Waltman, V. Triconi, G. E. Wilson, Jr., A. H. Lewin, N. L. Goldberg, M. M. Y. Chang, *Lancet* **1973-II**, 495 (1973).
19. In animal preference tests, one odor is operationally defined as preferred to another if the animal increases the probability of being stimulated by that odor over the probability of being stimulated by the other. See R. L. Doty, in *Methods in Olfactory Research*, D. G. Moulton, A. Turk, J. W. Johnston, Eds. (Academic Press, London, 1975), pp. 393-406. In sexually experienced dogs, conspecific estrous vaginal odors are clearly preferred to nonestrous vaginal odors, as well as to neutral control odors in such out-of-context test situations [F. A. Beach and A. Merari, *Proc. Natl. Acad. Sci. U.S.A.* **61**, 442 (1968); R. L. Doty and I. Dunbar, *Physiol. Behav.* **12**, 825 (1974)].
20. We thank the members of the Monell Chemical Senses Center and the Department of Obstetrics and Gynecology, University of Pennsylvania Medical School, for assistance on this project. Supported by Rockefeller Foundation grant RF-72018.

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Locus of Short-Term Visual Storage

Abstract. *A rod monochromat can preserve visual information in iconic memory even when the initial stimulus is invisible to the subject. Since the initial invisibility is due to rod saturation, it can be shown that all the information must have been stored inside the photoreceptors. Because the spectral sensitivity for producing icons in normal subjects is that of the rods, the conclusion is that in normal subjects, under ordinary viewing conditions, the photoreceptors are the primary store for iconic memory.*

After a brief exposure to an array of letters, a subject cannot usually report all the letters that he thinks he saw. This subjective phenomenon was demonstrated objectively in the classic study of Sperling (*1*), who compared complete and partial reports made by subjects. The complete report consisted of all the letters a subject could report from a 50-msec presentation of, for example, two rows of letters. In the partial report only sampled half the information available to the subject, the letter presentation. If the tone was of high frequency, the subject had to report only the letters in the top row. If the tone was of low frequency, the subject only reported the letters in the bottom row. Since the partial report only sampled half of the information available to the subject, the number of letters available is twice the number given in the partial report. This experiment demonstrated that there were more letters available for short delays than were recalled in a complete report.

This result led to the notion of a short-term visual store (STVS), also called iconic memory (*2*), which decays rapidly. Sperling tentatively identified the STVS with the persistence of sensation that follows the stimulus. This persistence, or visual image, is usually called an icon (*2, 3*). Various theories have suggested that STVS, or the icon, is located partly in the retina but also at the level of feature extraction or at other more cognitive levels. The data reported here demonstrate that under typical viewing conditions this STVS is located primarily in the retina at the level of the photoreceptors.

In the first experiment, stimuli consisted of two rows of four letters each, presented for 50 msec. Each letter was about 2° high and the pre- and postexposure fields were dark. The conditions were similar to those of Sperling except that a Maxwellian view apparatus was used instead of a tachistoscope. In the complete report condition, the subject had to report all the letters. In the partial report condition, the subject reported either the top or the bottom row, depending upon whether the auditory tone was of high or low frequency.

Figure 1 shows a typical result of this experiment, which repeats Sperling's demonstration that for short delays the number of letters available is greater than the number that can be given in a complete report (*4*). Thus the STVS contains more letters than can be reported.

The unusual thing about this experiment is that the subject was a rod monochromat. She has the usual characteristics of rod monochromats, including poor acuity, complete color blindness, and a breakdown of visual function at high luminance levels. These characteristics correspond to the properties of normal rods. As found for other rod monochromats, all of her visual functions tested were the same as rod functions in a normal individual. In particular, the iconic memory experiments produced data similar to those obtained for normal subjects.

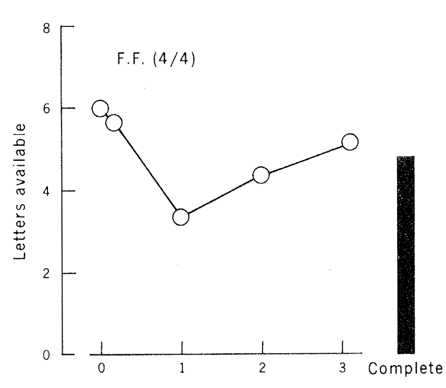

Fig. 1. Number of letters available (circles) in partial report as a function of delay of auditory tone. The bar indicates the average number of correctly identified letters in the complete report. The stimulus consisted of two rows of black letters, four per row, on a white background field that was about 14° wide by 10° high. Letter height was about 2° and the letters occupied a visual area about 10° wide by 7° high. The stimulus was presented for 50 msec and the delay of the tone was measured from the onset of the stimulus. A block design was used. Subject was a rod monochromat.

In the second experiment on this subject, an adapting field of about 20° in visual angle was used in the background. The letters were white and were added onto the white background. The background field was set to about 1000 scotopic trolands, and the letters were again about 2° high and were displayed for 50 msec. No matter how bright the letters were made, they could not be seen by the rod monochromat. She only saw the background field. However, if she closed her eyes after the letter presentation, she could see an icon of the background field and, superposed on it, a slightly brighter icon of the letters. That is, invisible letters produced ordinary discriminable icons after the rod monochromat closed her eyes. How is it possible for an icon to be produced by an invisible stimulus?

The letters were not seen on the background because of the phenomenon of rod saturation, discovered by Aguilar and Stiles (*5*) for normal rod vision and later demonstrated for rod monochromats (*6*). That is, the rod system saturates so that it cannot detect any increments above the critical intensity of about 1000 scotopic trolands. This is not due to exhaustion of the photopigment, since saturation occurs when only an infinitesimal amount of pigment has been used. The phenomenon of rod saturation is not noticed by normal subjects, because cones are operating when the rods become saturated. A rod monochromat, lacking cone function, cannot see any increments above the background when the rods are saturated, and, in particular, cannot see the letters in the experiment described. The background luminance used to demonstrate rod saturation is about the level of that in most tachistoscopes.

Although the rod monochromat had her rod system saturated and could not see the letters when they were presented, when she closed her eyes she *did* see the icon of the letters superposed on the icon of the background. Since the letters were eventually discriminable, the information about the letters must have been stored before (peripheral to) the first stage in the visual system that saturates. It could not be stored after the first stage that saturates because once saturation occurs, no discrimination is possible. The first stage that saturates produces identical signals from the background area and the area that received letters plus background. Therefore, all the information about the icon must have been stored before the first stage that saturates. Electrophysiological evidence indicates that the phenomenon of saturation occurs as early as the rod photocurrent in rats (*7*) and *Necturus* (*8*). If human rod photoreceptors are similar to those of rats and *Necturus* (*5–8*), then one would assume that the rod photocurrent in humans would saturate in a similar manner. Therefore, the first stage in the visual system that saturates is either the rod photocurrent or an earlier stage. Therefore, the information about the icon must be completely stored before the rod photocurrent, and thus inside the photoreceptor or at the membrane. The rods that received quanta from just the background and the rods that received quanta from the background plus the letters all send out the same maximum saturating signal so that from the photocurrent stage on to the brain there is no discrimination possible.

When the rod monochromat closes her eyes after the letters are presented, she in effect turns off the retinal illumination. However, there will still be retinal activity since the transduction process takes a finite amount of time. With the eyes closed, the rods start to recover so that the photocurrents will be below the saturating level. The finding that the rod monochromat can see the icon of the letters indicates that those rods that captured more quanta (letters plus background) are sending out a larger signal than those that only received the quanta from the background. It is this rod photoreceptor current that occurs after the stimuli are removed that leads to the sensation of the icon.

Although it is true that the rod monochromat shows normal-looking data in partial report experiments, one cannot conclude from this that the information about the icon is necessarily located in the photoreceptors in normal subjects, since normals also have cone vision and we do not know how this complicates matters. However, the next experiment demonstrates that iconic memory in normal subjects is basically a rod phenomenon, so that the conclusion derived for the rod monochromat also holds for normals.

The visual stimulus consisted of two

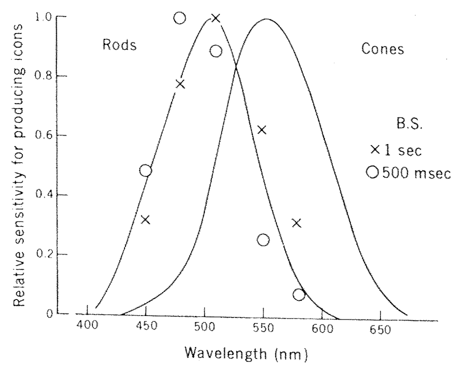

Fig. 2. Relative spectral sensitivity (inverse of energy needed in relative units) for producing 1-second and 500-msec icons. Smooth curves are known spectral sensitivities of normal rod and cone systems. The subject has normal vision. See text for details.

rows of six letters each, totaling about 12° wide by 5° high. Each letter was 1.7° high. The stimulus was produced by a slide with transparent letters on a black background. Interference filters of different wavelengths were placed in the beam so that the letters appeared to be colored on a black background. The subject had normal vision, both rod and cone vision. The stimulus was presented for 50 msec. A preliminary experiment had demonstrated that if an auditory click was presented at the onset of the visual stimulus, the click and the onset of the visual sensation appeared subjectively coincidental. In the actual experiment, an auditory click of 20 msec was presented 500 msec after the stimulus. The task of the subject was to vary the intensity of the light so that the end of the sensation of an image or icon of the letters subjectively matched the onset of the click.

This was done for various stimulus colors. The results are shown in Fig. 2. The spectral sensitivity to produce a 500-msec icon or a 1-second icon is approximately the same as the rod spectral sensitivity function, and is not even approximately close to the cone spectral sensitivity function. It is possible that cones play some role in iconic memory, but for the most part, the spectral sensitivity in producing icons is due to rod vision. This is consistent with the subjective sensation that when, for example, a green stimulus is used, one sees a clear crisp image of green letters which then changes into a diffuse white icon. That is exactly what one would expect if the rods are producing the 500-msec or 1-second icon. It may be that rods and cones are both producing icons. But the rods with their slower time course (*8, 9*) produce longer-lasting icons than the cones.

This experiment demonstrates that for the most part, under conditions of dark pre- and postadapting fields, the icon is a rod phenomenon in normal subjects, so that the conclusions reached about the rod monochromat also hold for persons with normal vision. Thus, under these conditions the information about the icon is stored primarily inside the rod photoreceptors.

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References and Notes

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3. There is substantial agreement that the terms icon, visual image, and persistence of sensation may be used interchangeably. But there is disagreement on whether or not the icon is an afterimage. Unfortunately, the term afterimage is not used consistently in the literature so it is not clear if the disagreement is a semantic or substantive one. Everyone agrees about the terminology of positive and negative afterimages following stimuli of high intensities. Since these are of retinal origin, some people think that the term afterimage can only be used when an image is proved to be of retinal origin. Others disagree. Another reason for the reluctance to use the word afterimage for the icon is the difference in subjective impression between them. The icon is a fleeting image whereas ordinary afterimages last for many minutes. Elsewhere I argue that all these images can be classified into three categories of afterimages (B. Sakitt, *Vision Res.*, in press). However since this report deals only with the icon and STVS, there is no reason to enter this controversy here; hence the word afterimage is avoided.
4. The dip in the curve is similar to that found in one of Sperling's subjects. Sperling attributed it to a guessing strategy. This seems to be true here since the dip corresponded to excellent performance for the top row and very poor performance for the bottom row. In later experiments, with more practice, there usually was no dip.
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10. Supported by NIH grant EY01336. I thank L. Ganz, G. Long, E. Smith, and G. Sperling for comments on this manuscript, and C. Bahlman and P. Hallenbeck for technical assistance.

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