Spatial Frequency and the Mediation of Short-Term Visual Storage

Abstract. *The perceived duration of a photopically illuminated, fixated grating presented for 50 milliseconds increased (from 300 to 500 milliseconds) with spatial frequency (0.9 to 15 cycles per degree). This suggests a sustained neural channel contribution to short-term visual storage, and argues against a pure photoreceptor, especially a rod, locus for such storage.*

Much work in vision has attempted to relate cortical electrophysiology to various perceptual phenomena and psychophysical measurements (*1*). Cognitive psychologists, on the other hand, have focused on the analysis of information processing in terms of discrete stages. One stage in this processing is short-term visual storage (STVS; iconic storage, or icon) whereby a visual impression is preserved for several hundred milliseconds after removal of the stimulus and acts as an input to more central memory systems (*2*).

Sakitt (*3*) claimed that STVS is basically a rod photoreceptor process. However, contrary evidence suggests that both cone and postreceptor neural elements comprise STVS. Square-wave gratings, containing orientation information, can generate icons similar to those produced with letter or shape targets that are more common in an information-processing context. Furthermore, the perceived duration of such a grating can be specifically decreased by selective adaptation to gratings of the same color and orientation (*4, 5*). Color-specific processes are incompatible with a rod icon [also see (*6*)]. These data do suggest a cone-produced icon with cortical filtering of its duration or a central iconic locus in orientation-specific populations.

We have measured the duration of icons produced by gratings of various spatial frequencies. Spatial frequency has been established as a crucial parameter for some types of cortical units (*7*) and in psychophysical studies believed to tap these populations (*1, 8*). We found that iconic duration increased with spatial frequency in a manner inconsistent with rods and more in accord with post-photoreceptor transient and sustained neural processes receiving cone input.

By means of a method of Meyer *et al*, (*4*) a subject was shown a grating of 50-msec duration and a blank field of variable length that were constantly alternating. With shorter blank intervals, the grating seemed continuously present, implying persistence of STVS for at least as long as the blank duration. The grating could be seen to go on and off with longer blanks. This discontinuity of grating perception indicates the termination of the icon. The point of change from perceived grating continuity to discontinuity provides a measure of the STVS length generated by the 50-msec target.

Five vertical square-wave gratings (0.9, 1.9, 3.8, 7.5, 15 cycles per degree) of 0.99 contrast, with bright bars at 10 footlamberts (1 footlambert is equivalent to 3.4 candela per square meter) subtending 5.25° vertically by 7.5° horizontally and presented for 50 msec were alternated with a variable duration blank of the same size (mean luminance, 5 footlamberts) in a six-channel tachistoscope (Scientific Prototype). A dim central fixation point was present throughout the entire stimulus exposure. Perceived grating durations were determined as follows. First, the observer adapted for 3 minutes to a 5-footlambert blank field to maintain a constant state of photopic light adaptation. The five gratings were then presented in a random order, and in response to the subject the experimenter adjusted the duration of the alternated blank to the discontinuity-continuity point for the grating's appearance.

The functions relating mean icon duration to spatial frequency of the 50-msec target grating are presented in Fig. 1. We (G.M. and W.M.) served as initial subjects; two naive subjects (M.M. and M.S.) were also tested. The STVS length significantly increased for all subjects with increasing spatial frequency [random block analysis of variance on the means for each subject for each spatial frequency, F (4, 12) = 24.37, $P < .01$]. The function was also duplicated for G.M. and W.M. when the data were analyzed according to the method of limits.

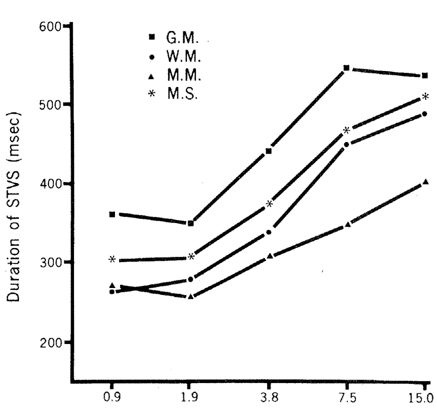

Fig. 1. Mean icon duration for subjects G.M., W.M., M.M., and M.S. as a function of spatial frequency. On each day the series of five gratings was repeated five times. G.M. was tested on 4 days for a total of 20 replications per grating. W.M. was tested on 2 days for a total of ten replications. M.M. and M.S. were both tested on 1 day for a total of five replications per grating.

It was not predicted a priori that STVS duration would increase as the target consisted of finer and finer lines. In fact, the result was slightly counterintuitive because the finer (higher spatial frequency) lines were harder to see, but this "harder-to-see" percept lasted much longer.

These data can be related to the dynamics and possible loci of STVS. If the icon had a pure photoreceptor locus one might expect the duration of STVS to follow the human contrast sensitivity function which, for steadily presented stimuli, exhibits a peak sensitivity around 3 cycles per degree (*9*). The duration of STVS, however, continues to grow (Fig. 1) through the highest frequencies measured. This suggests that the icon is mediated by a neural mechanism that exhibits different temporal characteristics for different spatial frequencies.

One explanation may be provided by the sustained and transient channel distinction current in both electrophysiological and psychophysical studies of vision. Neurons have been found in the retino-geniculate-striate visual pathways of cats and primates which show a consistent interaction in their responses to spatial and temporal frequencies and are usually divided into two classes: sustained and transient (*7, 10*). This distinction is also recognized in visual psychophysics where separate sustained and transient channels have been proposed. Transient channels are said to be sensitive to temporal events, to prefer lower spatial frequencies, and not to be critically concerned with pattern discrimination, whereas sustained channels are said to be relatively insensitive to temporal modulation, to prefer higher spatial frequencies, and to mediate pattern vision (*11–14*).

In our experiment, the subject is instructed to use a pattern discrimination criterion for finding the presence or absence of the grating. Kulikowski and Tolhurst (*14*), using either a flicker detection or pattern detection criterion, found that pattern sensitivity showed a low spatial frequency decline which flicker sensitivity did not. Also, flicker sensitivity declined at low temporal frequencies whereas pattern sensitivity did not. This suggests different information channels for pattern and flicker information, which may be, respectively, the sustained and transient systems with their different spatial frequency preferences. Our data show that alternation rates where subjects typically find the grating to be just continuous are far slower than the fastest temporal modulation (critical flicker fusion) (*15*) that can be detected at this luminance. At our point of continuity-discontinuity of grating appearance, there is obvious flicker in the field even though the pattern seems constant.

One might suspect that the increase in STVS reflects increased response persistence in the sustained system with increasing spatial frequencies. Breitmeyer and Ganz (*13*) cite evidence indicating that higher spatial frequencies increase persistence in the sustained channel.

It is interesting that gratings repeated for 500 msec on and 500 msec off appeared stationary at spatial frequencies greater than 1.2 cycles per degree, whereas lower spatial frequencies appeared temporally modulated (*12*). The appearance of stationariness of the higher spatial frequencies through a 500-msec offset is analogous to our estimates for long icons in the same spatial frequency range. These reports indicate a longer persistence in approximately the same spatial frequency region where the STVS durations increase, and support our suggestion that the higher spatial frequencies are responsible for longer icon durations [see (*16*)]. Physiological data also demonstrate longer response persistences to brief stimuli in cells classified as sustained (*10*).

These data imply that STVS has a post-photoreceptor component and thus conflict with Sakitt's proposal (*3*) that the major locus of the icon is in the rod photoreceptors. Our experiments suggest that major cone and post-photoreceptor processes are active in STVS. First, if only rods mediated STVS one would expect a "foveal" hole in the perceived icon because of the predominance of cones in central vision (*17*). In our study with fixation controlled, no such phenomenon was evident. Second, the increase in STVS duration with spatial frequency speaks against a pure photoreceptor icon. We can find no obvious reason to predict on a rod or cone level that finer gratings would produce longer icons. In fact, since the 15 cycle-per-degree grating yielded the longest perceived durations, one would have to postulate that if photoreceptors produced this icon, some neural process shortened the icons for the other gratings. More parsimonious is the suggestion of increasing sustained channel mediation of the icon with increasing spatial frequency.

The long duration of the 15 cycle-per-degree icon is doubly interesting. Such a grating, with its bars of 2 minutes of arc, is beyond or at best at the limits of rod acuity (*18*). It is unlikely that rods mediate the icon of a grating, centrally fixated, photopically illuminated and to which they have little resolution.

In summary, the duration of STVS increased with spatial frequency in a manner consistent with increasing sustained channel mediation. In cognitive psychology, the icon is assumed to maintain pattern vision despite interruptions of input and for further processing. Sustained channels may have the requisite properties for this task. Breitmeyer and Ganz (*13*) distinguish between a central, contour-specific iconic store called ISc and a peripheral icon, or ISp. Our data seem to represent manipulations of the ISc stage while Sakitt's (*5*) may refer to the ISp. However, a rod STVS would seem largely irrelevant to our normal photopic vision which includes fine acuity, foveal mediation, color, and bright lights, and not of major importance to most human information-processing paradigms. Cone or neural loci, or both, for STVS are certainly not excluded.

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References and Notes

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16. As shown in Fig. 1, STVS duration is relatively unchanged in the low spatial frequency region (0.9 to 1.9 cycles per degree) but shows a rapid increase from 3.8 to 15 cycles per degree. This might suggest a transition from transient to sustained processes which parallels other psychophysical findings [D. J. Tolhurst, *Vision Res.* **15**, 1151 (1975); *ibid.*, p. 1143; and see Kulikowski and Tolhurst (*14*)].
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19. We thank Werner K. Noell, Irving Biederman and especially Naomi Weisstein for making her advice and laboratory available. G.E.M. was supported by National Eye Institute grant 5T32 EY07019-01,02.
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Corneal Endothelium Damage with Intraocular Lenses: Contact Adhesion Between Surgical Materials and Tissue

Abstract. *Intraocular lenses destroy corneal endothelial cells by contact adhesion between the acrylic lens and endothelial surfaces during cataract surgery. Glass and rubber surgical glove surfaces produce similar cell damage. This phenomenon may be important in many surgical procedures and appears to be preventable if a hydrophilic polymer interface is interposed between contacting tissue and the surfaces of materials used.*

We became interested in the problem of cellular damage caused by surface adhesion from the standpoint of ophthalmic surgery and from the finding that corneal endothelial damage occurs during intraocular acrylic lens insertion. The cornea, the anterior transparent membrane of the eye, depends upon an intact living endothelial monolayer for its clarity. The endothelium serves as an aqueous barrier