the two discriminations was affected equally by the tasks the birds performed during phase 2 and, indeed, that the phase 2 activity should cause any forgetting at all would not be expected from what is known of RI in human long-term memory. One of the most widely accepted generalizations (*6*) holds that little or no interference occurs unless the discriminative stimuli that control responding in the first and second phases of training are reasonably similar. In our experiments the stimuli that controlled responding during phase 1 were completely absent during phase 2.

Our results are compatible with a model (*7*) based on the assumption that all the information a pigeon acquires during the course of these experiments is stored in a single memory of limited capacity, and that newly entered information destroys information already stored. On an empirical level, this research yielded two surprising results: (i) our procedure produced virtually complete forgetting, and (ii) the learning and relearning curves are nearly identical.

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5 May 1981

Disappearance of Stabilized Chromatic Gratings

Abstract. *When the image of a stationary, sinusoidal luminance grating is stabilized on the retina of a human subject, he becomes unable to detect this stimulus at contrasts that are readily visible in normal, unstabilized vision. At much higher contrasts, such stabilized gratings can still be seen over most of the normal range of spatial frequencies, although the threshold contrast may be increased by as much as 20 or 30 times. When the analogous experiment is performed with an isoluminance chromatic grating, however, there is no contrast that can restore the visibility of the stabilized grating; the threshold elevations for stabilized chromatic gratings are too great to measure. Saturated red/green gratings fade out and disappear at 100 percent contrast (even where this is 45 times the unstabilized threshold), and they do not reappear as long as stabilization is maintained. Without some kind of temporal variation of the proximal stimulus, the opponent-color pathways apparently do not respond to spatial patterns.*

The visual contrast sensitivity function for isoluminance chromatic gratings behaves differently from the luminous contrast sensitivity function measured under comparable conditions (*1*, *2*). The two sensitivity curves cross each other, with the chromatic sensitivity being greater at low spatial frequencies and the luminous sensitivity being greater at high spatial frequencies. [This is analogous to the relation between luminous and chromatic flicker sensitivity curves (*2*, *3*).] These results are believed to reflect the relatively coarse spatial organization of the opponent-color pathways, compared with that of the pathways that transmit achromatic information.

It has recently been shown that stabilizing the retinal image (that is, canceling the image motion due to eye movements) has profound effects on the luminous contrast sensitivity function. Although these effects vary somewhat with the experimental techniques used (*4*), complete absence of temporal variation greatly decreases sensitivity and changes the shape of the curve, moving the sensitivity peak to higher spatial frequencies (Fig. 1A).

I now report that attempts to measure the chromatic contrast sensitivity with image stabilization lead to a surprising result: Under stabilized-image conditions, the chromatic contrast sensitivity for isoluminance gratings cannot be measured because the stabilized chromatic threshold is always greater than 100 percent contrast. Chromatic gratings of the highest contrast that could be produced faded out and disappeared when the retinal image was stabilized and did not reappear as long as stabilization was maintained. This means that the chromatic threshold was elevated by a factor of more than 45 at low spatial frequencies (Fig. 1B). How much more, of course, is unknown.

This extreme behavior is not shown by the luminous contrast sensitivity under stabilized-image conditions. The maximum elevation of the luminous contrast threshold (Fig. 1A) is only 30 times, and this is the greatest elevation of the luminous contrast threshold so far reported (*4*).

To make the luminous and chromatic sensitivity measurements directly comparable, both were carried out with the same subject, under the same conditions, in the same apparatus. The only difference was a spatial phase shift of 180° between the red and green components of the two stimuli. When the red and green gratings were in phase, the stimulus was a yellow luminous grating, variable in contrast from 0 to 100 percent. When they were out of phase, the stimulus was an isoluminance red/green grating.

Because the maximum chromatic contrast obtainable under these conditions depends on the chromaticities of the red and green components, these primary colors were made as saturated as possible (*5*). Both were derived from the P22 phosphors of a standard (RCA) color television screen. The P22 red component is nearly a spectral color. The green is not, but its luminance is almost twice as great as that of the red. It was therefore possible to greatly increase the saturation of the green component while approximately balancing the red and green luminances by viewing the display through a yellow (Wratten 16) filter. The final setting of the red/green balance was then made by adjusting the modulation of the green component relative to that of the red; this was done by flicker photometry. Thus, the apparent color contrast of the chromatic gratings (viewed without stabilization) was very high, while their (flicker photometric) brightness contrast was imperceptible (*6*).

Once a stabilized chromatic grating of this kind has disappeared, a striking chromatic afterimage can be seen by suddenly reducing the stimulus contrast to zero. Although the subject is then viewing a uniform yellow field, he sees a red/green chromatic grating of opposite phase to the stimulus. The strength of these chromatic afterimages (as measured by the chromatic contrast required to produce a just-detectable afterimage) is generally less than that of comparable luminous afterimages (measured in the same way) (*4*, *7*). This is the opposite of what might be expected from the data of Fig. 1 if the elevation of the stabilized threshold and the formation of the afterimage are merely different aspects of the same local adaptation process (*8*). Thus, there may be important differences between these two processes (in either the

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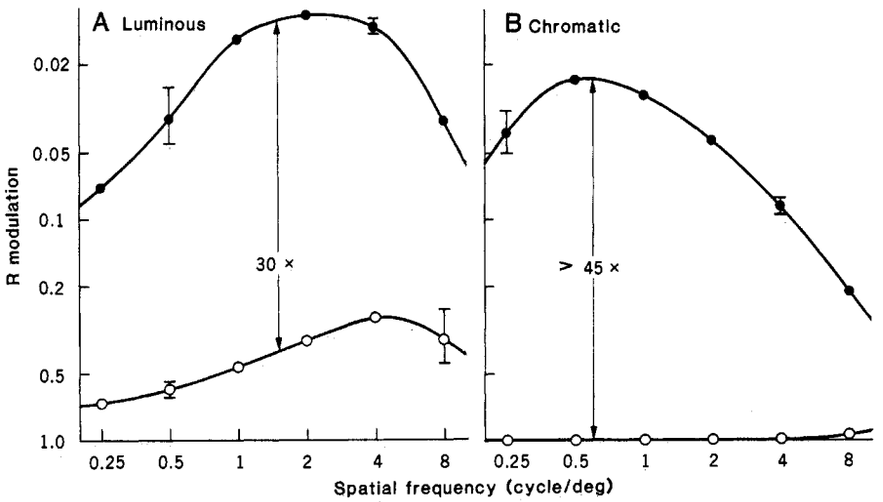

Fig. 1. Contrast sensitivity for stabilized (open circles) and unstabilized (filled circles), luminous and chromatic, sine-wave gratings 8° in diameter, with dark circular surround, viewed monocularly with the natural pupil. Each point represents the mean of five trials; the greatest and smallest standard deviations obtained at any spatial frequency are shown on each curve. The characteristic shapes of the unstabilized curves are in agreement with previous studies (*1*, *2*); the chromatic sensitivity is greater than the luminous sensitivity for spatial frequencies below 0.7 cycle/deg, but less than the luminous sensitivity at higher frequencies. Each stimulus is composed of a red (*R*) grating and a green (*G*) grating, matched in luminance by flicker photometry, and superimposed. The same contrast scales are used in both graphs. (A) the red and green components have the same spatial phase, producing a yellow grating with luminous contrast but no chromatic variation. (B) The same components are superimposed 180° out of phase, producing an isoluminance red/green grating with only chromatic contrast. In the stabilized case, chromatic sensitivity cannot be measured, because the stabilized chromatic grating disappears even at 100 percent modulation.

chromatic or achromatic pathways, or both).

For achromatic gratings, even very slow movement of the stimulus (for example, 0.01 deg/sec) greatly increases the stabilized contrast sensitivity. As the velocity is increased from zero, the sensitivity increases smoothly from the minimum values shown in Fig. 1A up to a maximum as great as the unstabilized contrast sensitivity (*9*). I have now found that the chromatic contrast sensitivity behaves in a similar way, although its zero-velocity values are unmeasurably low (Fig. 1B).

Figure 2 shows the chromatic contrast sensitivity for a stabilized, isoluminance (red/green) grating, with a spatial frequency of 1 cycle/deg, drifting at velocities from 0.015 to 16 deg/sec (which are numerically equal to the local temporal frequencies in this case). Except for the effects of stabilizing the retinal image, these data should be comparable to previous studies of chromatic flicker sensitivity with a constant spatial pattern (*2*, *3*); the results are very similar for temporal frequencies greater than 0.5 Hz. With the stabilized, drifting-grating technique, however, accurate data can be obtained at much lower frequencies (*10*). Below 0.5 Hz, the sensitivity decreases with a slope approaching 1.0, as would be expected if the chromatic response is proportional to the local time derivative of the stimulus. This differentiating behavior confirms the results of Fig. 1B: Stabilized chromatic gratings do disappear, but this result can be approached only at temporal frequencies well below 0.01 Hz (*11*).

There is also some suggestion of a low-frequency falloff as a function of spatial frequency in the unstabilized data of Fig. 1B and in previous studies (*1*, *2*). Without stabilization, however, this cannot be unequivocally attributed to the spatial structure of color-opponent receptive fields; it might be a temporal artifact

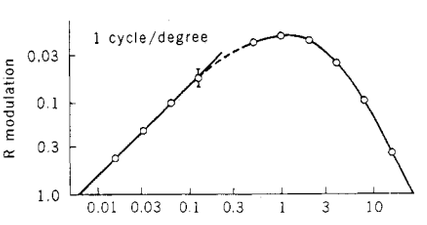

Fig. 2. Contrast sensitivity for stabilized, 1-cycle/deg, chromatic gratings as a function of drift velocity (or flicker frequency); other conditions are as in Fig. 1B. At frequencies above 0.5 Hz, the results agree with previous chromatic sensitivity data (including those obtained with counterphase flicker). At frequencies below 0.2 Hz, the sensitivity function resembles that of a perfect differentiator (slope of 1). Only at frequencies below 0.01 Hz does the chromatic sensitivity approach the unmeasurably low values obtained with stationary, stabilized gratings.

introduced by uncontrolled eye movements. Aside from this possibility, the data of Fig. 2 have no direct bearing on such spatial characteristics, of course; they depend only on the temporal frequency of the stimulus.

It has been shown (*12*) that the residual response to stationary, stabilized images differs from the response obtained when the visual stimulus is temporally modulated by eye movements or otherwise; some of the established properties of normal spatial vision are completely absent under stabilized conditions. But the analogous result in the chromatic case is even more startling: there are no responses to stabilized chromatic stimuli. We may infer that the opponent-color pathways require some sort of temporal modulation to transmit any spatial information about the stimulus. Although they respond well to transient stimuli, these chromatic mechanisms (unlike the achromatic ones) are evidently incapable of sustained responses.

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5. The color contrast of the chromatic grating is proportional not only to the modulation of each component but also to the distance between the two primary colors in chromaticity space. Thus the maximum color contrast for a given modulation is obtained by using red and green primaries that are as far apart as possible.
6. There are no standard units for specifying the color contrast of an isoluminance pattern; this has been done in various ways in the literature (*1*, *2*). In order to specify both luminous and chromatic stimuli in the same units, I used the contrast scales shown in Fig. 1, where the standard Michelson contrast, $(I_{max} - I_{min})/(I_{max} + I_{min})$, is given for the red component only. Ideally, the red and green scales would be identical, but they were allowed to differ somewhat to completely eliminate luminance modulation in the chromatic stimulus. This produces a slight shift in chromaticity when the luminance contrast of the yellow grating is varied from zero to maximum, but it does not affect the results.
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10. The studies cited in (*2*, *3*) varied somewhat in their low-frequency limits (De Lange, 1 Hz; Van der Horst and Bouman, 0.5 Hz; and Kelly and Van Norren, 0.37 Hz). Kelly and Van Norren did obtain a significant decrease in sensitivity below 1 Hz, but Van der Horst and Bouman did not (perhaps because their stimulus was an unstabilized drifting grating).
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13. Supported by NIH grant EY 01128.

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