

19.0 Physiology

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Three or four studies have been issued in the past year from the laboratory of nervous physiology. These are diverse and will be treated separately. We report only on that work is now in print or are ready to be published.

19.1 Strategies of Perception

Gad Geiger, Jerome Lettvin

Three years ago we began studies on peripheral vision. Two papers have been issued, announcing some of the results.^{1,2} These papers are explicit and do not much go beyond the data. It is useful to lay forth here a more general account of the underlying ideas and the meaning of our results. These results are presented first in a cursive way.

There is a visual process, called “lateral masking,” by which aggregates of forms take on a textural quality. For example, text presented a few degrees away from the center of gaze is clearly text, but not easily read. It is as if the letters in a group interfere with each other, so that the clear perception of any one letter is compromised. This can be shown not to depend on acuity, which is quite high for peripheral vision in the vicinity of the fovea. For perception such an aggregate seems to possess at best a statistics rather than a precise spatial order. There is a distribution of letter like things, and in this distribution the interior members are clear but not distinct. That is easy enough to check by fixing your eye on some letter in the middle of a line and finding that you can't read those words of three or more letters in length, that lie two words away from the point of fixation.

We showed that the information needed to identify an ordinarily masked letter in the near peripheral field, is not lost by some early visual process since the letter can be made to stand out from the texture when its twin is presented at the point of fixation.

In the course of these experiments we noted that a few subjects did not seem to show much lateral masking in the near periphery. They scored remarkably accurately in identifying each of the letters in short strings of letters presented as far as 10 (degrees) away from the point of fixation. These subjects, interviewed after the study was completed, shared a common property, dyslexia.

Accordingly we were led to compare dyslexics with ordinary readers. To put the results succinctly, dyslexics tend to have visual masking in and around the center of gaze, and much less a few degrees away from that center - the reverse of what holds for ordinary readers.

We devised a series of simple tests that distinguished clearly three populations: ordinary readers, residual dyslexics (who had learned to read), and severe dyslexics (who could hardly read). In the severe adult dyslexics we then showed what we had

suspected - that they could learn to read using their peripheral vision. When members of this last group learned to read, they began to show increased masking in the further periphery and a relief of the severe masking immediately around the region of foveal vision. (We now have about fifteen such cases but this material is not yet published).

Our view is that masking is a learned process, strongly task-dependent. It is not intrinsic to visual process in the sense that it follows immutably from some anatomical and physiological imperative. Instead it is a convenient learned way of reducing task-irrelevant detail to texture, while preserving task-relevant detail as form. Most important to us, learning the strategy of masking depends strongly on the motor aspects of practice in performing tasks. This much can be inferred by analogy with the studies on hand-eye coordination done by Richard Held, Ivo Kohler and others. We took advantage of this prior work in designing the pedagogy by which we could bring adult dyslexics from 3rd grade level to 10th grade level over about four months.

But we have gone further in our concept of such processing. We feel that most of us have several task-determined strategies between which we switch on the instant, (tantamount to flipping between modes of operation), as the task requires. Again, such switching has been described for more complex forms of perception by Kohler, Held, and others, so it should come as no surprise that the same principle may hold on elementary levels. What is most interesting is that, as with dyslexics, a strategy can become "frozen."

Since we can now show these attributes of vision both psychophysically and clinically, we feel that the ideas have some strength. Clearly a more precise account is needed, and, indeed, we have one, but it is not easily compressed to the sort of sketch appropriate here.

19.2 Image Sharpening in the Photoreceptor Layer of the Eye

Jerome Lettvin and Gill Pratt

A century ago, Helmholtz remarked that he would summarily discharge anyone who brought him a human eye as a good optical device. The reason is obvious. Under optimum focus and aperture of the normal eye, a star-point at infinity is given in the image as a more or less Gaussian distribution of light some 5-10 cones in diameter. Yet whoever possesses a normal eye can see distinctly two stars as two light points when they are separated by a cone-width or even less in the visual field. In short, we see better than is accounted by the optical transfer function.

This argues for a sharpening operation in the retina, somewhat akin to that used conventionally nowadays in computer-aided image processing. Conventional opinion holds that such process occurs in the neural components of the retina, e.g., bipolar and horizontal cells, those neurons that receive information from the receptors. But aside from economy, several reasons have inclined us to reject that view and we are about to publish a working model by which the needed image sharpening is provided by the receptor layer itself.

The basic problem with image sharpening taking place after the receptors is that the receptors are interconnected resistively along the image plane. There are, in fact, two levels of this connectivity between photoreceptors, and the connections are well attested physiologically and anatomically. The lateral spread of signal, with the receptors as nodes in a resistive net, would be even more conducive to informational blur than the optics itself. Thus, if image-sharpening is deferred to the post-receptor nervous tissue, the two blurring factors, taken together, optical and electrical, make for a far worse condition than the blur alone.

Accordingly, on the thesis that poor engineering is not preserved in evolution, we reconsidered the problem. There is, of course, an obvious advantage to a resistive net if the nodes, the receptors, are made voltage sensitive current sources. That is, given a transduction of light to signal voltage at each receptor, and an individual production of current in each receptor that clamps that voltage, the receptor acts as a voltage source in the net, and the current used to clamp that voltage measures the Laplacian between the receptor and its surrounding neighbors. Given that the receptors are effectively AC devices, the Laplacian is the preferred sharpening function to be applied to the image.

This is easy enough to show both formally and by a simple two stage (two transistor) model, and it works quite ideally.

Required for the usefulness of the model is that there are at least: 1) an ionic conductance in the outer segment of the photoreceptor, and that it is governed by photon capture; 2) a voltage-sensitive pump (current generator) for the same ionic species in the inner segment; and 3) a lateral resistive connectivity between receptors.

All three features have been established by physiologists so that the model we propose is not without merit. We have prepared a note on this matter. It has rather more technical detail, and we are submitting it for publication.

19.3 Tectal Processing of Visual Information in a Frog

Arthur Grant, Thomas Sciascia, Jerome Lettvin

Optic tectum is the most massive part of the visual brain in the frog. Its fine anatomy is fairly regular, a sheet of processing columns that map the visual field. But there is no firm description yet of the internal connections.

All of the errors that beset the interpretation of electrical records are first order in this structure. For example, in the uncurarized frog, the axons of the tectal neurons are quite active, but the cell-bodies seldom fire so that the easily had cell-body records are most often useless, while the axons are well-nigh unrecordable above noise level. In addition, there are many cells without axons, and many with what Székely and Lazar thought to be electrically active dendritic parts. However they had no specific evidence for that conjecture. We can now supply it.

One of the puzzles has been to account for the signals that seem to be from the optic nerve fibers themselves. These are the most salient and reliable transients recorded in the tectum, well-matched to the activity of single fibers in the optic nerve. However,

we have found them to be due to the firing of dendritic appendages of tectal neurons so that they do not have a one-to-one relation with the retinal axons. What is more, these appendages are connected among themselves as Szekely and Lazar have shown so that they form nets. This fact has provided a strong tool for parsing some of the tectal processing. It will be submitted for publication soon.

References

- ¹ G. Geiger and J.Y. Lettvin, "Enhancing the Perception of Form in Peripheral Vision," *Perception* 15, 119 (1987).
- ² G. Geiger and J.Y. Lettvin, "Peripheral Vision in Persons with Dyslexia," *New England J. Med* 316, 1238 (1987).