Stabilized images: Functional relationships among populations of orientation-specific mechanisms in the human visual system*

MARTY J. SCHMIDT, MARK P. COSGROVE, and D. R. BROWN
Purdue University, Lafayette, Indiana 47907

Two experiments are presented in which fading rates of stabilized line stimuli were measured following prolonged adaptation to nonstabilized grating patterns in various orientations. Results indicated that some orientation-specific effects are sensitive to small variations of orientation around an optimal orientation, as well as to stimuli rotated 90 deg from the optimal orientation. These data were interpreted in terms of interactions among populations of orientation-specific mechanisms in the human visual system.

A number of recent neurophysiological studies have described single neurons in animal visual systems which respond with a high degree of specificity to orientation characteristics of line stimuli. Hubel and Wiesel, for example, have determined that some cortical cells are capable of coding orientations of line stimuli within a tolerance of 10-15 deg in the cat (Hubel & Wiesel, 1965) and within 5-10 deg in the monkey (Hubel & Wiesel, 1968). These and similar observations have prompted psychophysical investigators to search for behavioral correlates of these orientation-specific channels, or mechanisms. While it is undeniably premature to equate psychological phenomena with specific neurophysiological events, the emerging isomorphism between the two classes of data is encouraging. For example, Campbell and Kulikowski (1966), using a masking paradigm, determined that an orientation difference of 12 deg between mask and test stimuli reduced masking effects by a factor of two from the masking level obtained when both stimuli shared a common orientation. These authors suggested that the visual system includes a number of orientation-specific channels, each tuned to a specificity of about 12-15 deg. These and other data indicate that orientation-specific mechanisms are fundamental units of organization in the visual system.

The studies presented here are part of a series designed to apply stabilized image techniques to examine various pattern processing operations in the human visual process. Previous studies in this series (Brown, Schmidt, Cosgrove, & Zuber[1]; Cosgrove, Schmidt, Fulgham, & Brown, in press; Fulgham, Schmidt, Cosgrove, & Brown[2]; Schmidt, Fulgham, & Brown, 1971) have demonstrated that fade durations and fading rates of stabilized stimuli are sensitive indices of pattern and orientation characteristics of simple stimuli. The present paper is intended to describe and clarify further characteristics of orientation-specific mechanisms and, in particular, to examine functional relationships among them.

EXPERIMENT 1

Brown et al[1] examined the effects of horizontal and vertical adaptation gratings on fading rates of stabilized vertical test lines. Adaptation to nonstabilized grating stimuli produced orientation-specific effects on the fading of stabilized line stimuli; the same effects were obtained dichoptically, indicating that they were probably of postretinal origin. Experiment 1 in the present study was designed to provide a more complete analysis of the functional relationship between adaptation grating orientation and the visibility of a stabilized test stimulus. Specifically, fading rates of a vertical test line were measured following prolonged adaptation to a grating viewed in one of seven different orientations. It was predicted that results would be consistent with earlier psychophysical studies (e.g., Campbell & Kulikowski, 1966; Fidell, 1970; Fulgham et al[2]) which indicated that pattern mechanisms may be specific to orientations within a range of 5-15 deg. Additional evidence (Bouma & Andriessen, 1968, 1970; Gibson & Radner, 1937) suggests that orientation-specific mechanisms are in some way affected by orientations outside this range. Accordingly, this experiment was designed to reveal both the "tuning range" of a specific orientation mechanism and the nature of its more general response to a wide range of other stimulus orientations.

Method

Subjects. Two of the authors, M.C. and M.S., 24 and 25 years of age, respectively, served as Os. Vision was corrected to 20/20 in the left viewing eyes with individually fitted scleral contact lenses worn during all experimental sessions. Both Os were well practiced in stabilized image viewing.

Stimuli. Eight adapting fields were used. Black bars on a light background created a grating pattern which was viewed in seven different orientations, rotated 0, 5, 15, 45, 75, 85, and 90 deg from the vertical. A light-filled circular field without grating bars was included as a control condition. In all cases, field diameter was 5 deg 12 min. Grating bars were parallel, 2 min in width, and separated by 10 min of light background. Thus, a periodic grating pattern of 5 cycles/deg was formed. Adaptation stimuli of these dimensions have produced orientation-specific effects on the fading of stabilized line stimuli in a previous study (Brown et al[1]).

The test stimulus for all sessions appeared as a vertical black line segment 2 min in width and 50 min in length, centered in a circular (5 deg 12 min) light-filled field.

Optical system. An optical system similar to that described by Clowes and Ditchburn (1959) was modified to include two channels, each capable of presenting O with an image in either stabilized or nonstabilized Maxwellian view. Each channel consisted, essentially, of a tungsten ribbon-filament source lamp, a target slide, lens train, and heat filter. A very similar version of the stabilization system has been described in detail elsewhere (Fulgham et al[2]; Schmidt et al, 1971). Basically, stabilization was achieved by means of an optical lever reflected from a small mirror fixed to a contact lens worn on the viewing eye. Nonstabilized Maxwellian view was obtained in the same system by shifting the O's biteboard laterally, allowing the primary projection path to pass directly through the O's pupil, thus avoiding the contact lens mirror and optical lever. This procedure was identical to that used in an earlier study (Brown et al[1]).

Shutters operated by stepping motors were located in each channel to permit selection of either channel. Field luminance under all viewing conditions was adjusted to a measured 2.0 fL and was maintained by continuous monitoring of filament current at each source lamp.

Procedure and Experimental Design
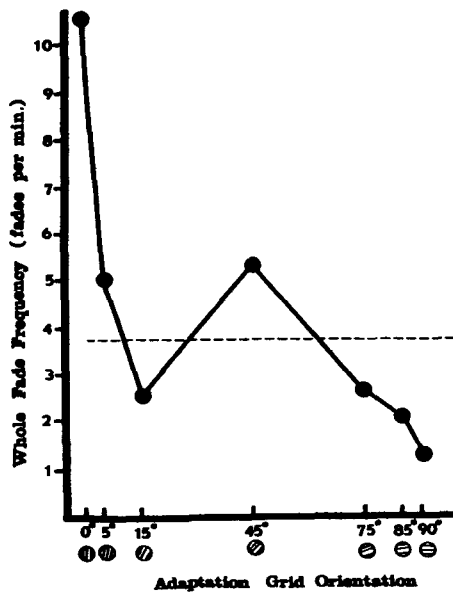
Eight experimental conditions were

Fig. 1. Whole-fade frequency of a stabilized vertical test line following different nonstabilized adaptation conditions. Each data point represents the mean whole fades per minute for the 15-min viewing session following a given adaptation condition. The dotted line represents the mean fade frequency of the test line following adaptation to a blank field.

defined by the seven orientations of the adaptation grating and the blank (control) adapting field. For each grating orientation, an equal number of clockwise and counterclockwise rotations were presented in a random sequence. Each O was tested under all conditions twice, with conditions randomly assigned to 16 days of testing for each O.

Each experimental session consisted of an adaptation phase, in which O viewed one of the eight adaptation fields for 15 min in nonstabilized Maxwellian view, and a test phase, in which the test line was viewed for 15 min in stabilized Maxwellian view.

Prior to the adaptation phase, O inserted the contact lens and assumed the appropriate position for nonstabilized viewing. The adaptation field was then presented through Channel 1. Following the adaptation interval, O shifted position to obtain stabilized viewing of the test field which was presented through Channel 2. Transitions between nonstabilized and stabilized viewing positions required a few seconds.

Responses to the stabilized test pattern were recorded by means of two telegraph keys under O's left hand. During the test phase of each session, two categories of responses were recorded: whole fades and partial

fades. The O responded to a whole fade whenever the entire stimulus was faded from view by pressing the appropriate key. A partial fade was recorded when any part, but not all, of the line was faded from view. Whole and partial fade frequencies (in fades per minute) were obtained from a two-channel event recorder which was activated by the telegraph keys.

Results and Discussion

Orientation-specific adaptation effects were clearly reflected in whole fade rates of the test line; mean fade rates following each adaptation condition for the 15-min viewing session are shown in Fig. 1. Partial fade rates, in contrast, did not produce consistent effects with respect to differences among adaptation conditions and are not shown here. For whole fade rates, an analysis of variance of the 8 (adaptation conditions) by 2 (Os) design, using interactions with Os as error estimates, showed that the main effect associated with adaptation condition was significant ($F = 25.5$, $df = 7,7$ $p < .001$). Results for both Os were highly similar; differences between Os were not statistically significant ($F < 1$). A similar analysis applied to the partial fade rates did not yield any significant effects. Since our interest here was primarily with orientation-specific effects, discussion below is concerned only with whole fade rates.

Orientation-specificity of the adaptation effect is seen most clearly by comparing the effects of vertical and horizontal adaptation gratings. Whole-fade rates of the vertical test line, following adaptation to the vertical and horizontal gratings, were 10.6 and 1.4 fades/min, respectively. When the fade rate for the test line following blank field adaptation (3.7 fades/min) is considered as a reference, or baseline, adaptation to a vertical grating facilitated fading and adaptation to the horizontal grating suppressed fading. While this suppression effect is not statistically significant, the obvious floor effect must be considered. In addition, inspection of the data showed this suppression effect to be consistent across the 15-min viewing period.

Figure 1 indicates that other orientations of the adaptation grating also produced either facilitation or suppression of test line fade rates. With respect to the baseline rate, the direction and degree of the effect suggest a functional relationship between adaptation grating orientation and the degree of effect over a 90-deg range of adaptation grating orientations. Three general characteristics of this relationship are

suggested in Fig. 1: (1) The fading rate of a stabilized vertical test line was elevated by adaptation to vertical or near-vertical (within 5 deg) gratings. (2) With one exception, the fading rate of a vertical test line was suppressed by adaptation to grating orientations outside of this range. Maximum suppression of fading occurred when the adaptation grating and test stimulus differed by 90 deg in orientation. Cosgrove et al (in press) have shown that for line stimuli of this size, changes in fade frequency are accompanied by corresponding changes in total fade duration. Thus, suppression of fading represents increased visibility. When they differed by 75 or 85 deg, the suppression of fading appears to be less pronounced. (3) Adaptation to a grid rotated 45 deg from the vertical produced a slight elevation in the fading rate of the vertical line.

EXPERIMENT 2

Results of the first study indicated that, while the effect on visibility of adapting to different orientations is "tuned" to some extent, fading of the vertical stimulus is also influenced by adaptation gratings outside of this range. Experiment 2 was designed to examine the generality of these data for other orientations. In this study, distinction was also made between effects observed during the first and last 6 min of the 15-min test session.

Method

The methodology in Experiment 2 was identical to that used in Experiment 1, with the exception of the experimental design. Four adaptation conditions were used: grating stimuli were viewed at 0-, 45-, and 90-deg rotations from the vertical, and a blank field adaptation condition was included as a control. Three test conditions were defined by three orientations of the test line: 0-, 45-, and 90-deg rotations from the vertical. Twelve different viewing conditions were defined by crossing the four adaptation fields with the three test conditions. All conditions were viewed twice by each O and were independently randomized for 24 viewing sessions for each O.

Results and Discussion

In a previous study using similar stimuli (Brown et al[1]), it was observed that adaptation effects were most pronounced during the first 6 min of stabilized viewing. The final 6 min of a 15-min viewing session were often marked by an apparent "recovery" from the orientation-specific effects. Since our intention in Experiment 2 was to examine subtle differences among hypothesized vertical, diagonal,
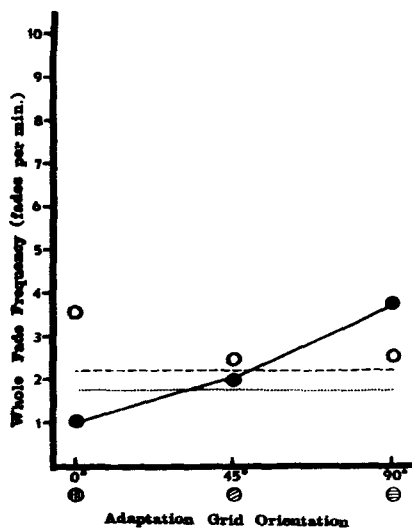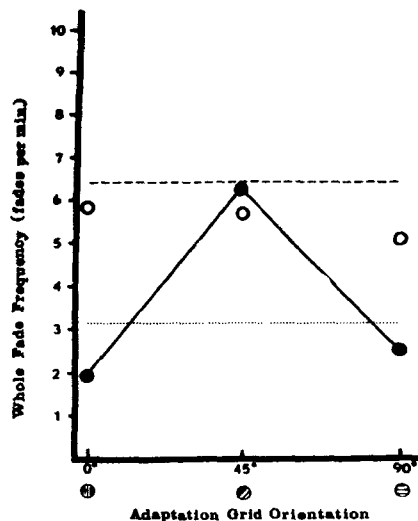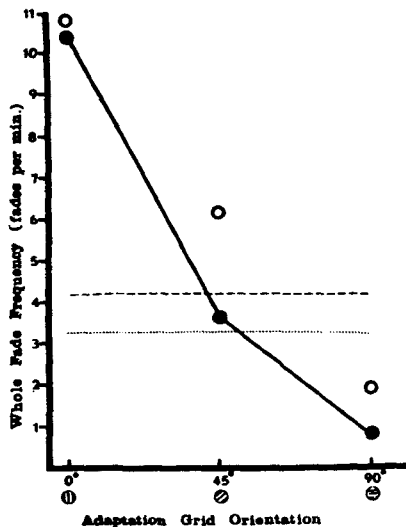
Fig. 2. Whole-fade frequencies of a stabilized vertical (top), diagonal (middle), and horizontal (bottom) test line following different nonstabilized adaptation conditions. Each solid data point represents the mean frequency with which the test line faded during the first 6 min of the stabilized viewing period following adaptation. Each open data point represents the mean frequency with which the test line faded during the last 6 min of the stabilized viewing period. The lower dotted line on each graph represents the mean fade frequency in the first 6 min of viewing of the test line following blank field adaptation. The upper dotted line in each case represents the mean fade frequency during the last 6 min of stabilized viewing following blank field adaptation.

and horizontal mechanisms, analysis of these data was restricted to whole-fade rates of the test lines during the first 6 min of the test session. Whole-fade rates of the vertical, diagonal, and horizontal (0-, 45-, and 90-deg rotations, respectively) are summarized in Fig. 2 (top, middle, and bottom, respectively). Fade rates obtained during the final 6 min of each 15-min viewing session are included to suggest the degree of "recovery" from the effects of adaptation.

Figure 2 shows, in general, that when adaptation grating orientation and test line orientations were the same, fading rate of the test stimulus was above the rate produced by the control condition. When adaptation grating and test line orientation differed, however, fading rate of the test line was either unaffected or suppressed below the control fade rate. When adaptation and test orientation differed by 90 deg (Fig 2, top and bottom), fading rate of the test line was clearly suppressed. When they differed by 45 deg, the suppression effect was either very slight (Fig. 2, middle) or not present (Fig. 2, top and bottom). It is interesting that Fig. 1 shows an elevation of fading of the vertical test line after adaptation to a 45-deg grating, while in Fig. 2 (top), the elevation effect is much smaller in magnitude. It is likely that Fig. 2 (top) is a more accurate representation of the effect produced by the 45-deg adaptation grating, since the elevated fade rate of the vertical test line in Experiment 1 was due to an unexplained increase in fading rate during the final 6 min of test viewing. A similar increase in fading was not seen in the horizontal test line following adaptation to the 45-deg grating.

Comparison of Fig. 2 (top, middle,

and bottom) suggests that fade rates of the horizontal test line were influenced to a lesser degree by the various adaptation conditions than were the fade rates of the diagonal and vertical test lines. These impressions were supported by statistical tests. For each stimulus condition, a separate analysis of variance of the 4 (adaptation conditions) by 2 (Os) design was computed, using the pooled within-cell variance for all 12 viewing conditions as an error estimate. For the vertical test stimulus, the effect associated with adaptation conditions was highly significant (F = 26.09, df = 3,12, p < .001); for the diagonal test stimulus, the effect was also significant (F = 5.71, df = 3,12, p < .05); but for the horizontal test stimulus, the effect was not significant. This last result may be in part due to the very low fade rate of horizontal lines and the limited statistical power of this design.

GENERAL DISCUSSION

The results of Experiment 1 indicated that the vertical mechanism is "tuned" within limits of 5-15 deg from the vertical and horizontal orientations. The effect produced by a grating rotated only 5 deg from vertical was substantially reduced from that produced by a vertical grating. When the adaptation grating was rotated as much as 15 deg from the vertical, the direction of the effect was reversed, i.e., whole fade rates of the test line were depressed below the baseline rate. These observations are consistent with a number of earlier psychophysical data (Andrews, 1967; Campbell & Kulikowski, 1966; Fidell, 1970; Fulgham et al[2]). In addition, our data show that the vertical mechanism is sensitive to small variations in adaptation grating orientation when adaptation and test orientations differ by 75-90 deg. Suppression of fading was successively greater for 75-, 85-, and 90-deg rotations from the vertical (Fig. 1). These results are consistent with earlier studies which indicated that orientation-specific mechanisms are influenced by stimuli outside the optimal orientation range for that mechanism (Brown et al[1]; Campbell & Maffei, 1971; Gibson & Radner, 1937; Gilinsky, 1967). It is suggested here that these phenomena are evidence of functional relationships among different orientation-specific mechanisms.

Results of Experiment 2 indicated that horizontal and vertical mechanisms exhibit similar inhibitory and facilitatory effects on each other. Adaptation to the diagonal grating apparently did not influence fading (or visibility) of stabilized vertical and

horizontal lines, but fading of a stabilized diagonal line was suppressed somewhat following adaptation to other orientations. If the effects observed in Experiment 2 do, in fact, represent mutual interactions among different orientation-specific mechanisms, then our data are predicted by a model that has already been described in the literature, namely, a class of orientation-specific neurons described by Hubel and Wiesel (1965). These authors have reported a higher-order hypercomplex cell in Area 19 of cat cortex that responds maximally to two orientations of line stimuli 90 deg apart. This cell also responds with a reduced firing rate to all other orientations of stimuli, reaching a minimal firing rate when stimuli are midway between the two optimal orientations. In view of the known anatomical and physiological organization of this region, Hubel and Wiesel suggested that these cells receive afferent connections from lower-order hypercomplex cells having receptive field orientations 90 deg apart. Lower-order hypercomplex cells that, presumably, provide input to higher-order hypercomplex cells are characterized by increased (above baseline) firing rates to stimuli in a preferred orientation and decreased (below baseline) firing rates to stimuli rotated 90 deg from the preferred orientation. Hubel and Wiesel suggested that the properties of hypercomplex cells are most easily explained by assuming that afferent synapses for a given cell are both excitatory and inhibitory in nature. Thus, firing rates of the higher-order hypercomplex cell described above may be determined by interactions between two antagonistic mechanisms. If the optimal stimulus orientations for this cell were horizontal and vertical, then prolonged presentation of a horizontal stimulus would, presumably, diminish the influence of the "horizontal" input component and, by comparison, enhance the influence of the "vertical" input component. Prolonged adaptation to a line rotated 45 deg from both optimal orientations would influence both input components equally. If one assumes that collective firing rates from populations of such cells are correlated with visibility of line stimuli, then the extrapolation of this model to our data is straightforward.

With respect to interactions between mechanisms having optimal orientations separated by 90 deg, our data apply only to horizontal and vertical orientations. They do not indicate, for example, if the same effects would be obtained between mechanisms optimally sensitive to 45- and 135-deg rotations from the vertical.

However, our data have important implications for other evidence, which indicates that horizontal and vertical mechanisms process information more efficiently than other mechanisms. Over three decades ago, Gibson and Radner (1937) measured the strength of aftereffects produced by viewing lines of various orientations and suggested that horizontal and vertical orientations function as "spatial standards." This hypothesis has received some recent support. Andrews (1967) and Bouma and Andriessen (1968, 1970) have demonstrated that errors of orientation perception are usually made in the direction of the nearest horizontal or vertical axis; these errors decrease in magnitude as the physical stimulus approaches horizontal or vertical. Also, acuity for line or grating stimuli is maximal for vertical or horizontal orientations (Andrews, 1967; Campbell, Kulikowski, & Levinson, 1966). Finally, earlier stabilized image studies in the present series (Cosgrove et al, 1972; Schmidt et al, 1971) have demonstrated that, in extended stabilized image viewing sessions, horizontal and vertical stimuli tend to resist fading to a greater degree than do diagonal stimuli.

One possible explanation for the organized character of fading in stabilized images is that, when a significant proportion of the population of analyzers for a particular stimulus are adapted, that stimulus fades from view. With respect to the vertical and diagonal test lines, the horizontal test line (Experiment 2) was least influenced by prolonged adaptation to either horizontal or vertical adaptation conditions. It is possible that the population of horizontal-specific mechanisms is substantially larger than populations of, say, vertical orientation channels and is, therefore, more difficult to adapt.

The studies presented here, admittedly, represent only a cursory examination of relations among orientation-specific mechanisms. Nevertheless, these results are consistent with earlier psychophysical data and extend our understanding of the operation of these mechanisms.

Furthermore, they emphasize the utility of stabilized image techniques in psychophysical approaches to human pattern vision.

REFERENCES

ANDREWS, D. P. Perception of contour orientation in the central fovea, Part I: Short lines. Vision Research, 1967, 7, 975-997.
BOUMA, H., & ANDRIESSEN, J. J. Perceived orientation of isolated line segments. Vision Research, 1968, 8, 493-507.
BOUMA, H., & ANDRIESSEN, J. J. Induced changes in the perceived orientation of line segments. Vision Research, 1970, 10, 333-349.
CAMPBELL, F. W., & KULIKOWSKI, J. J. Orientational selectivity of the human visual system. Journal of Physiology, 1966, 187, 437-445.
CAMPBELL, F. W., KULIKOWSKI, J. J., & LEVINSON, J. The effect of orientation on the visual resolution of gratings. Journal of Physiology, 1966, 187, 427-436.
CAMPBELL, F. W., & MAFFEI, L. The tilt after-effect: A fresh look. Vision Research, 1971, 11, 833-840.
CLOWES, M. B., & DITCHBURN, R. W. An improved apparatus for producing a stabilized retinal image. Optica Acta, 1959, 6, 252-265.
COSGROVE, M. P., SCHMIDT, M. J., FULGHAM, D. D., & BROWN, D. R. Stabilized images: Dependent variable specificity of pattern-specific effects with prolonged viewing. Perception & Psychophysics, 1972, 10, 295-299.
FIDELL, L. S. Orientation specificity in chromatic adaptation of human "edge detectors." Perception & Psychophysics, 1970, 8, 235-237.
GIBSON, J. J., & RADNER, M. Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. Journal of Experimental Psychology, 1937, 20, 453-467.
GILINSKY, A. S. Masking of contour-detectors in the human visual system. Psychonomic Science, 1967, 8, 395-396.
HUBEL, D. H., & WIESEL, T. N. Receptive fields and functional architecture in two non-striate areas (18 and 19) of the cat. Journal of Neurophysiology, 1965, 28, 229-289.
HUBEL, D. H., & WIESEL, T. N. Receptive fields and functional architecture of monkey striate cortex. Journal of Physiology, 1968, 195, 215-243.
SCHMIDT, M. J., FULGHAM, D. D., & BROWN, D. R. Stabilized images: The search for pattern elements. Perception & Psychophysics, 1971, 10, 295-299.

NOTES

1. Brown, D. R., Schmidt, M. J., Cosgrove, M. P., & Zuber, J. J. Stabilized images: Pattern processing and non-pattern processing operations. Submitted for publication.
2. Fulgham, D. D., Schmidt, M. J., Cosgrove, M. P., & Brown, D. R. Stabilized images: Selected characteristics of receptive fields for line stimuli. Submitted for publication.