Reprint Series
9 April 1982, Volume 216, pp. 204–205

SCIENCE

# Receptive Fields and the Optimal Stimulus

David G. Stork, John Z. Levinson, Duane G. Albrecht, Russell L. De Valois, and Lisa G. Thorell

Copyright © 1982 by the American Association for the Advancement of Science

## Receptive Fields and the Optimal Stimulus

Albrecht *et al.* (*1*) have suggested that the "spatial frequency channel" hypothesis provides more insight into the functional nature of visual cortical neurons than does the bar-width, or "size" view. They also pointed out that their results—that such cortical cells in both the cat and the monkey are more sharply tuned to gratings than to bars—are consistent with an opponent center-surround receptive field (RF) with subsidiary disinhibitory flanks.


0036-8075/82/0409-0204$01.00/0 Copyright © 1982 AAAS

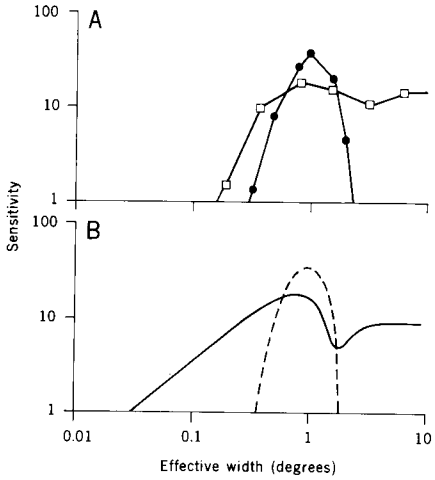


Fig. 1. (A) Sensitivity for bars (squares) and gratings (circles) for a complex cell in the striate cortex of a cat [from (*1*)]. (B) Theoretical functions.

We convolved a simple, one-dimensional RF, such as they suggested, with bars and gratings. The computer-generated curves contain virtually all the salient features of the Albrecht *et al.* data (relative bandwidths and amplitudes, lack of drop-off of bar sensitivity at large effective widths, and so forth) (Fig. 1). The overall concordance between experiment and theory suggests that "frequency channels" and "bar detectors" imply each other, and that a cell's response might also be well characterized in terms of the RF directly.

Albrecht *et al.* stated, "The optimum stimulus for a cell is conventionally considered to be that which evokes the largest response." They, and others, searched for this largest response on the basis of the constraint of constant stimulus contrast, or equivalently (for a linear system), they vary the contrast until a criterion response is elicited. Motivated by the significance of the RF itself, we suggest an alternate constraint, that of constant "energy," $E$, defined (in analogy to the energy in a physical wave) as:

$$E = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} |s(x,t)|^2 \, dx \, dt$$

where $s(x,t)$ gives the deviation of the luminance from its mean value as a function of position and time (*2*). The stimulus that maximizes response under this constraint, we call the "optimal stimulus."

The virtue of this criterion is that the optimal stimulus gives quantitatively the detailed spatial and temporal properties of the RF: Its spatial distribution is that of the RF, and its temporal history (reversed in time) "matches" the system's impulse response function (*3*). Thus, by successive approximations through a set of trial stimuli, or appropriate response-stimulus feedback loop, the spatiotemporal properties of the system can be deduced (*4*). These properties include phase information, which is not revealed by grating and flicker sensitivity curves.

In short, the frequency channel and optimal stimulus (or RF) descriptions are compatible and both should be in the repertoire of the physiologist and psychophysicist.

DAVID G. STORK
*Departments of Physics* and
*Psychology, University of Maryland, College Park 20742*
JOHN Z. LEVINSON
*Department of Psychology, University of Maryland*

### References and Notes

1. D. G. Albrecht, R. L. De Valois, L. G. Thorell, *Science* **207**, 88 (1980).
2. J. Z. Levinson, *J. Opt. Soc. Am.* **58**, 1558 (1968).
3. G. L. Turin, *IRE Trans. Inf. Theory* **IT-6**, 311 (1960).
4. Since submission of the original version of this comment, A. Watson, H. Barlow, and J. Robson reported optimal stimuli for humans, determined psychophysically (paper presented to the annual meeting of the Association for Research in Vision and Ophthalmology, Sarasota, Fla., 26 April to 1 May 1981).
5. This work was supported by grant EY01640 from the National Institutes of Health. We would like to thank D. S. Falk and R. M. Steinman for helpful comments.

29 July 1980; revised 18 September 1981

Using a relatively simple set of geometric patterns (lines, edges, spots), Hubel and Wiesel (*1*) were able to derive the spatial receptive field (RF) properties of visual cortical neurons. We and others (*2, 3*) have since characterized the spatial properties through the use of spatial frequency grating patterns. In a linear system, these two descriptions (space domain and frequency domain) are mathematically equivalent; we have in fact demonstrated the equivalence of these two descriptions for simple cells (*4*). Thus, while not surprising, it is nevertheless reassuring to know that Stork and Levinson (*5*) were able to generate theoretical predictions (based upon linear assumptions and a receptive field structure such as the one we, and others, have demonstrated) in agreement with the results of our experiments (*6*).

However, it is erroneous to equate the space domain description of striate cells (the spatial RF) with the term "bar detector" (an error Hubel and Wiesel were careful *not* to make). It must be emphasized that a linear spatial filter with tuning comparable to what is found in the striate cortex would make an extremely poor bar detector, providing totally ambiguous information concerning bar width. The main point of our experiment was the demonstration that cortical cells are simply not selective along the dimension of bar width. An adequate bar detector would require a different type of RF structure than what is found in the visual cortex. This fact is evident in the empirical results of our study as well as the theoretical results of Stork and Levinson.

When considering the functional significance of the spatial-analytic capabilities of striate cells, one must keep in mind the idealized nature of these mathematical descriptions: no physical system can span the infinite distance required to isolate a single sine wave for a pure frequency domain description, and similarly no physical system can isolate an infinitesimal spatial impulse for a pure space domain description. Practical considerations force the essential dual characteristic. An ideal system should provide maximum conjoint localization in both domains—space and frequency—comparable to the spatial tuning of visual cortical neurons (*7*). We certainly agree that the analytic tools of vision research should include both descriptions: spatial receptive fields and spatial frequency tuning.

DUANE G. ALBRECHT
*Department of Psychology, University of Texas, Austin 78712*
RUSSELL L. DE VALOIS
*Department of Psychology, University of California, Berkeley 94720*
LISA G. THORELL
*IBM Corporation, Kingston, New York 12401*

### References and Notes

1. D. H. Hubel and T. N. Wiesel, *J. Physiol. (London)* **148**, 574 (1959); *ibid.* **160**, 106 (1962); *ibid.* **195**, 215 (1968).
2. See, for example, references 8 and 9 in (*3*); R. L. De Valois and K. K. De Valois, *Annu. Rev. Psychol.* **31**, 309 (1980).
3. D. G. Albrecht, R. L. De Valois, L. G. Thorell, *Science* **207**, 88 (1980).
4. D. G. Albrecht, thesis, University of California (1978); R. L. De Valois, D. G. Albrecht, L. G. Thorell, in *Frontiers of Visual Science*, S. J. Cool and E. L. Smith, Eds. (Springer-Verlag, New York, 1978); L. G. Thorell, thesis, University of California (1981); J. A. Movshon, I. D. Thompson, D. J. Tolhurst, *J. Physiol. (London)* **283**, 53 (1978).
5. D. G. Stork and J. Z. Levinson, *Science* **216**, 205 (1982).
6. In (*3*), we emphasized that our results were consistent with the notion of "linear summation of excitation and inhibition within receptive fields with spatially antagonistic regions" (p. 88); we have shown elsewhere (*4*) that the linear filter predictions are in accord with the measured bar versus grating responses; further, we interpreted our data within both the space domain and the frequency domain perspectives (*3*, p. 90).
7. Guided by analogies to quantum mechanics, Gabor has investigated this dual characteristic of an information sampling system and has provided an elegant and rigorous discussion of the basic issues [D. Gabor, *J. Inst. Elect. Eng.* **93** (Part 3), 429 (1946)]; Marcelja has clearly demonstrated the relevance of Gabor's "theory of communication" to visual cortical function [S. Marcelja, *J. Opt. Soc. Am.* **70**, 1297 (1980)].

26 January 1982