

## RESEARCH NOTE

# LARGE LOSS OF VISUAL SENSITIVITY TO FLASHED PERIPHERAL TARGETS

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**Abstract**—Threshold measurements of flashed peripheral test spots are shown to be affected by continuous presentation. With repeated presentations of a tiny test flash, thresholds rose progressively, sometimes reaching more than 10 times the initial value. This large loss in sensitivity is not simply due to retinal light adaptation. Habituation to repetitive stimulation proceeds more rapidly with frequent flash presentation but is still conspicuous when flashes occur every 2–3 sec. With 15 min of rapid flash presentation, there is an initial sharp recovery in sensitivity after which there remains some loss of sensitivity even after 35 min. Habituation occurs within both rod and cone systems and transfers between them. The effect is specific to the size and spatial frequency, but not the orientation, of the habituating stimulus.

When visual sensitivity is measured by finding threshold intensities for detection, the usual assumption is that such threshold stimuli are too weak to change observers' thresholds. This report concerns a case where that assumption fails: with repeated presentations of a tiny test spot in peripheral vision (but not in foveal vision), the threshold may rise dramatically and progressively, eventually reaching more than ten times its initial value.

Figure 1a shows the increases in two observers' thresholds for a 4' blue (486 nm) test flash that was detected by rods and presented on a concentric 7° deep-red (Wratten 70) background. Observers took care to maintain steady fixation during the long period of repetitive stimulation. We noted that, once the effect had been well established, flashes at the elevated threshold intensity were occasionally perceived with striking clarity. These infrequent apparent lapses of the effect were disregarded by the observer in setting threshold, on the assumption that they were caused by inadvertent eye movements. The experimental conditions made it difficult to attribute the large rise in threshold to receptor light adaptation: the flashes were brief—50 msec; they were at very low intensity—near threshold; and they were presented at a slow rate—one flash every 2.5 sec. Some post-recep-

toral habituation to repetitive stimulation seemed a more likely explanation.§

More or less similar losses of sensitivity have been observed with repeated flashes in peripheral vision by Ronchi and Salvi (1973), Heijl (1977), Baker and Bargoot (1977), and Singer *et al.* (1977). Baker and Bargoot and Singer *et al.* reported effects quantitatively comparable to those we observed. Experiments in which the disruptive effects of eye movement are reduced or eliminated by stabilizing the retinal image (Barlow, 1963; Cosgrove *et al.*, 1974) or by the use of entoptic phenomena (Sharpe, 1972) have also shown a loss of sensitivity with prolonged repetitive stimulation. Visual sensitivity is also reduced by continuous observation of a stationary pattern without image stabilization (Gilinsky, 1968; Lennie and MacLeod, 1973), bipartite fields with chromatic and luminance borders (Buck *et al.*, 1977; Frome *et al.*, 1981), a moving pattern (Pantle and Sekuler, 1968; Blakemore and Campbell, 1969), or a flickering field (Granit and von Ammon, 1930; Le Grand and Geblewicz, 1937). It is not yet clear to what extent these various phenomena, as well as those reported here, may result from a common process. We have examined in more detail several characteristics of the loss of sensitivity in the peripheral retina, including a crossover effect between rods and cones and between sizes or spatial frequencies. Not only are these habituation effects of interest *per se*, these losses of sensitivity could lead to spurious conclusions from other psychophysical experiments.

In experiments to define some properties of the visual habituation process, a 4' spot (usually set at 16 times threshold) was used as the habituating stimulus and a 4' test spot was used to measure threshold. The stimuli could each be presented at the center of a 7° background field, positioned 7° from the line of sight in the temporal retina. A 50-msec flash occurred

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§ The loss of sensory excitability dealt with here is termed habituation because we have found it to exhibit seven of the nine characteristics of behavioral habituation listed by Thompson and Spencer (1966); the two other characteristics refer to dishabituation, the recovery of the habituated response upon presentation of a strong, irrelevant stimulus. We conducted no direct tests for dishabituation.

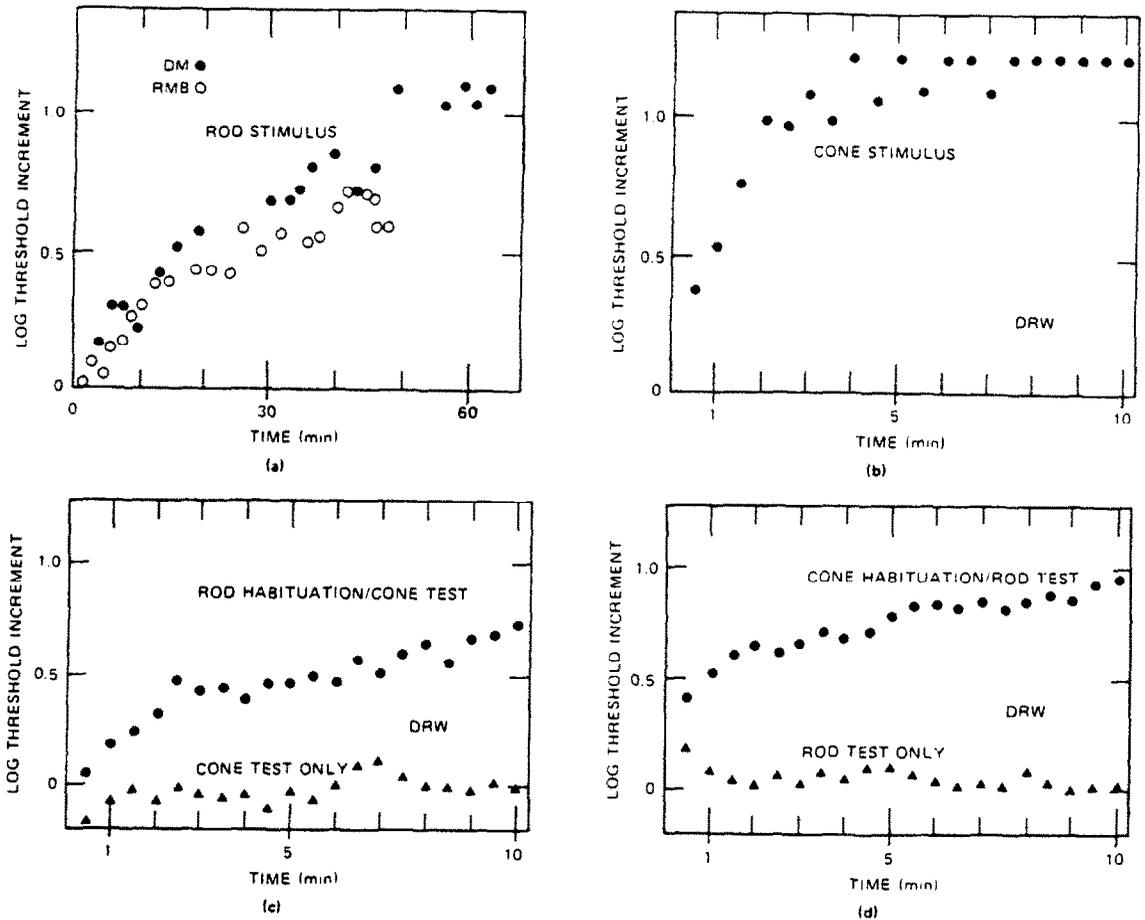


Fig. 1. Increase in log increment threshold as a function of time. These threshold observations are quite precise, as one standard error is smaller than the size of plotted point. (a) Rod-mediated thresholds as tracked by two observers for blue (486 nm) 50-msec flashes presented every 2.5 sec on a deep red (Wratten 70) background. (b-d) Filled circles indicate thresholds taken in 10-min sessions with a 50-msec flash occurring every 0.5 sec. The observer viewed 25 sec of the flashing habituation spot which was 1.2 log units above initial threshold. This was then replaced with the flashing test spot for 5 sec, during which the observer adjusted the test flash to threshold: (b) Cone-mediated thresholds of two observers for a 619 nm red test spot on a 500 nm blue-green background. (c) The filled circles represent cone thresholds taken after 25-sec habituation periods to a rod stimulus. The filled triangles represent cone thresholds when no habituating flashes were presented. During the 25-sec habituation phase, the subject viewed only the background. (d) The filled circles represent rod thresholds taken after 25-sec habituation periods to a cone stimulus. The filled triangles represent cone thresholds when no habituating flashes were presented.

every 0.5 sec; the observer viewed the flashing habituating spot alone for 25 sec, and then the test spot alone for 5 sec while adjusting it to threshold. The alternation of 25 sec of habituation and 5 sec of threshold adjustment was maintained for 10 min. When habituation was to a rod stimulus, a blue 486 nm spot was used on a deep-red (Wratten 70) background. When habituation was to a cone stimulus, a red 619 nm spot was used on a blue-green 500 nm background. Observers viewed the stimuli from a biteboard in a three-channel Maxwellian view optical system. At least two observers were run under all conditions described, with little difference in the qualitative or quantitative aspects of the results.

Figure 1b shows habituation to a deep-red stimulus that was detected by cones, rather than by rods as in

Fig. 1a. With this procedure, in which the habituation stimulus was presented at a higher intensity and more frequently than with the threshold tracking procedure, the change in threshold becomes asymptotic after 5 or 6 min.

When the same procedure was used but when habituating and test stimuli were detected by rods rather than cones, the size and time course of the effects were similar (data not shown). Baker and Bargoot (1977) also noted the similar behavior of rods and cones, as did Granit and von Ammon (1930) in their study of flicker adaptation.

We found in addition that a stimulus detected by cones raises the threshold for a stimulus detected only by rods and vice versa. The filled circles in Fig. 1c represent cone thresholds for the red test spot taken

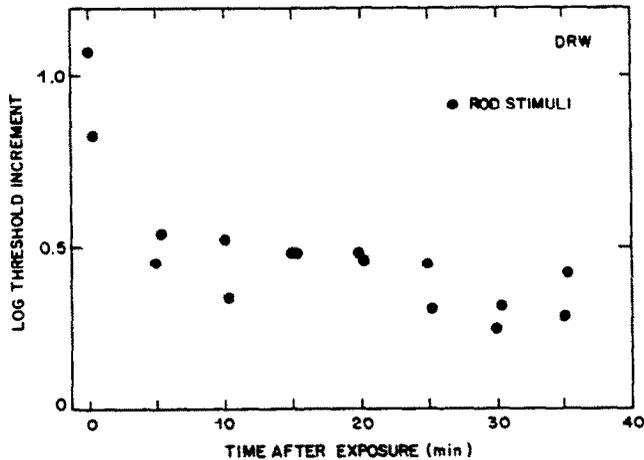


Fig. 2. Long-lasting increase in log increment thresholds for a rod stimulus after 15 min of prior habituation. Recovery in sensitivity is shown as a function of time from the end of a 15-min session with a blue 50-msec flash presented on a steady red background every 0.5 sec at 1.2 log units above initial threshold. The observer then adjusted a test flash to threshold twice every 5 min. The two threshold judgments (represented as points) were separated by 15 sec.

during habituation to a rod stimulus. The blue habituation stimulus, seen against a deep red background, was 10 times rod threshold, but still below cone threshold, since it could not be detected during the cone plateau phase of dark adaptation. The filled triangles at the bottom are thresholds for the test stimulus, which was detected by cones, when no habituating stimulus was presented during the session. In this case, the observer viewed the steady red background during the 25-sec habituation periods. Clearly, the 5-sec periods of exposure to the test flash alone had little effect on cone threshold. In contrast, the upper points show a clear change in cone threshold as a result of habituation to a stimulus detected by rods.

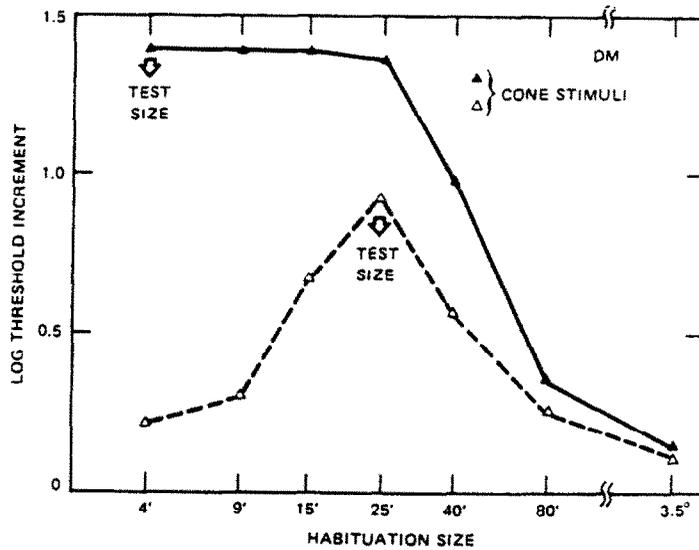
Similarly, habituating to a stimulus detected by cones raised rod thresholds significantly (filled circles, Fig. 1d). The red habituation stimulus was detected by cones since: (i) cones were more sensitive to the red stimulus than rods, even in the dark adapted eye; (ii) cones were more than 10 times as sensitive as the rods to the red stimulus after suppressing rod function with the blue-green background; (iii) we ran a control experiment using a blue habituation stimulus that was equivalent to the red one in its effect on rods. Although this habituation stimulus was equal to the red one in its effect on rods, it was barely, if at all, visible and had only a feeble effect on rod threshold. These results clearly show that habituation occurs central to the visual receptors.

Figure 2 shows a long-lasting effect with 15 min of habituation. There seems to be an initial sharp recovery in sensitivity over the first 5 min, after which there remains some loss of sensitivity even after 35 min. Such long-lasting aftereffects are reminiscent of findings of shifts in perception after adaptation to gratings. (e.g. Frome *et al.*, 1975; see Harris, 1980, and the references given therein.) We also found that a second

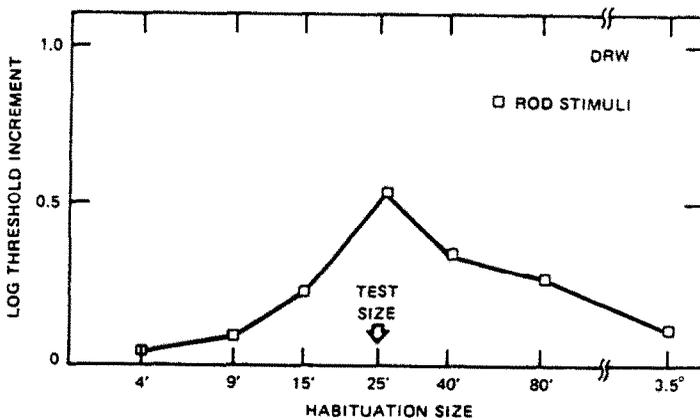
period of habituation following 10 min of recovery from the first exposure to 10 min of habituation showed a more rapid loss of sensitivity and a more prolonged period of recovery than that associated with the initial period of habituation (data not shown).

Several lines of evidence suggest that the habituation effect is associated with neural pathways excited by pattern. First, changes in the appearance of the test spot accompanied the large rise in both rod and cone thresholds. Subjects noticed that the appearance of the test spot changed over time from small and sharp to relatively diffuse and amorphous. This change was particularly pronounced in rod vision. However, a change in fixation of less than 15' arc restored the appearance of such a blob at threshold to a bright (i.e. suprathreshold) tiny spot. Second, our experiments also show size selectivity within both rod and cone systems. In these variable-size experiments, the test spot was either 4' or 25' dia, and the habituating spot ranged in size from 4' to 3.5', with luminance held constant. Figure 3 shows that the maximum habituation effect occurred with the same size habituating spot as test spot and was relatively reduced as the habituation spot differed in size from the test spot. In one case, a 6' habituating stimulus was used for 10 min and there was no change in the threshold for a 4' arc spot. This provides strong additional evidence that the threshold rise is the result of habituation, rather than receptor light adaptation.

The habituation and test spots were replaced with sinusoidal gratings. When both gratings were the same frequency (2 or 0.5 c/deg), there was a rise in threshold in our data (not shown) of about 0.8 log units. However, a grating two octaves away from the habituating stimulus (0.5 or 2 c/deg) showed only a small change in threshold. The rise in threshold due



(a)



(b)

Fig. 3. Threshold for the test spot as a function of the size of the habituation spot (plotted on a logarithmic scale). The arrows indicate the size of the test spot for which threshold judgments were made. (a) Thresholds taken with cone stimuli as both habituation and test spots. (b) Thresholds taken with rod stimuli as both habituation and test spots.

to habituation was much smaller for large spots or coarse gratings than for small spots or fine gratings. Our observations differ in this respect from results with flicker adaptation, which have reported either no effect of area (Granit and von Ammon, 1930), or a greater effect for large areas (Le Grand and Geblewicz, 1937).

We found very little evidence for orientation selectivity. Orthogonal (vertical and horizontal) habituating and test gratings showed nearly as much habituation effect as did gratings of the same orientation. Habituation was also found not to transfer binocularly. That is, we have not been able to find any evidence that presenting a habituating stimulus to one eye has any influence on the threshold for a stimulus presented to the other eye. This differs from the observations of Singer *et al.* (1977) who found binocular transfer and no size selectivity. This raises the possi-

bility that there may be more than one type of visual habituation in humans or that the apparent properties of habituation may differ when measured by means of different procedures.

#### DISCUSSION

Several lines of evidence make it likely that our findings are the result of habituation, and not of light adaptation. First, habituation to a rod stimulus raised the threshold for cone stimuli and vice versa. Secondly, a large-diameter habituating spot fails to raise threshold for appreciably smaller spots presented to the same patch of retina. And thirdly, habituation can be induced at near-threshold intensities of the habituating spot. Since lights of that intensity would not appreciably change the receptors' state of light adaptation, the rise in threshold is diffi-

cult to reconcile with any receptor light adaptation mechanism.

The site of habituation appears to be located in monocular pathways involving size- or spatial-frequency-selective neural units. Electrophysiologically, habituation of a single cell's response by repeated presentation of its optimal stimulus is conspicuous in the cortex (Hubel and Wiesel, 1965; Maffei *et al.*, 1973; Vautin and Berkley, 1977). Vautin and Berkley show convincingly that the habituation they observed was cortical rather than precortical in origin. Habituation of cortical cells could underlie both our results and the frequency-selective-adaptation effect observed with gratings (e.g. Gilinsky, 1968; Pantle and Sekular, 1968; Blakemore and Campbell, 1969; Frome *et al.*, 1979). One difference is that the cells implicated in detection of small flashed peripheral targets must lack any sharp orientation specificity. Some monocularly excitable cells in striate cortex satisfy this requirement (e.g. Poggio and Fischer, 1977). Habituation of lateral geniculate cells could also underlie our results since LGN cells can show habituation (Monnier *et al.*, 1976), very little orientation specificity, and very little binocular transfer of excitatory signals (Hubel and Wiesel, 1961; Wiesel and Hubel, 1965). Finally, habituation could be mediated as peripherally as the inner plexiform layer of the retina. Recent findings of physiological mechanisms that respond to repetitive stimulation bear a striking resemblance to the psychophysical results reported here. The primary source of physiological habituation has been identified at the inner plexiform layer of the proximal retina (Karwoski and Proenza, 1980).

These findings have an important implication for all psychophysical increment threshold experiments using peripheral vision: these habituation effects can be large (greater than a log unit) and may obscure other results of interest. One way to minimize these effects would be to have subjects successively fixate a number of fixation points at the same distance from the test stimulus, in order to space repeated flashes to a specific retinal area further apart in time.

Although habituation can certainly be a problem in laboratory experiments, visual habituation may be useful in suppressing persisting background stimuli (of external or entopic origin) that have little interest to the organism. The absence of the effect in foveal vision makes sense from this viewpoint, since the fovea is directed by choice to regions of the environment where an interesting stimulus is present.

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