

PSYCHOPHYSICAL RELATIONSHIPS AMONG MECHANISMS SENSITIVE TO PATTERN, MOTION AND FLICKER

MARC GREEN*

School of Optometry, University of California, Berkeley, CA 94720, U.S.A.

(Received 21 April 1980; in revised form 23 January 1981)

Abstract—Sensitivity to drifting gratings was measured both before and after adaptation to a uniform flickering field. In the first experiment, it was found that viewing uniform flicker with one eye impaired sensitivity for drifting gratings presented to the same or contralateral eye. Likewise, adaptation to drifting gratings increased flicker detection thresholds. In the second experiment, temporal tuning of the adaptation effect was determined by adapting observers to several different flicker frequencies and testing with gratings of different drift rate. The data suggested the existence of broadly tuned temporal channels which respond to both flicker and motion. In a third experiment, spatial tuning of uniform flicker adaptation was evaluated by employing test gratings of different spatial frequency. The threshold elevation curves were low-pass in shape and exhibited an upper cut-off at 3–4 c/deg. Moreover, the 3–4 c/deg limit was found even when observers explicitly set thresholds for detecting temporal change. The results of the three experiments are consistent with the view that the human visual system contains separate sustained and transient mechanisms. Contrary to previous suggestions that the two systems play specialized roles in perception, however, our data indicate that both transient and sustained mechanisms can signal motion.

INTRODUCTION

In 1881, Bowditch and Hall suggested that perception of stationary and moving objects is mediated by different centers in the brain. A new version of their proposal has recently surfaced in the guise of the "sustained-transient dichotomy" (for reviews, see Breitmeyer and Ganz, 1976; MacLeod, 1978). This model suggests that the human visual system contains two separate mechanisms for the processing of spatio-temporal luminance variations. One mechanism, the transient system, is most sensitive at low spatial and moderate temporal frequencies. A second mechanism, the sustained system, is optimally stimulated by low temporal and moderate spatial frequencies. The sustained-transient model, however, goes far beyond simply proposing different spatiotemporal sensitivities for the two mechanisms. It suggests that each mechanism plays a specialized role in perception: the transient system codes temporal change while the sustained system signals stationary, clearly defined pattern.

The specialized nature of the two mechanisms is frequently demonstrated by determining separate thresholds for perception of spatial and temporal luminance change (e.g. Kulikowski and Tolhurst, 1973). For example, suppose an observer is presented with a sine-wave grating modulated at a moderate temporal frequency. At detection threshold for a low

spatial frequency grating observers report the perception of temporal change without the presence of distinct spatial structure. This is usually interpreted as meaning that detection was mediated by the transient system (see Fig. 1(a)). When contrast is raised to a sufficiently high level, the sustained system reaches threshold and well-defined contours become visible. At higher spatial frequencies, transient system sensitivity falls off rapidly and detection is mediated by the sustained system. As a result, stationary stripes are seen at threshold, and more contrast is then required to stimulate the transient system and to perceive temporal change. The assumption here is that the sustained system signals not just pattern, but *stationary* pattern (Tolhurst, 1973; Kulikowski and Tolhurst, 1973). Perception of temporal change must always (except perhaps at very low temporal and very high spatial frequencies) be signaled by the transient system, so that the perception of clearly visible objects in motion normally results from a combination of sustained and transient system activity.

While much attention has been focused on the possible dichotomy between mechanisms for signaling spatial and temporal luminance variation, remarkably little note has been taken of the fact that there exists two categories of temporal information, i.e. temporal change with (motion) and without (flicker) a directional component. The first study (Van Nes *et al.*, 1967) to determine separate spatial and temporal thresholds employed flicker perception as a transient criterion and motion perception as a pattern criterion. In subsequent studies, however, experimenters have generally failed to explicitly differentiate between flicker and motion and have even used the terms

* Research supported by NSF Research Grant BNS7914096 and, in part, by NEI Grant EY01175. Reprints may be obtained from the author at the School of Optometry, 360 Minor Hall, University of California, Berkeley, CA 94720, U.S.A.

interchangeably (Tolhurst *et al.*, 1973). The general implication seems to be that motion and flicker are both signaled by the transient system, on one hand, and stationary pattern by the sustained system on the other.

The purpose of the present study was to test the validity of the sustained-transient model outlined above. Specifically, experiments were aimed at determining whether (1) flicker and motion are processed by mechanisms sharing a common stage in the transient system and (2) there is a separate sustained system which signals only the presence of stationary pattern. To anticipate the data, results confirmed the sustained-transient model only partially. Evidence was found to support the idea of a transient system tuned to low spatial frequencies and a sustained system which is more sensitive at higher spatial frequencies. However, it appears that the transient system operates at spatial frequencies only as high as 3–4 c/deg and that motion in higher spatial frequency targets is signaled by the sustained system. Therefore, the degree of perceptual specialization of the two systems is not absolute.

METHODS

Rationale for the use of uniform flicker

The primary method used in our research was the selective adaptation paradigm. Although the rationale behind this technique is based on a number of tenuous assumptions, it has frequently been used to identify the filter properties of visual mechanisms (Braddick *et al.*, 1978). The novel feature of the present research was the use of a uniform flickering field as a tool to determine the selectivities of visual mechanisms. There are several advantages to the use of this stimulus in adaptation experiments. A uniform flickering field contains temporal change but no spatial structure (within the display borders). As a result, it should be invisible to the sustained system but stimulate the transient system. In fact, if one accepts the view that the transient system can be described as a low-pass filter in the spatial frequency domain (e.g. Kulikowski and Tolhurst, 1973; Sekuler *et al.*, 1978), then uniform flicker should be the optimal stimulus for the transient system. As a result, prolonged viewing of uniform flicker should therefore have the advantage of producing a highly selective adaptation effect. A temporally modulated grating, on the contrary, is likely to stimulate mechanisms which signal pattern as well as those which signal temporal change. Even when gratings are presented in a stationary mode, eye movements may produce temporal components in the retinal image.

Observers

In addition to the author, three other observers were employed in various phases of the study. Observer J.V.O. had partial knowledge of the aims of the

experiments while the other two, M.C. and R.K., were experimentally naive.

Apparatus and procedure

Observers viewed stimuli generated on the face of a CRT screen by the standard television technique. The screen contained a fixation point in the center and was masked down to a circular field with black paper. For dichoptic presentations, observers viewed two CRTs matched in color and luminance. Since different CRT displays were used in different phases of the study, exact field size and mean luminance varied somewhat across experiments. These details are described in the figure legends. Each session began with three minutes of pre-adaptation to sinusoidal flicker of the unpatterned screen. Unless otherwise stated, depth of flicker modulation was adjusted to be 1.5 log units above detection threshold. Two psychophysical methods were employed to obtain data. Method of adjustment data were obtained with a series of cycles consisting of nine seconds of flicker adaptation alternating with 1.3-sec test intervals. During the test interval, a sine-wave grating was switched on and off with no change in mean luminance. The observers' task was to set the test grating to contrast threshold by turning a featureless knob. As many cycles as required could be viewed, but typically 8–12 were sufficient. In addition to gratings, a uniform flickering

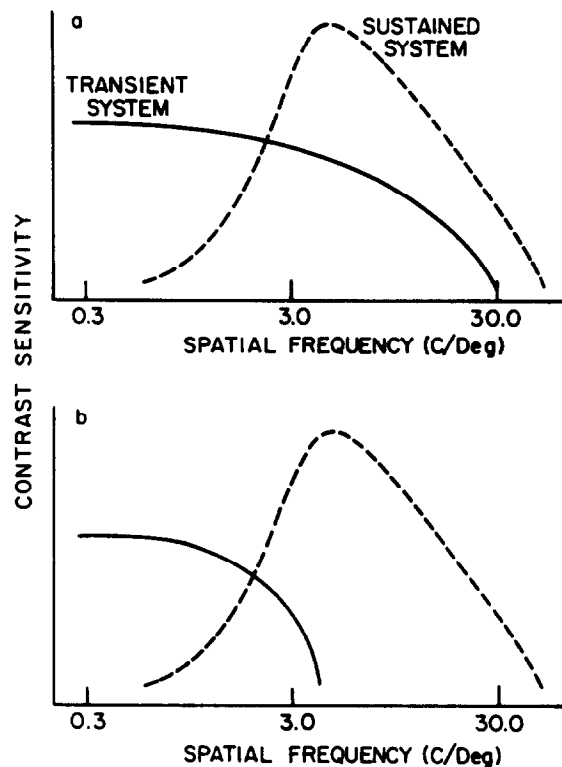


Fig. 1. Schematic representation of the spatial frequency tuning of the sustained and transient mechanisms. Top panel shows sensitivity of the two mechanisms as proposed by Kulikowski and Tolhurst (1973). Relative sensitivities suggested by Legge (1978) are shown in the bottom panel.

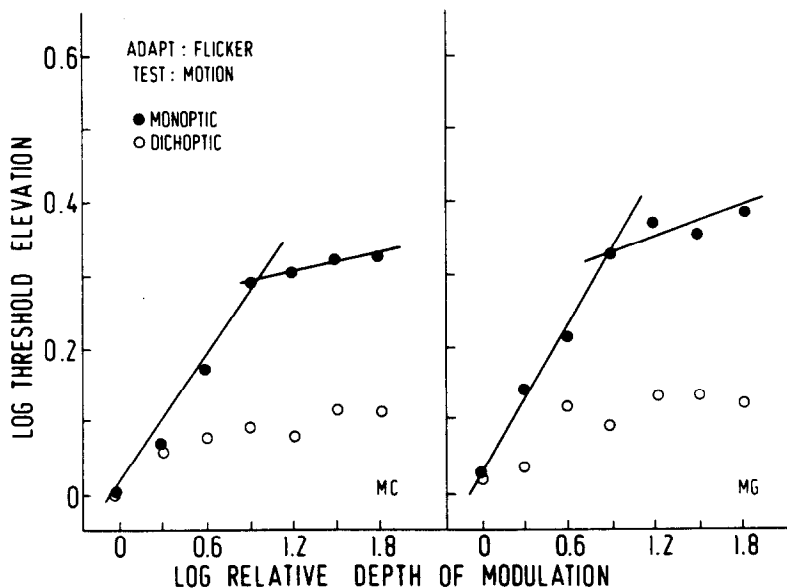


Fig. 2. Effect of relative flicker amplitude on detection gratings presented to the same (solid symbols) or contralateral (open symbols) eye. Temporal frequency of both gratings and flicker was 9 Hz. The visual field was 6.5° and had a mean luminance of 40 cd/m^2 . Straight lines were fitted by the method of least squares. Left panel: observer M.C.; right panel: observer M.G.

field was also used as a test stimulus. Observers set threshold for flicker by turning a knob which controlled depth of modulation. Unadapted control thresholds were obtained by replacing the flickering adaptation field with a steady field of the same time-averaged luminance. Each data point was determined by averaging five threshold settings. Data were also collected by a two-alternative forced-choice procedure. Testing was performed with a series of continuously cycling trials. Each trial consisted of 7 sec of flicker adaptation followed by the first 1.5-sec observation interval, a 3-sec re-adaptation period and a second 1.5-sec observation interval. A grating was switched on and off gradually with a cosine temporal envelope during one of the test intervals. The observer verbally indicated which interval contained the test grating. Threshold was tracked by altering contrast in a manner contingent on the observer's accuracy. Three correct responses in a row resulted in a 0.1 log unit decrease in contrast, while an error at any time produced a similar size contrast increment. This procedure produces a detection level corresponding to the 79.6 percent correct point on a psychometric function (Wetherill and Levitt, 1965).

RESULTS AND DISCUSSION

Experiment 1. Adaptation to flicker and motion—interocular transfer

The first experiment was designed to test whether (1) adaptation to flicker would impair sensitivity to moving gratings and (2) whether motion adaptation would likewise raise flicker detection thresholds. Figure 2 shows results for observers who detected a 0.6 c/deg grating which drifted rightward at 9 Hz. The

test grating was presented alone or in conjunction with adaptation to 9 Hz uniform flicker presented to the same (monoptic condition) or contralateral (dichoptic condition) eye. Under both monoptic and dichoptic viewing, uniform flicker adaptation raised thresholds for detecting moving gratings. Size of the monoptic effect increased as a power function with depth of flicker modulation up to a level of 0.9 log unit (a factor of 8) above threshold. Increasing flicker amplitude beyond this point produced little additional threshold elevation. Due to the small degree of interocular transfer, it is not entirely clear whether a similar breakpoint occurs in the dichoptic data. The curve for observer M.G. exhibits some signs of an inflection point, but this is less apparent for observer M.C. It was somewhat surprising to obtain any dichoptic effect since previous papers (Smith, 1971; Hanly and MacKay, 1979) have reported failures to find any interocular transfer of uniform flicker adaptation.

Figure 3 shows results for reversed adaptation, where observers detected flicker before and after adaptation to motion. In both monoptic and dichoptic conditions, low suprathreshold adapting stimuli produce a magnitude of sensitivity loss similar to that resulting from flicker adaptation. However, no plateau occurs in reversed adaptation, and threshold elevation continues to grow with adapting contrasts as high as 1.8 log units above threshold. As a result, reversed adaptation produced a larger threshold elevation with highly suprathreshold adaptation stimuli. Although the maximum size of the threshold elevation differed, amount of interocular transfer was 25–29% for both flicker and motion adaptation. The impairment of sensitivity produced by flicker and

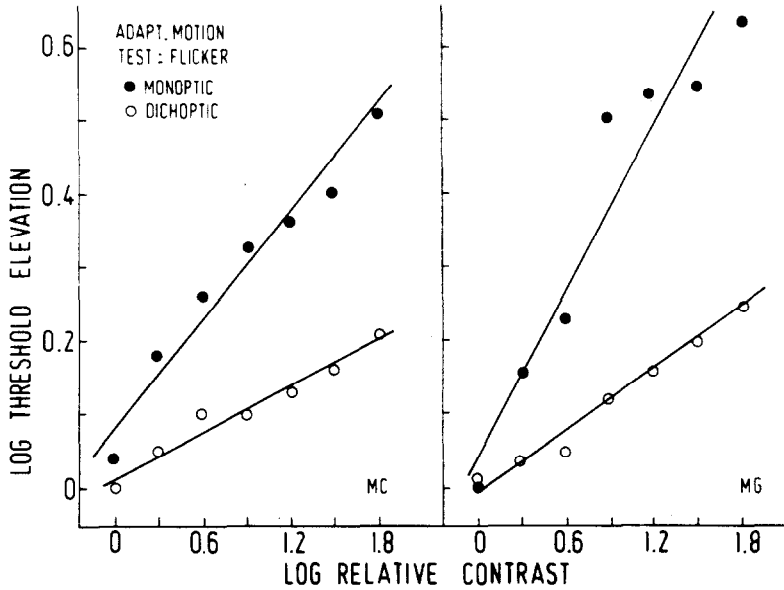


Fig. 3. Effect of relative grating contrast on detection of flicker presented to the same or contralateral eye. Details were the same as in Fig. 2.

motion on one another supports that idea that the two forms of temporal modulation share a common stage of processing in the transient system.

Uninterrupted power function relationships between threshold elevation and amplitude of the adaptation stimulus have been reported in studies using stationary gratings (Stecher *et al.*, 1973) and uniform flicker (Smith, 1971). However, Pantle *et al.* (1978) have noted that when direction-specific adaptation is measured with drifting gratings, curves exhibit a plateau very similar to that found in the present data. In the context of the sustained-transient dichotomy, it might be imagined that detection is mediated by the transient system prior to adaptation. Low amplitude flicker reduces sensitivity of the transient system below that of the sustained system. Since detection is then mediated by the sustained system, further increase in flicker amplitude should have little effect. No plateau presumably occurs with flicker detection since this stimulus is always detected by the transient system (Wilson, 1980). Anecdotal reports of the observers lend some support to this interpretation. Before adaptation, the gratings appeared as a diffuse motion containing no definite spatial structure. Following adaptation, bars could be discerned and the grating appeared to move much more slowly. However, the postadaptation percept was never that of a stationary grating, as would be expected if detection were mediated by the sustained system. This suggests that (1) the interpretation is incorrect or (2) the sustained system can signal motion. Data favoring the second alternative will be presented in the subsequent experiments.

Experiment 2. Temporal tuning between flicker frequency and drift rate

Previous studies have found that the human visual

system contains a number of independent channels tuned to different spatial frequencies (Blakemore and Campbell, 1969). The possibility of a similar multiple channel arrangement in temporal vision has been investigated with respect to flicker frequency (Smith, 1970; Pantle, 1971; Smith, 1971; Nilsson *et al.*, 1975) and velocity (Pantle and Sekuler, 1968). These studies have found that although well-defined channels are not present, some degree of temporal tuning exists. If flicker and motion are processed by a common stage in the transient system, then temporal tuning between flicker and motion might be expected. This was investigated by measuring sensitivities to gratings moving at a variety of drift rates before and after adaptation to different flicker frequencies. A second goal of the study was to determine whether flicker adaptation effects were restricted to rapidly moving gratings or would also be demonstrated with gratings moving more slowly.

Figure 4 shows the threshold elevation curves obtained when observers adapted to 15.0, 7.5 and 2.5 Hz uniform flicker and detected 0.5 c/deg gratings drifting at temporal frequencies ranging from 0.6 to 20 Hz. All three flicker frequencies raised detection thresholds for gratings of all drift rates. In spite of the broadness of the adaptation effect, the data suggest a weak temporal tuning and cannot be explained with a single temporal channel. Curves produced by different flicker frequencies are similar for low drift rates but differ at rapid drift frequencies. Following 15.0 Hz flicker adaptation, size of the threshold elevation diminishes only with decreasing drift rate. For the two lower flicker frequencies, threshold elevation curves exhibit both a low- and a high-frequency attenuation. There is some suggestion for observer M.G. (left panel) that the 2.5 Hz curve shows a sharper high-frequency attenuation than the 7.5 Hz

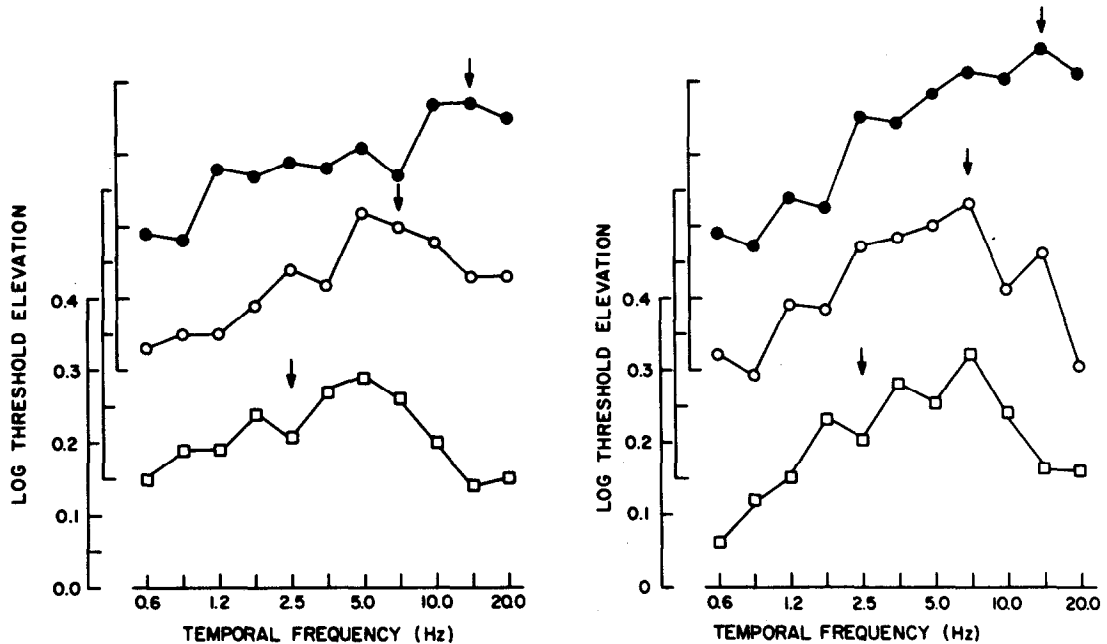


Fig. 4. Threshold elevation curves for a 0.5 c/deg grating detected following adaptation to uniform flicker. Curves have been displaced upward by 0.15 log unit for clarity. Arrows indicate the frequency of flicker for which each curve was obtained. The visual field was 7° dia. and had a mean luminance of 11 cd/m^2 . Adaptation periods were reduced from 9 to 7 seconds. Left panel: observer M.G.; right panel: observer J.V.O.

curve. This trend is less pronounced for observer J.V.O. (right panel). In general, however, little differentiation is apparent between the 7.5 and 2.5 Hz curves with both peaking at the same drift rates. Displacement of the peak of the 2.5 Hz curve to drift rates an octave or more higher in frequency suggests the absence of a channel centered at low temporal frequencies.

The degree of tuning found here is comparable to that found in previous studies (Smith, 1971; Pantle, 1971; Nilsson *et al.*, 1975) which employed uniform flicker as both adaptation and test stimuli. The similarity between the present data and those of Smith (1971), who used flicker frequencies similar to those employed here, is especially strong. With regard to temporal tuning for rate of motion, there is some disagreement over sharpness of tuning. The channels reported by Pantle and Sekuler (1968) are very broad and resemble those found with uniform flicker. Tolhurst *et al.* (1973), on the other hand, suggest that when observers use perception of motion rather than of form as the threshold criterion, then temporal channels are very well defined. However, this conclusion should be taken with some caution because Tolhurst *et al.* employed only two closely spaced adaptation frequencies (6 and 10 Hz). Although their threshold elevation curves are peaked in the 6–10 Hz range, the present data suggest that similar curves would be obtained with any low to moderate temporal rate. Moreover, there is little differentiation between 6 Hz curves and the 10 Hz curves, which actually peak at 8 Hz for two of three observers. In sum, except for the Tolhurst *et al.* study, the degree of

temporal tuning found in previous studies which employed only flicker or only motion is similar to that found in the present experiment. This further supports the idea that flicker and motion share a common processing stage in the transient system.

Flicker adaptation raised thresholds for gratings moving as slowly as 0.6 Hz. Stromeyer *et al.* (1979) have concluded that directionally tuned mechanisms can detect gratings drifting even more slowly than those employed here. The threshold elevation for slow drift is doubtless limited to very low spatial frequencies. We have found that adaptation had no effect on detection of slow gratings of 2.0 c/deg drifting at 0.6 Hz. This was not surprising since these gratings were seen as stationary at threshold and therefore were likely detected by the sustained system both before and after adaptation.

Experiment 3. Spatial frequency tuning of uniform flicker adaptation

The transient system is presumed to have poor spatial resolving power and therefore mediates detection only at low spatial frequencies while a separate sustained system detects fine gratings. As a result, flicker adaptation should only impair sensitivity when low spatial frequency gratings are employed. This prediction was tested by determining thresholds with and without flicker adaptation for gratings ranging in spatial frequency from 0.5 to 16 c/deg.

Comparison of counterphase flickering and drifting gratings. Figure 5 shows sensitivity for gratings which sinusoidally flickered in counterphase at 16 Hz.

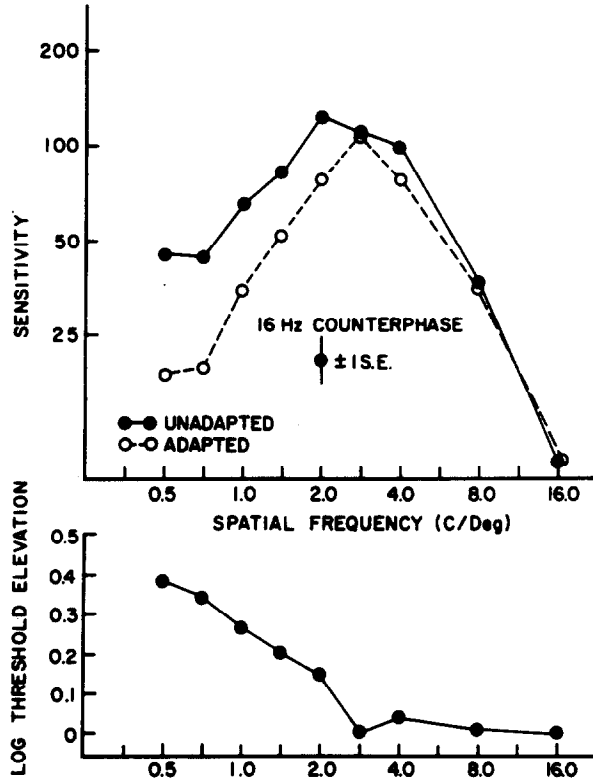


Fig. 5. Contrast sensitivity to 16 Hz sinusoidal counterphase flickering gratings before and after adaptation to 16 Hz flicker. Closed circles represent data for unadapted thresholds and open circles data for adapted thresholds. Error bar in the middle shows ± 1 SE for the most variable point in all three experiments. Variability was generally about half this size. The lower panel shows threshold elevation as a function of spatial frequency. Data were collected with a field size 4.0° dia. at a mean luminance of 100 cd/m^2 . Method of adjustment was employed. Observer: M.G.

Curves obtained both before and after adaptation to 16 Hz uniform flicker exhibit a low spatial frequency attenuation not usually found with rapidly flickering gratings, although similar data have been reported (Tolhurst *et al.*, 1973). This was likely due to the relatively few bars in the field at low spatial frequencies (Howell and Hess, 1978; McCann *et al.*, 1978) as well as the dark edges of the surround (McCann and Hall, 1980). Use of a larger field reduced the low spatial frequency attenuation (see Fig. 9). The major effect produced by flicker adaptation was to reduce sensitivity for low spatial frequency gratings. The size of the threshold elevation was largest with the coarsest grating of 0.5 c/deg, diminished with increasing spatial frequency, and was absent above 3–4 c/deg. This result is consistent with previous data (Legge, 1978; Wilson, 1980) which suggests that in the spatial frequency domain the transient system can be described as a low-pass filter with a cut-off of about 3–4 c/deg.

Counterphase flickering gratings can be mathematically decomposed into the sum of two half-amplitude components which move in opposite directions (Levinson and Sekuler, 1975). It would therefore be expected that flicker adaptation should produce a similar threshold elevation in detection of linearly drifting and counterphase flickering gratings. This was tested by replacing the 16 Hz counterphase flick-

ering grating with a grating drifting leftward at 16 Hz and again determining thresholds with and without adaptation. Results from this experiment, shown in Fig. 6, confirmed that the threshold elevation curve for drifting gratings was similar to that obtained with counterphase flickering gratings. The sensitivity loss was about the same size and the curve also shows a low-pass shape, going to 0 at about 3–4 c/deg. In addition to grating targets, the effect of flicker adaptation on an identical uniform flickering test field was measured. Threshold elevation with a uniform flicker test target was greater than for any of the gratings. This is consistent with the results of the first experiment where observers exhibited larger threshold elevation when detecting flicker than when detecting gratings.

Since counterphase flickering gratings contain only half-amplitude moving components, sensitivity to drifting gratings should be twice as great for the flickering gratings, but only when detection is mediated by direction-selective mechanisms. In the present data, sensitivity for the drifting gratings was about twice that for counterphase drifting gratings for spatial frequencies as high as 8.0 c/deg. At 16 c/deg, counterphase flickering and drifting gratings produced similar thresholds, indicating that detection was no longer mediated by direction-selective mechanisms. The fail-

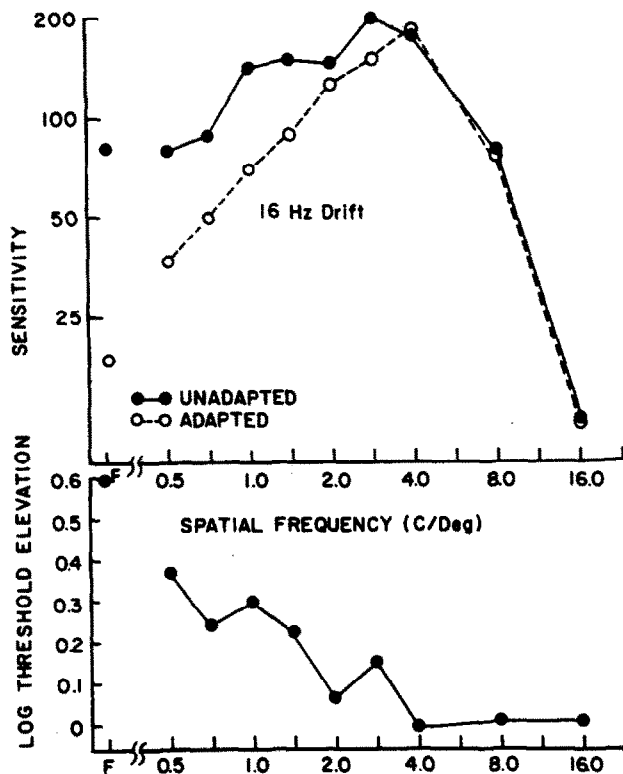


Fig. 6. Contrast sensitivity to 16 Hz drifting gratings before and after adaptation to 16 Hz flicker. The symbol "F" on the horizontal axis represents a condition in which the test stimulus was a uniform flickering field. Other details are the same as in Fig. 5. Observer: M.G.

ure to find doubled sensitivity for drifting gratings at 16 c/deg was surprising since Stromeyer *et al.* (1978) measured detection thresholds for 15 c/deg gratings with a temporal frequency of 15 Hz and found that drift produced twice the sensitivity of counterphase flicker. The reason for the disparity of results is not clear. Although the 4.0 and 8.0 c/deg gratings were therefore presumably detected by directionally selective mechanism, adaptation produced no threshold elevation. This suggests that motion in high spatial frequency targets is detected by a mechanism which is not sensitive to uniform flicker.

Effects of changing experimental conditions on spatial frequency tuning of flicker adaptation. The previous experiment was performed with very rapidly drifting gratings. The goal of the subsequent study was to determine whether a similar spatial tuning for flicker adaptation would be obtained with a slower drift rate. In Fig. 7 results are shown for an experiment in which flicker and drift frequencies were slowed to 8 Hz.

The threshold elevation curve exhibits a form similar to that found with the 16 Hz temporal frequency. Figure 8 shows further results from an 8 Hz experiment in which data were collected by a two-alternative forced-choice method, luminance was reduced by almost a log unit (from 100 to 11 cd/m²) and field size was increased (from 4.0° to 5.2°). These changes reduced the low spatial frequency attenuation of grat-

ing sensitivity. However, the threshold elevation curve retains a low-pass shape and the 3–4 c/deg cutoff. In a more recent study (Green, in preparation) it has been found that the threshold elevation produced by a uniform flicker mask has the same 3–4 c/deg upper limit even when the flicker frequency and drift rate are as low as 2.2 Hz. Spatial frequency tuning of the flicker adaptation effect therefore is highly consistent over a large range of experimental conditions.

Separate "detection" and "transient" threshold criteria. As mentioned in the introduction, the sensitivities of the sustained and transient systems are often (e.g. Keesey, 1972; Kulikowski and Tolhurst, 1973) determined by employing separate thresholds for detection of spatial and temporal luminance change. The logic is that when temporal change is seen at threshold, then detection is mediated by the transient system while a threshold percept of stationary pattern indicates that detection was mediated by the sustained system. If uniform flicker desensitizes only transient mechanisms, then adaptation should raise thresholds for temporal but not spatial change. To test this, an experiment was designed in which separate spatial and temporal thresholds were to be determined before and after adaptation. Unfortunately, it was not possible to establish a consistent pattern criterion for temporally modulated low spatial frequency gratings. We therefore switched to a slightly different strategy of employing separate

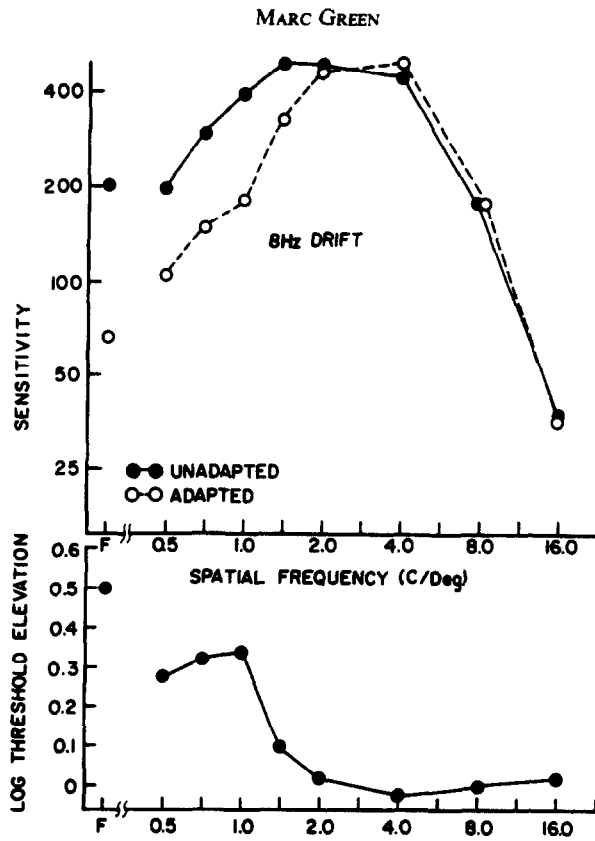


Fig. 7. Contrast sensitivity to 8 Hz drifting gratings before and after adaptation to 16 Hz flicker. The symbol "F" on the horizontal axis represents a condition in which the test stimulus was a uniform flickering field. Other details are the same as in Fig. 5. Observer: M.G.

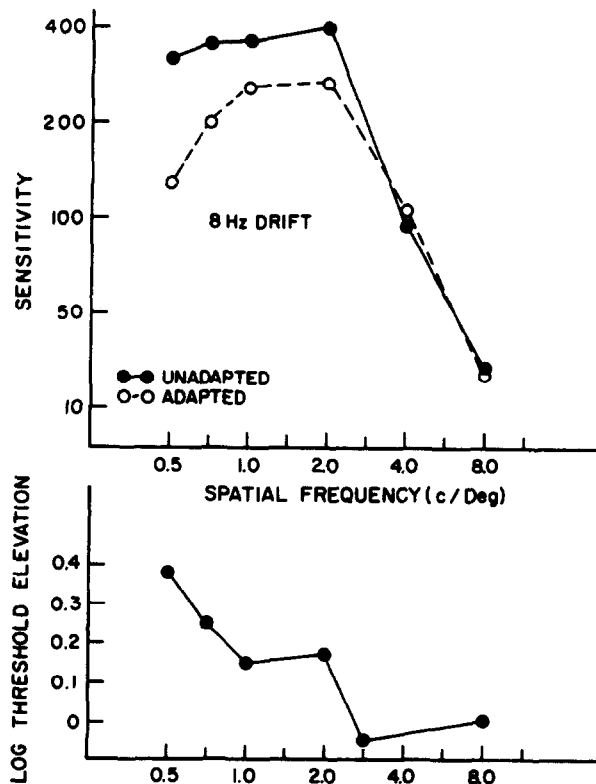


Fig. 8. Contrast sensitivity to 8 Hz drifting gratings before and after adaptation to 8 Hz flicker. The display was 5.2° dia with a mean luminance of 11 cd/m². Two-alternative forced-choice method was employed. Observer: R.K.

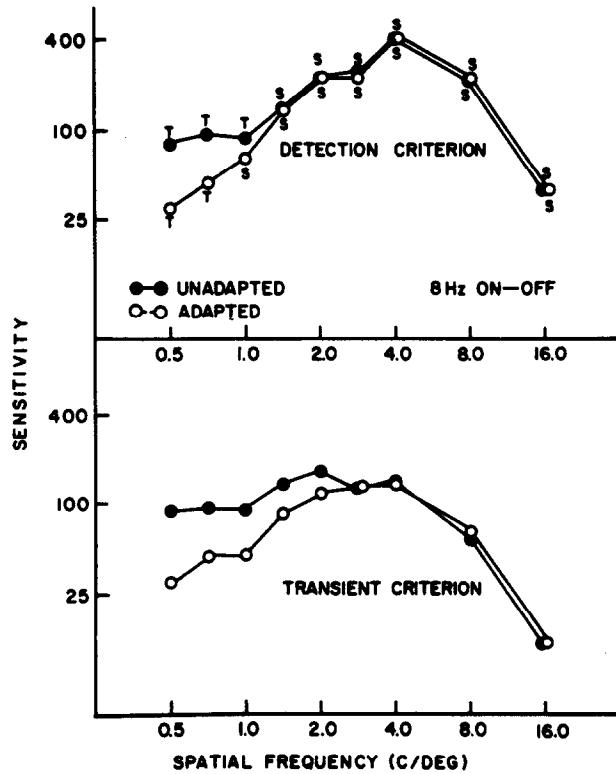


Fig. 9. Contrast sensitivity for 8 Hz on-off flickering gratings before and after adaptation to 8 Hz flicker. Upper panel shows data obtained with detection criterion and lower panel data obtained with transient criterion. The symbol "S" signifies that the grating appeared stationary at threshold and "T" that gratings were perceived as temporally modulated. Other details are the same as in Fig. 5. Observer: M.G.

"detection" and "transient" criteria (cf. Watson and Nachmias, 1977). With the detection criterion, observers simply set threshold for the perception of any just-detectable luminance modulation on the CRT screen but stated whether the target appeared temporally modulated (and presumably detected by the transient system) or stationary (and detected by the sustained system). If the grating appeared stationary, then the observer increased the contrast until the transient criterion, i.e. detection of temporal change, was reached. Gratings were modulated with 8 Hz sinusoidal on-off flicker since it proved relatively easy to employ the two different criteria with this form of temporal change. On-off flicker is like counterphase flicker in that it contains two components of equal amplitude moving in opposite directions. However, on-off flicker also contains a stationary component not present in counterphase flicker (Sekuler *et al.*, 1978).

The results obtained with the detection criterion are shown in the top panel of Fig. 9. As might be expected, low spatial frequency gratings were seen as temporally modulated (T) at threshold, while higher spatial frequency gratings appeared stationary (S). The threshold elevation was again obtained only at low spatial frequencies with no effect found above 1.5 c/deg. This is lower than the 3-4 c/deg limit found with counterphase flickering and drifting gratings.

The difference may have been due to detection of the stationary component on the on-off flicker. Most importantly, when gratings appeared stationary prior to adaptation, flicker adaptation failed to have any influence on threshold. This result supports the idea that flicker adaptation desensitizes the transient system but has no effect on a separate sustained system. The present data are complemented by previous experiments which demonstrated that when care is taken to switch the stimuli on and off very gradually, flicker adaptation (Green, 1979) and masking (Klein *et al.*, 1977) have no effect on detection of stationary gratings even at low spatial frequencies.

The bottom panel of the figure shows results obtained with the transient criterion. Changing criterion had the effect of increasing the size of the threshold elevation and increasing the spatial frequency at which it could be obtained from 1.5 to the ubiquitous 3-4 c/deg. A comparison of the threshold elevations produced by the two criteria is shown in Fig. 10 where it is obvious that in spite of the fact that observers were explicitly setting thresholds for temporal change, flicker adaptation again failed to have any influence on high spatial frequency sensitivity. This experiment has been repeated with drifting rather than flickering gratings and similar results were obtained. These data, then, provide more evidence that temporal change at high spatial frequencies is

processed by a mechanism separate from the transient system.

The role of display edges in flicker adaptation

It has been suggested above that flicker adaptation effects are obtained only with low spatial frequency gratings because they are detected by the transient system. A final observation was made to test a plausible alternative to this interpretation. The black edges of the CRT surround created spatial frequency components. Since these components would be low in spatial frequency, they would be expected to produce greatest adaptation effects on low spatial frequency test gratings (Blakemore and Campbell, 1969). A control procedure was performed to evaluate the significance of the display edges. An observer viewed two CRT screens combined to form a single channel by means of a beam splitter. One CRT contained drifting gratings as before, while the second was placed near the beam splitter so that it covered a visual angle of over 100° . Flicker produced on the second CRT therefore covered most of the visual field and created virtually no components within several octaves of the spatial frequency range of the test gratings. Under these conditions, flicker adaptation still produced a loss in sensitivity to drifting gratings. This result is consistent with the view that the transient system can be considered as a single low-pass channel in the spatial frequency domain (Legge, 1978; Wilson, 1980). Our conclusion therefore is that the display edges do not play a significant role in producing the flicker adaptation effect.

DISCUSSION

Evaluation of the sustained-transient dichotomy

In general, the results of the flicker adaptation experiments supported the idea that the human visual system contains separate transient and sustained systems. The threshold elevation produced by adaptation to uniform flicker was restricted to low spatial frequencies where gratings are presumably detected by the transient system (Kulikowski and Tolhurst, 1973). At high spatial frequencies, when detection is mediated by the sustained system, no adaptation effect was found. Evidence for separate sustained and transient mechanisms has also been found in several previous studies which employed flickering of flashed uniform fields. Green (in preparation) has shown that flickering fields mask drifting gratings only up to a spatial frequency of 4.0 c/deg, while Stromeyer *et al.* (1979) found that flickering fields greatly mask broad flickering bars but had minimal effect on detection of narrow bars. Similarly, it has been demonstrated that flashed uniform fields result in a transient masking effect on low but not high spatial frequency gratings (Green, 1981).

Data from previous experiments further support the present results in suggesting that the transition point where mediation of sensitivity switches from the transient to the sustained system occurs at about 3-4 c/deg. Kulikowski (1971) compared sensitivity for on-off and counterphase flickering gratings with the assumption that transient mechanisms would be twice as sensitive to the counterphase flicker. Counterphase sensitivity proved to be twice as great, but only for

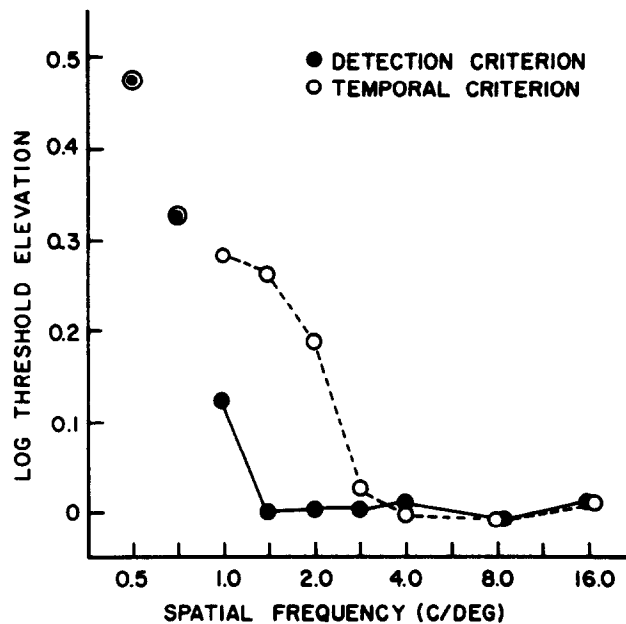


Fig. 10. Threshold elevation for 8 Hz on-off flickering gratings before and after adaptation to 8 Hz flicker. Open circles represent data obtained with a transient criterion and closed circles with a detection criterion. Observer: M.G.

gratings below 3 c/deg. More recently, Legge (1978), using a spatial frequency masking paradigm, and Wilson (1980), employing subthreshold summation between aperiodic stimuli, also have concluded that the transient system mediates detection only when spatial frequencies are below 3–4 c/deg.

Although the notion of separate transient and sustained systems is generally supported by the present data, our results do not entirely agree with the most commonly expressed version of the dichotomy, which was outlined in the introduction of this paper. The major point of inconsistency can be seen by comparing Figs 1(a) and (b). Figure 1(a) shows the spatial frequency sensitivity of the two systems proposed by Kulikowski and Tolhurst (1973). The transient system mediates detection of drifting low spatial frequency gratings but becomes less sensitive than the sustained system at higher spatial frequencies. However, the transient system continues to mediate perception of temporal change up to 30 c/deg. Our data are more consistent with a representation of the sustained and transient system sensitivities proposed by Legge (1978) and shown in Fig. 1(b). Here the transient system is totally insensitive above 3 c/deg. As a result, motion at higher spatial frequencies must be detected by the sustained system. Two pieces of evidence from the present experiment support this model. First, the threshold elevation produced by flicker adaptation was limited to spatial frequencies below 4 c/deg in spite of changes in drift rate, luminance, and psychophysical method. Moreover, even when thresholds for perception of temporal change were determined, no threshold elevation was obtained above the 4 c/deg limit. Second, it was found that drifting gratings were twice as detectable as counterphase flickering gratings except at 16 c/deg. This suggests that up to 8.0 c/deg, gratings were detected by direction-selective mechanism (Levinson and Sekuler, 1975). Failure of flicker adaptation to raise thresholds at 4.0 and 8.0 c/deg suggests that motion at these spatial frequencies is not detected by the transient system. This conclusion is supported by a more recent experiment (Green, in preparation) where it was found that flicker had no effect on detection of drifting 4.0 c/deg gratings even though direction of motion could be discriminated at threshold. The present data therefore suggests that temporal change at high spatial frequencies is processed by the transient system but rather by the sustained system. This view contradicts a basic tenet of the sustained-transient dichotomy which states (e.g. Tolhurst, 1973; Kulikowski and Tolhurst, 1973) that the sustained system plays a specialized role in perception by signaling only stationary pattern. However, physiological data (e.g. Hubel, 1959; Goodwin *et al.*, 1975) showing that simple cells, which presumably play a large role in form vision, are often directionally selective support the view that neural elements which code pattern can also code motion.

The idea of separate sustained and transient motion detection mechanisms has recently been proposed in

other papers (Bonnet, 1977; Lovegrove *et al.*, 1979). In fact, the notion that the human visual system must contain at least two distinct motion detection mechanisms goes back over a hundred years. Although originally invoked to explain differences between real and apparent motion (Exner, 1875), recent authors (e.g. Leibowitz, 1955; Braddick, 1974; Pantle, 1973; Bonnet, 1977; Anstis, 1978) have developed more sophisticated two-process models with the defining characteristics of each of the two mechanisms differing somewhat from paper to paper. Taken together, however, there does seem to be some consensus among authors that pattern information plays a role in the operation of only one of the two mechanisms. The first motion detection system directly codes velocity by processing point-by-point changes of the retinal light distribution. A different mechanism first segregates out spatial structure and only then senses motion by correlating changes in the position of the form information. Such a scheme is quite consistent with the idea of separate sustained and transient motion detection mechanisms and suggests an explanation for why flicker adaptation failed to increase threshold for motion in high spatial frequency gratings. Flicker adaptation was shown to have no effect on detecting spatial structure. The sustained motion mechanism was presumably not affected by flicker adaptation because it first detects spatial structure and only then processed motion.

Response of sustained and transient mechanisms to uniform flicker

It is interesting to speculate on why sustained and transient mechanisms differ in their responsiveness to uniform flicker. The response of a visual neuron depends on the distribution of light falling in its receptive field. Light falling in some areas is excitatory and increases the output of the neuron, while light falling in other regions has an antagonistic inhibitory effect. When the entire receptive field of the neuron is evenly illuminated, no net response would occur if the excitatory and inhibitory components (1) were of equal strength and (2) developed with the same time course. Absence of either of these properties could result in a response to uniform flicker. There is some psychophysical evidence that visual mechanisms operating at low spatial frequencies, where the transient system presumably is sensitive, respond with delayed inhibition. For example, the presence of a delayed inhibitory response can be demonstrated by determining the temporal frequency sensitivity of a visual mechanism. If there is asynchrony between excitation and inhibition, the temporal frequency response will be band-pass in nature, exhibiting a low-frequency attenuation. Conversely, a low-pass response would be obtained when no delayed inhibitory component was present in the mechanism's response. The band-pass response is, in fact, usually found only with low spatial frequency gratings, and several studies (e.g. Robson, 1966; Koenderink and

van Doorn, 1979) have found that the division between band-pass and low-pass temporal frequency curves occurs at about 4 c/deg. Further, Watson and Nachmias (1977) determined the temporal development of excitation and inhibition by measuring sub-threshold summation between gratings presented for only 4 msec. Even though the very short durations highly favored detection by the transient system, delayed inhibition was found only when low spatial frequency gratings were employed.

In summary, the present study has employed adaptation to uniform flicker as a tool to distinguish sustained and transient visual mechanisms. The results suggest a conclusion which is intermediate between the more extreme viewpoints that (1) perception of spatial and temporal luminance change is mediated by two functionally distinct visual elements (Tolhurst, 1973; Kulikowski and Tolhurst, 1973) and (2) spatio-temporal vision can be explained by a single mechanism (Lennie, 1980). While our data support the view that separate transient and sustained mechanisms exist, it appears that the two systems are not completely specialized with regard to their roles in perception. The transient system responds to uniform flicker and motion and seems to be primarily concerned with signaling temporal change. Although the sustained system may be a form analyzing mechanism, it is also capable of signaling motion perceptions. Finally, the distinguishing characteristics of these two systems may be the synchrony with which excitatory and inhibitory responses develop.

REFERENCES

- Anstis S. M. (1978) Apparent movement. In *Handbook of Sensory Physiology: Vol. VIII, Perception* (Edited by Held R., Leibowitz H. W. and Teuber H. L.), pp. 656-673. Springer-Verlag, Berlin.
- Blakemore C. and Campbell F. W. (1969) On the existence of neurons in the human visual system selectively sensitive to orientation and size of retinal images. *J. Physiol.* **203**, 237-260.
- Bonnet C. (1977) Visual motion detection models: features and frequency filters. *Perception* **6**, 491-500.
- Bowditch H. P. and Hall G. (1981) Optical illusion of motion. *J. Physiol.* **3**, 296-301.
- Braddick O. A. (1974) A short-range process in apparent motion. *Vision Res.* **14**, 519-527.
- Braddick O., Campbell F. W. and Atkinson J. (1978) Channels in vision: basic aspects. In *Handbook of Sensory Physiology: Vol. VIII, Perception* (Edited by Held R., Leibowitz H. W. and Teuber H. L.), pp. 3-38. Springer-Verlag, Berlin.
- Breitmeyer B. and Ganz L. (1976) Implication of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. *Psychol. Rev.* **83**, 1-36.
- Exner S. (1875) Über das Sehen von Bewegungen und die Theorie des zusammengesetzten Auges. *Sitz. Akad. Wissen. Wien* **72**, 156-190.
- Goodwin A. W., Henry G. H. and Bishop P. O. (1975) Direction selectivity of simple striate cells: properties and mechanisms. *J. Neurophysiol.* **38**, 1500-1522.
- Green M. (1979) Effects of flicker adaptation on grating detection. *Invest. Ophthalm. visual Sci.* **18**, 91.
- Green M. (1980) Detection and discrimination of moving gratings masked by flicker. In preparation.
- Green M. (1981) Spatial frequency effects in masking by light. *Vision Res.* **21**, 861-866.
- Hanly M. and MacKay D. M. (1979) Polarity-sensitive perceptual adaptation to temporal sawtooth modulation of luminance. *Expl. Brain Res.* **35**, 37-46.
- Howell E. and Hess R. (1978) The functional area for summation to threshold for sinusoidal gratings. *Vision Res.* **18**, 375-378.
- Hubel D. H. (1959) Single-unit activity in striate cortex of unrestrained cats. *J. Physiol.* **147**, 226-238.
- Klein S., Stromeyer C. and Madsen J. (1977) Counterphase flickering and moving gratings masked with spatially uniform, flickering fields. *Invest. Ophthalm. visual Sci. Suppl.* **16**, 10.
- Koenderink J. and van Doorn A. (1979) Spatiotemporal contrast detection threshold surface is bimodal. *Opt. Lett.* **8**, 32-34.
- Kulikowski J. J. (1971) Some stimulus parameters affecting spatial and temporal resolution of human vision. *Vision Res.* **11**, 83-93.
- Kulikowski J. J. and Tolhurst D. J. (1973) Psychophysical evidence for sustained and transient detectors in human vision. *J. Physiol.* **232**, 149-162.
- Legge G. (1978) Sustained and transient mechanisms in human vision: temporal and spatial properties. *Vision Res.* **18**, 69-82.
- Leibowitz H. (1955) The relation between the rate threshold for the perception of movement and luminance for various durations of exposure. *J. exp. Psychol.* **49**, 209-214.
- Lennie P. (1980) Perceptual signs of parallel pathways. *Phil. Trans. R. Soc. B* **290**, 23-37.
- Levinson E. and Sekuler R. (1975) The independence of channels in human vision selective for direction of movement. *J. Physiol.* **250**, 347-366.
- Lovegrove W., Over W. and Broerse J. (1979) Color selectivity in motion after-effect. *Percept. Psychophys.* **25**, 157-159.
- MacLeod D. (1978) Visual sensitivity. *Ann. Rev. Psychol.* **29**, 613-645.
- McCann J. and Hall J. (1980) Effects of average-luminance surrounds on the visibility of sine-wave gratings. *J. opt. Soc. Am.* **70**, 212-219.
- McCann J., Savoy R. and Hall J. (1978) Visibility of frequency sine-wave targets: dependence on the number of cycles and surround parameters. *Vision Res.* **18**, 891-894.
- Nes F. L. van, Koenderink J. J., Nas H. and Bouman M. A. (1967) Spatiotemporal modulation transfer function of the human eye. *J. Opt. Soc. Am.* **57**, 1082-1088.
- Nilsson T., Richmond C. and Nelson T. (1975) Flicker adaptation shows evidence of many channels selectively sensitive to temporal frequency. *Vision Res.* **15**, 621-623.
- Pantle A. (1971) Flicker adaptation I: Effect of visual sensitivity to fluctuations of light intensity. *Vision Res.* **11**, 943-952.
- Pantle A., Lehmkuhle S. and Caudill S. (1978) On the capacity of directionally selective mechanisms to encode different dimensions of moving stimuli. *Perception* **7**, 261-267.
- Pantle A. and Sekuler R. (1968) Velocity-sensitive elements in human vision: initial psychophysical evidence. *Vision Res.* **8**, 445-450.
- Robson J. G. (1966) Spatial and temporal contrast sensitivity functions of the human eye. *J. opt. Soc. Am.* **56**, 1141.
- Sekuler R., Pantle A. and Levinson E. (1978) Physiological basis of motion perception. In *Handbook of Sensory Physiology: Vol. VIII, Perception* (Edited by Held R., Leibowitz H. W. and Teuber H. L.), pp. 67-96. Springer-Verlag, Berlin.

- Smith R. A. (1970) Adaptation of visual contrast sensitivity to specific temporal frequencies. *Vision Res.* **10**, 275-279.
- Smith R. A. (1971) Studies of temporal frequency adaptation in visual contrast sensitivity. *J. Physiol.* **216**, 531-552.
- Stecher S., Sigel C. and Lange R. (1973) Spatial frequency channels in human vision and threshold for adaptation. *Vision Res.* **13**, 1691-1700.
- Stromeyer C., Madsen J., Klein S. and Zeevi Y. (1978) Movement-selective mechanisms in human vision selective to high spatial frequencies. *J. opt. Soc. Am.* **68**, 1002-1005.
- Stromeyer C., Madsen J. and Klein S. (1979) Direction-selective adaption with very slow motion. *J. opt. Soc. Am.* **69**, 1039-1041.
- Stromeyer C., Zeevi Y. and Klein S. (1979) Response of visual mechanisms to stimulus onset and offset. *J. opt. Soc. Am.* **69**, 1350-1354.
- Tolhurst D. J., Sharpe C. R. and Hart G. (1973) Analysis of the drift rate of moving sinusoidal gratings. *Vision Res.* **13**, 2545-2555.
- Watson A. B. and Nachmias J. (1977) Patterns of temporal interaction in the detection of gratings. *Vision Res.* **17**, 893-902.
- Wetherill G. B. and Levitt H. (1965) Sequential estimation of points on a psychometric function. *Br. J. Math. Stat. Psychol.* **18**, 1-9.
- Wilson H. (1980) Spatiotemporal characterization of a transient mechanism in the human visual system. *Vision Res.* **20**, 443-452.