. R. C. Harrison, *J. Exptl. Zool.* **17**, 521 (1914).
  2. P. Weiss, *Arch. Entwicklungsmech. Organ.* **116**, 438 (1929).
  3. ———, *Intern. Rev. Cytol.* **7**, 391 (1958).
  4. M. D. Rosenberg, *Proc. Natl. Acad. Sci. U.S.A.* **48**, 1342 (1962).
  5. K. B. Blodgett, *J. Am. Chem. Soc.* **57**, 1007 (1935).
  6. I. H. Sher and H. Sobotka, *J. Colloid Sci.* **10**, 125 (1955).
  7. G. O. Gey, *Harvey Lectures, Series L* (Academic Press, New York, 1954); A. C. Taylor and E. Robbins, *Develop. Biol.*, in press.
  8. This research is supported by grants from the American Cancer Society and the National Institutes of Health, U.S. Public Health Service, to Paul Weiss as principal investigator.
- 2 January 1963 ■

## Selective Sensitivity to Direction of Movement in Ganglion Cells of the Rabbit Retina

**Abstract.** *Among the ganglion cells in the rabbit's retina there is a class that responds to movement of a stimulus in one direction, and does not respond to movement in the opposite direction. The same directional selectivity holds over the whole receptive field of one such cell, but the selected direction differs in different cells. The discharge is almost uninfluenced by the intensity of the stimulus spot, and the response occurs for the same direction of movement when a black spot is substituted for a light spot.*

The great sensitivity of retinal ganglion cells to movement of a pattern of light over the retina has been recognized since Hartline's work on the frog (1). Hubel and Wiesel presented evidence that certain cells in the cat's cortex respond, not to any movement, but only to movement in a particular direction (2). Reports of similar directional selectivity have been made on the retina and optic tectum of frog (3), on the cortex of cat (4), on the lateral geniculate of rabbit (5), and most re-

cently on the retina of pigeon (6) and the tectum of rabbit (7). The extraction of information as to direction of motion is a surprisingly complex task for a few synaptic layers to perform, and some doubt remained in our minds as to whether a simpler explanation of apparent directional selectivity had been adequately excluded.

Hartline showed that "off" units in the frog responded to any diminution in the total contribution from all parts of the receptive field to the ganglion

cell (1). As well as responding to dimming of a uniform light, they also responded to movement of a spot of light away from the most sensitive central zone of the receptive field. In such a unit, if a stimulating spot is moved to and fro over the edge of the receptive field one may easily obtain records showing a discharge to movement in one direction, and not in the opposite direction. It would be misleading, however, to call this directional selectivity, for if other regions of the receptive field are explored the direction of movement giving the maximum discharge will not be constant; it will always tend to lie on a line away from the center of the receptive field. On the other hand, a unit showing true selectivity for direction should show the same direction of preference in all parts of its receptive field. A similar argument applies to contrast; a unit which is genuinely selecting out direction of motion should show the same preference regardless of contrast, whereas Hartline showed that the frog's "off" units discharged when a shadow moved towards the center of the receptive field, not away from it as with bright stimulus spots.

The receptive fields of most of the cells for which directional sensitivity has been reported are more complex than those of the "off" units investigated by Hartline, and we originally felt that an explanation in terms of a change in the pooled excitatory and inhibitory contributions from all parts of the receptive field had not been excluded except for certain cortical neurons (2). However, we have found that about one-third of the units isolated in the rabbit's retina show a movement sensitivity in which the direction of preferential response is invariant in different parts of the receptive field, and is invariant for changes in contrast. We think this excludes simple explanations of the type outlined above, and shows that retinal units can be genuinely directionally selective.

Single retinal units were isolated by a technique similar to that of Kuffler (8). The rabbits were lightly anesthetized with urethane, or in some cases decerebrated under ether. Figure 1 shows the response of a unit to movement of a spot of light all the way across its receptive field. It is clear that movement in a posterior-anterior direction evokes a vigorous discharge, whereas movement from anterior to posterior evokes none. We were sure

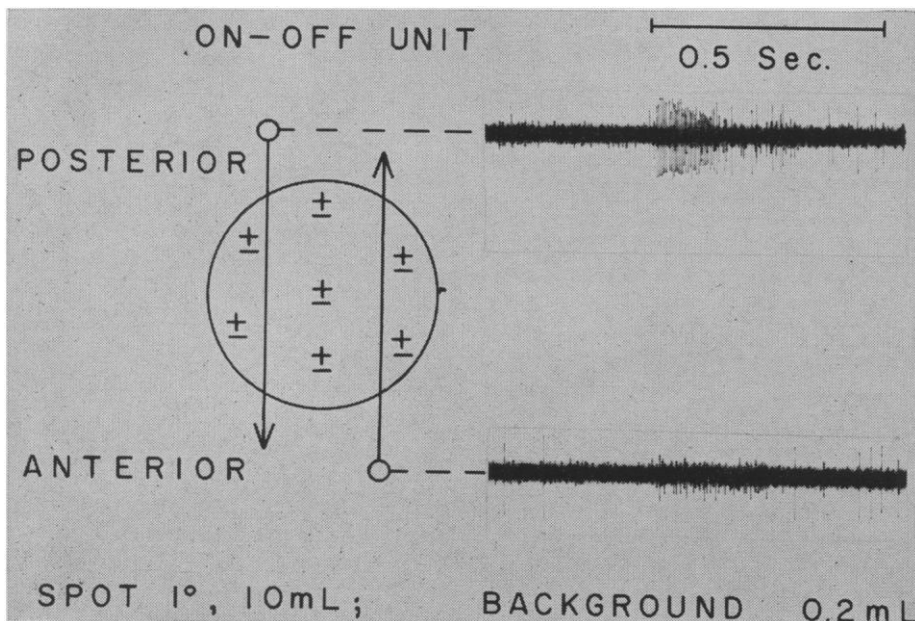


Fig. 1. A spot of light is moved right across the receptive field of an "on-off" unit. It responds to movement from posterior to anterior, but not to movement from anterior to posterior. Thus it shows directional selectivity. A second unit is visible which responds to antero-posterior movement.

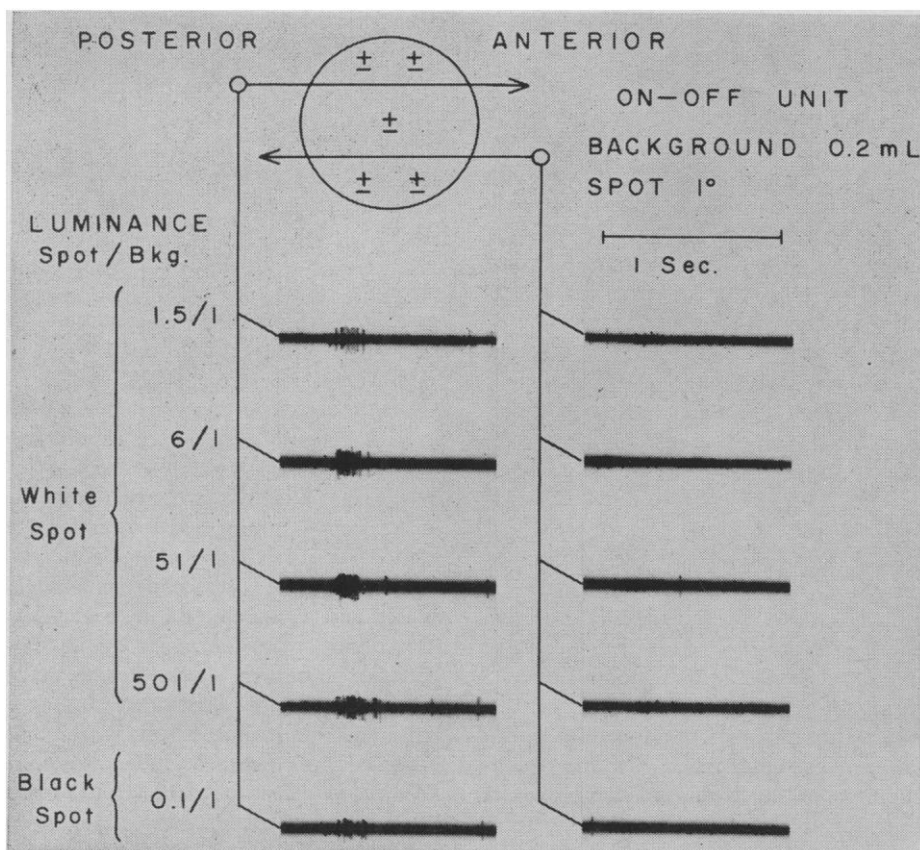


Fig. 2. Effect of intensity and reversal of contrast on response to movement. The spot is moved through the field of an "on-off" unit first from posterior to anterior, then in the reverse direction. For the top four records the spot was brighter than the background, the ratio of luminances being indicated on the left. The ratio just eliciting a discharge was about 1.2 to 1. However, when the spot was darker than the ground a response was again obtained and occurred for the same direction of motion as with a bright spot.

that the spot traversed the whole receptive field because this had previously been explored by turning on and off the same stimulus spot (10 millilamberts,  $1^\circ$  diameter, background illumination 0.2 mlam). As in most units showing directional selectivity, discharges were obtained at both "on" and "off," even at the center of the receptive field. They are thus similar to the "on-off" units in the frog (9). However directional selectivity is not only found in association with this type of field; we have occasionally found it in units for which "on" and "off" thresholds differed greatly.

Many units in the rabbit have concentric "on" and "off" zones, as in the cat (8). These are sensitive to movement, but the greatest discharge tends to occur for centrifugal or centripetal motion. The receptive fields of the units shown in Figs. 1 and 2 were approximately  $5^\circ$  in diameter.

It has been suggested that the asymmetry of the directionally selective units was caused by damage or optical effects of the electrode itself. This is excluded by the fact that we have observed it when recording from fibers, in which case the field is some distance from the electrode.

Figure 1 shows an expected, smaller, second set of action potentials which appear for movements that cause little activity in the larger unit. This is important for it shows that the selected direction of sensitivity is diversified, and is not the same in all units.

Figure 2 shows invariance of response for changes in contrast. Changing the intensity of the moving spot over a range of 1000 : 1 has little influence on the discharge. The lowest line shows the response when a black dot on a large white card is moved through the receptive field. Reversing the contrast only reduces the discharge in the favored direction by a small amount and does not result in a greater discharge in the opposite direction.

In summary, four main characteristics differentiate units that have genuine directional selectivity from other types of units. First, movements of a spot of light completely across their receptive fields produce a discharge from certain directions only. Second, the same directional preference is shown for spots darker or brighter than the background. Third, the discharge varies little for big changes in intensity of a bright spot. And fourth, these units commonly (but not invariably) yield both "on" and

"off" responses at all points within their borders.

We believe these observations exclude simple explanations of movement sensitivity in terms of pooled effects from "on" and "off" zones of the receptive field. Exploration with a stationary spot turned on and off, and noting the phase at which a discharge occurs, does not provide a sufficient basis for predicting the response to a moving spot. In addition it is clear that two synaptic layers can abstract direction of motion from the spatio-temporal pattern of light falling on the retina, and that the rabbit possesses such a system of directionally selective ganglion cells in its retina (10).

HORACE B. BARLOW\*

RICHARD M. HILL

University of California, Berkeley 4  
School of Optometry

#### References and Notes

1. H. K. Hartline, *Am. J. Physiol.* **130**, 690 (1940).
  2. D. H. Hubel, and T. N. Wiesel, *J. Physiol.* **148**, 574 (1959); **160**, 106 (1962).
  3. J. Y. Lettvin, H. R. Maturana, W. S. McCulloch, W. H. Pitts, *Proc. I.R.E. (Inst. Radio Engrs.)* **47**, 1940 (1959).
  4. J. O. Grüsser, personal communication (1962).
  5. G. Arden, personal communication (1962).
  6. H. Maturana, Information Symposium Proceedings of the XXIII International Union of Physiological Sciences, Leiden (1962).
  7. K. P. Schaeffer, *Proc. Intern. Union Physiol. Sci. Part 2*, **1**, 496 (1962).
  8. S. W. Kuffler, *J. Neurophysiology* **16**, 37 (1953).
  9. H. K. Hartline, *Am. J. Physiol.* **121**, 400 (1938); H. B. Barlow, *J. Physiol.* **119**, 69 (1953).
  10. The work was supported by U.S. Public Health Service grants B-3843 and B-3154.
- \* On leave of absence from the Physiological Laboratory, Cambridge, England.

23 November 1962

### Bonding in Xenon Fluorides and Halogen Fluorides

**Abstract.** *The bonding in rare gas fluorides is similar to that in halogen polyfluorides, and the stability of such compounds should depend primarily on the ionization potential of the central atom. This theory is consistent with findings for all known compounds of the system and yields predictions concerning other systems.*

The very interesting discovery of stable xenon and radon fluorides (1) raises questions concerning the nature of the chemical bonding in these molecules. Two notes have been published on this topic (2), but neither offers a criterion of stability for rare gas fluorides, nor do they consider the various interhalogen compounds, such

as BrF<sub>5</sub>, which should be closely related to rare gas fluorides. Since there may be real advantage in considering these two types of molecules at the same time, further discussion seems desirable.

The properties of the interhalogen compounds have been reviewed recently (3), hence only a few of the most pertinent features are mentioned here. The diatomic species such as ClF have normal electron pair bonds and may be considered analogous to the rare gas atoms in that their normal valence shells are filled. It is the bonding of additional fluorine atoms to the chlorine of ClF to yield ClF<sub>3</sub> (or to yield BrF<sub>3</sub> or BrF<sub>5</sub> from BrF) (4) that is analogous to the formation of XeF<sub>2</sub> and XeF<sub>4</sub>.

The structures of ClF<sub>3</sub>, BrF<sub>3</sub>, BrF<sub>5</sub>, and IF<sub>5</sub> all show a pattern of approximately 90- and 180-degree bond angles with one especially short X—F bond and one or two pairs of linear three-atom arrays, F—X—F, with slightly longer X—F distances. The result is a planar T-shaped structure for the XF<sub>3</sub> and a square pyramid for the XF<sub>5</sub> molecules, respectively. These structures are readily explained by *dsp*<sup>3</sup> and *d<sup>2</sup>sp<sup>3</sup>* valence shells for the central atom, with the two and the one position occupied by unshared electron pairs, respectively, for XF<sub>3</sub> and XF<sub>5</sub>. However, the data on the nuclear quadrupole coupling indicate that the central atoms have a substantially smaller electron population than would be expected for covalent bonds on this pattern (5).

Since the fluorine nucleus has no quadrupole moment, one cannot apply this method of determining electron population to the terminal atoms in the fluorides, but it has been applied in the case of the iodine chloride molecules and ions. Cornwell and Yamasaki (6, 7) have shown that in the series ICl, ICl<sub>2</sub><sup>-</sup>, ICl<sub>4</sub><sup>-</sup>, the chlorine atoms carry a substantial negative charge (over 1/2 *e* in the negative ions), while the iodine atoms are correspondingly positive. These results, which follow from the *p*-orbital populations, as determined by the quadrupole-coupling results, account quite well for the electron population, leaving at most a small participation of *d* orbitals for these compounds.

There seems every reason to expect that the more electronegative fluorine atoms are similarly negative and that the bonding pattern proposed by Yamasaki and Cornwell (7) for the iodine chlorides is applicable equally to the

Table 1. Ionization potentials of the atoms of interest and the fluorides reported to form in each case.

Atom	Ionization potential (ev)	Fluorides formed
I	10.44	IF, IF <sub>5</sub> , IF <sub>7</sub>
Br	11.84	BrF, BrF <sub>3</sub> , BrF <sub>5</sub>
Xe	12.13	XeF <sub>2</sub> , XeF <sub>4</sub>
Cl	13.01	ClF, ClF <sub>3</sub>
Kr	14.00	

halogen fluorides and the xenon fluorides. In this pattern there are two molecular orbitals involved in the bonding of each linear array of three atoms (for example, F—Br—F or Cl—I—Cl). The first molecular orbital is composed of the central-atom *p* orbital along the particular axis, together with the antisymmetric (bonding) combination of terminal-atom *σ* orbitals. The second molecular orbital is composed primarily of the symmetric combination of terminal-atom *σ* orbitals and has only very small components of central-atom *d* or *s* orbitals. It is evident that the filling of these two molecular orbitals yields essentially a half covalent bond and a half ionic bond for each linkage.

Let us now consider the process in which an array F—X—F is formed from *X* (for example, ClF or Xe) and F<sub>2</sub>. The net energy change may be written as

$$\Delta E = I(X) - E(F) + D(F_2) - B(F-X-F) \quad (1)$$

Here, *I* is the ionization potential of *X*, *E* is the electron affinity of F, *D* is the dissociation energy of F<sub>2</sub>, and *B* is the binding energy of F—X—F formed from X<sup>+</sup> + F<sup>-</sup> + F. *B* contains effectively the electrostatic energy of the ionic bond, together with the covalent bond energy diminished by any non-bonded repulsive terms. The two middle terms in  $\Delta E$  do not depend on *X* at all, and it seems unlikely that the dependence of *B* on *X* is very great (8). Consequently, we may expect that *I*(*X*) will be the factor which effectively decides whether or not these F—X—F linkages are stable.

Table 1 gives the ionization potentials of the atoms of interest, together with the fluorides reported to form in each case. It is interesting to note that for the reaction XF<sub>3</sub> = XF + F<sub>2</sub> the literature values (3) for  $\Delta H$  are 1.1 ev for ClF<sub>3</sub> and 2.1 ev for BrF<sub>3</sub>. The difference of 1.0 ev is close to the difference in ionization potential (1.17 ev), as expected from our theory. It