TIME-COURSE OF SPATIO-TEMPORAL ADAPTATION; WITH RESPECT TO THE EXISTENCE OF SEPARATE SPATIAL AND TEMPORAL VISUAL MECHANISMS

STEVEN CHAIM PANISH

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TIME-COURSE OF SPATIO-TEMPORAL ADAPTATION; WITH RESPECT TO THE EXISTENCE OF SEPARATE SPATIAL AND TEMPORAL VISUAL MECHANISMS

Abstract
A series of experiments examined the hypothesis that spatial and temporal variation are processed by separate visual mechanisms. The first set of experiments determined that contrast thresholds set using spatial and temporal criteria covaried for counterphase-flickered gratings over a wide range of spatial and temporal frequencies. The two threshold curves appeared more independent when gratings were drifted, but this probably resulted from different patterns of eye movements within the two tasks.

A second set of experiments measured the time-course of adaptation under conditions designed to isolate the two hypothetical mechanisms, in an attempt to record a temporal "fingerprint" characterizing each mechanism. A test-probe procedure was used to determine contrast thresholds over 60 seconds of adaptation rise-time and 128 seconds of decay. Time constants of exponential curves fit to these data showed no pattern which could be related to the two mechanism hypothesis. A corresponding experiment categorized the appearance of near-threshold gratings during adaptation buildup and decay. When corrected for false-alarm rates, the perception of the stimuli were always pattern, or both pattern and flicker, even when a temporal mechanism should have performed the detection. These results uniformly fail to support the two mechanism hypothesis.

Keywords
Psychology, Experimental
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WITH RESPECT TO THE EXISTENCE OF
SEPARATE SPATIAL AND TEMPORAL VISUAL MECHANISMS

by

STEVEN CHAIM PANISH
B.A., Dickinson College, 1974
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DISSERTATION

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Durham, New Hampshire
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ABSTRACT

TIME COURSE OF SPATIO-TEMPORAL ADAPTATION;
WITH RESPECT TO THE EXISTENCE OF SEPARATE
SPATIAL AND TEMPORAL VISUAL MECHANISMS

by

STEVEN CHAIM PANISH

University of New Hampshire, September, 1982

A series of experiments was conducted to examine the hypothesis that spatial and temporal variation are processed by independent visual mechanisms. The first set of experiments used a two-criterion threshold technique to determine that spatial and temporal thresholds of counterphase flickered sinusoidal gratings covaried over a wide range of spatial and temporal frequencies. This contradicts previous reports. When drifting gratings were used, the two threshold curves appeared more independent. However, this apparent independence probably resulted from different patterns of eye movement within the two tasks.

A second set of experiments measured the time-course of adaptation under conditions designed to isolate the hypothetical spatial and temporal mechanisms. This procedure attempted to use adaptation time-course as a fingerprint to characterize the mechanism being tested. A test probe insertion procedure was used to determine contrast thresholds during 60 seconds of adaptation rise
time and 128 seconds of decay time. The resulting rise time and decay time threshold elevation curves were fit with exponential functions. The time constants of the fits showed no pattern which could be explained in terms of the two mechanisms hypothesis. A corresponding experiment enabled the subject to categorize the perception of the same test gratings at a series of near-threshold contrasts during adaptation buildup and decay. The two-mechanism hypothesis would predict that a temporal system would yield the perception of flicker at detection threshold, and a spatial system would yield the perception of form. However, this pattern was not observed during testing under the conditions designed to isolate each of the two mechanisms. When corrected for false alarm rates, the perception of the stimulus at threshold was always either form or both form and flicker, irrespective of which mechanism should have performed the detection.

It is clear that the time-course of adaptation differs when using different spatial and temporal stimulus parameters. However, no meaningful pattern emerges from these data which suggests the existence of separate spatial and temporal mechanisms. Neither the adaptation time-course experiments nor the two-criterion threshold experiments conducted in this study provide support for the two-mechanisms hypothesis.
I. INTRODUCTION

Results from several areas of research suggest a dissociation in the processing of spatial information (form) and temporal information (motion or flicker). Different contrast thresholds for the detection of pattern and flicker have been interpreted as resulting from functionally different processing mechanisms. These hypothetical mechanisms have been referred to as temporal and spatial, or transient and sustained (Tolhurst, 1973, 1975). Other experimenters consider it more likely that there exists a continuum of mechanisms subserving spatial and temporal perception (Graham, 1980, personal communication). Results from psychophysical adaptation experiments suggest the existence of functionally defined information carrying mechanisms, also referred to as channels, having varying, limited ranges of spatial and temporal sensitivity (Tolhurst, 1973). Channels responsive to flicker are thought to be optimally responsive (tuned) to low and moderate spatial frequencies (0-3 cycles/degree), while channels responding to spatial aspects of the stimulus are predominantly tuned to higher spatial-frequencies (2 c/d and up to the limits of acuity). There exists an intermediate range of spatial and temporal conditions where both sorts of channels are presumed to function (Tolhurst, 1975a). Neurophysiologists have categorized cells which differ in sensitivity and form of response to temporally modulated
spatial stimuli (Ikeda and Wright, 1972) and have related these categories to the psychophysical data. However, the validity of both the electrophysiological and the psychophysical categorizations have been disputed (Rowe and Stone, 1977, 1979; Arend and Lange, 1979).

Several experimenters have used adaptation paradigms to demonstrate the proposed divergence in processing of spatial and temporal information. The paradigms have used tests of both contrast threshold (Tolhurst, Sharpe and Hart, 1973) and spatial-frequency identification (Panish, Swift, and Smith, 1980). However, the physiology of adaptation is poorly understood despite its wide use in psychophysics.

Adaptation is a functional description of effects arising from the prolonged presentation of a stimulus. In the aforementioned studies, adaptation to a grating results in alterations in the contrast sensitivity function and in the perception of spatial frequency. The physiological process(es) underlying these aftereffects are not known, although the most often cited hypotheses involve either fatigue of a neural mechanism following overstimulation, or a buildup of inhibition between channels.

Adaptation time-course has not been the focus of any major studies, although it was considered (in a limited manner) in some of the early studies of spatial adaptation (Blakemore and Campbell, 1969; Blakemore, Munsey, and Ridley, 1973). A few recent studies have dealt directly with time-course, but these have also been quite limited in scope, utilizing few of the many parameters relevant to
adaptation (Bodinger, 1978; Daugman, 1979). Results have conflicted in such matters as the relationship between adaptation time and magnitude of contrast reduction, and the existence of a maximal or full adaptation beyond which no further effects take place. The relationship between adaptation parameters and the duration of contrast reduction has been only sketchily examined, and comparison of adaptation effects using different measures (contrast sensitivity, suprathreshold contrast matching, contrast discrimination, and spatial discrimination such as the spatial-frequency shift) are nonexistent.

It is not known whether spatial adaptation occurs at one or many levels of processing in the visual system. If we assume adaptation has multiple loci, it is possible the adaptation originating in different locations may display different parameters, especially temporal parameters. Thus, the proposed mechanisms mediating temporal and spatial perception might differ in the form of their decay functions, as they appear to differ in their sensitivities.

This study investigated the decay of grating adaptation to find a qualitative difference between the temporal and sustained systems. The project first attempted to replicate the separate flicker and form sensitivity functions which were reported by Kulikowski and Tolhurst (1973). Adaptation experiments were then conducted, using a test stimulus having spatial and temporal parameters at which the hypothetical spatial and temporal mechanisms had equal
sensitivity. In each session, parameters of the adaptation stimulus were biased towards the preferred parameters of one of the two proposed mechanisms. This procedure should have preferentially adapted that mechanism. Contrast thresholds were tested throughout the rise and decay of adaptation. It was predicted that the adaptation time-course of the less adapted (hence more sensitive) mechanism would be revealed by the threshold tests. If these thresholds are correlated with the appearance of the test stimulus at threshold, it should allow identification of the system performing the detection. This was accomplished through use of a subsequent experiment in which the subject categorized the appearance of test stimuli at near-threshold contrasts, using a bias-corrected, multiple-choice rating procedure.
II. EVIDENCE BEARING ON THE SPATIAL-TEMPORAL DICHOTOMY

The two spatial and temporal mechanisms proposed in the psychophysical literature originated by analogy to related classificatory schemes that had been proposed in the neurophysiological literature.

A. Electrophysiological Evidence

Enroth-Cugell and Robson (1966) characterized cat retinal ganglion cells in terms of their spatial summation properties, denoting cells with approximately linear summation x-cells and cells with highly non-linear summation y-cells. The y-cells were shown to increase their response rate when gratings drifted across the field, while x-cells did not.

A related classificatory scheme was put forth by Cleland, Dubin and Levick (1971) who suggested use of the terms sustained and transient response types for the cat x- and y-cells respectively. Their classificatory scheme considers the temporal profile of the cell's response to be a proper determinant for classification. This proposition has been strongly contested by Rowe and Stone (1977, 1979) who favor a more explicitly functionalist classification. (Although the terminology originally referred to the response characteristics of the cell, the experimenters noted that sustained and transient also came close to describing the presumed function of the cells (Cleland et
It is in this latter sense that the terms have come to be accepted within the psychophysics community, although the use of the terms remains somewhat ambiguous.

Presented with a small target spot, transient cells showed a sharp on-response, then slowed their discharge, returning to the pre-exposure baseline after a few seconds. The sustained cells showed some decrement after the initial response, but continued to fire above the baseline level for the one-minute exposure period.

Sustained retinal ganglion cells modulated their discharge to moving gratings about a mean rate, until the gratings were of high enough spatial-frequency to produce no change in response (4 c/d). Transient cells initially showed similar modulation, but it was replaced by an unmodulated increase in mean discharge rate which was maintained as long as the grating was moving. High frequency gratings (4 c/d) produced only a brief on-response when movement began. The transient cells also responded to gratings moving at higher velocity than did the sustained cells. Optimal spatial frequency was lower for the transient cells. Sustained retinal ganglion cells had lower conduction velocities than the transient cells. The experimenters also found that cat LGN cells could be classified in the same manner as the retinal ganglion cells.

Subsequent studies have utilized (separately) both the x/y and sustained/transient classifications. Both schemes have been expanded to account for cells resisting pigeonholing. The x/y categories are now the w/x/y (Stone
and Hoffman, 1972; Rodieck, 1973). The term w was chosen so that the alphabetical sequence w/x/y would correspond to increasing axonal velocities, but w-cells also differ from x- and y-cells in other properties: being generally smaller, having larger receptive fields and responding in both a phasic (sustained response) and tonic (transient response) manner with different stimulus parameters. The expansion of the sustained and transient classification has come from Cleland and Levick (1974) who proposed a complex scheme which retains use of the differing sustained/transient response characteristics and also considers the form of the receptive fields. This classification is essentialist in that it stresses the nature (essence in the Aristotelian sense) of the response. The w/x/y scheme is more functionalist in that its categories are primarily concerned with hypotheses regarding the functional niche of the cell rather than specific qualities of the cell (Rowe and Stone, 1977). In spite of the differences of approach, the creators of both schemes have at heart the concept that the two categories fulfill differing roles with respect to pattern and temporal vision. Both schemes are thus functionalist in intent if not precisely so in practice.

Ikeda and Wright (1974) applied the sustained/transient classification to cat cortical cells. Sustained cortical cells generally had peak response at higher spatial frequencies than the transient cortical cells, as well as narrower spatial-frequency bandwidths.
Essentially similar results, showing sustained and transient responding cells, have been obtained with primates. Gouras (1969) and Scobey and Horowitz (1976) have classified monkey retinal ganglion cells as tonic (sustained) or phasic (transient). Other experimenters have used the x/y classification, but results are substantially similar. Transient cells were found to have higher conduction velocities and decreased high spatial-frequency sensitivity relative to cells which yielded sustained response to stationary high frequency patterns (Marrocco, 1976; Sherman et al, 1976).

More recent studies have explored the reliability of the categorizations. A recent review (Lennie, 1980) cites several studies which find that the x/y (or sustained/transient) distinction breaks down under a variety of stimulus conditions. The problem is particularly acute for the sustained/transient schema. For instance, at low contrast the response of cat x- and y-cells showed little difference (Shapely and Victor, 1978). The properties of the different cell types also differ relative to retinal eccentricity, with both types of cells tending to give more transient response toward the periphery (Cleland and Levick, 1974). With respect to the relationship of these cell types to the psychophysically defined spatial and temporal mechanisms, Lennie (1980) comments that cat y-cells and x-cells are equally sensitive to low spatial-frequencies.
B. Psychophysical Evidence for the Sustained-Transient Dichotomy

Psychophysical evidence bearing on the sustained-transient dichotomy has been obtained with a variety of procedures.

i. Detection Thresholds. Several experimenters have noted that different contrast detection thresholds can be set for a moving or temporally modulated (flickering) stimulus. One is the threshold for the perception of flicker, or movement; the other the contrast at which the spatial form of the stimulus becomes visible (Keesey, 1972; Kulikowski and Tolhurst, 1973; Kingsmith and Kulikowski, 1975).

Kulikowski and Tolhurst (1973) and Tolhurst (1973) postulated the existence of spatial and temporal mechanisms which were defined in terms of these distinct psychophysical thresholds. The spatial mechanism was most sensitive at high spatial-frequency and low temporal frequency, and was proposed to be responsible for the perception of form. The temporal system was most sensitive at low spatial-frequency and high temporal frequency, and was proposed to underly the sensations of motion and flicker. These psychophysically defined mechanisms were considered analogous to the x/y and sustained/transient categories of the neurophysiologists.

This two-criterion threshold technique has been used in conjunction with other procedures to identify the system
performing a detection task. Kulikowski and Tolhurst (1973) measured sensitivity to spatial-frequency gratings which were flickered either in an on-off fashion (the contrast was cycled from 0 to peak value, but the bars remained stationary), or in spatial counterphase (contrast was cycled as in the on-off case, but at 0 contrast the spatial phase shifted by 180 degrees). In the counterphase-flickered condition, each point in the spatial cycle undergoes twice the luminance variation that it does in the on-off condition. Over a spatial-frequency range from 1 to 12 c/d, the ratio of the contrast detection thresholds (the contrast at which the screen was first perceived to be non-uniform) for the two kinds of flicker decreased from 2 to 1. Use of the detection threshold showed this ratio of 2 only below 1.5 c/d. When the task was changed to one of identifying flicker in the stimulus (the flicker threshold), a ratio of 2 was maintained over the entire spatial-frequency range tested. This was interpreted as showing that the flicker identification task was tapping a postulated transient system which showed twice the sensitivity to counterphase-flickered gratings as to on-off flickered gratings. Below 1.5 c/d, the temporal system was believed to be performing the detection during both tasks by virtue of its superior sensitivity at low spatial-frequencies.

The decline of the sensitivity ratio above 1.5 c/d was interpreted to mean that a postulated spatial system was active in the high spatial-frequency region. The authors
explain the difference in sensitivity as reflecting the nature of the response properties of the two proposed systems. The temporal system was believed to generate a transient response to temporal changes in luminance. Luminance varied twice as much at any one point in the counterphase condition than in the on-off condition, so the postulated temporal system would show twice the sensitivity to counterphase flicker as to on-off flicker. The spatial system responded to the variation of luminance from a mean level, by varying response about a mean level of discharge. Both forms of flicker had the same depth of modulation at peak contrast, so the spatial system would be equally sensitive to them.

Burbeck (1981) used a novel discrimination procedure to determine criterion-free thresholds for flicker and form. Her procedure involved a complex paradigm in which the subject was forced to detect flicker in a choice between a flickering low-contrast grating and a non-flickering grating of the same spatial-frequency. The gratings had to be matched for apparent contrast, and false alarm rate was monitored by the use of catch trials. A corresponding condition tested pattern sensitivity by forcing the subject to discriminate between flickering gratings and flickering uniform fields. The resulting data constitute threshold surfaces for the perception of flicker and form. Temporal response functions from these surfaces were quite different from those resulting from the early method of adjustment studies of Keesey (1971), Kulikowski and Tolhurst (1973),
and Harris (1980). Pattern thresholds were generally found to be lower than flicker thresholds. The pattern threshold surface largely corresponded to the detection threshold surface. Pattern sensitivity was higher than flicker sensitivity at all but the highest temporal frequencies tested. However, when Burbeck attempted the classic method of adjustment procedure, she obtained results of the usual form, which showed flicker to be more perceptible at low spatial frequencies, and pattern to be more perceptible at high spatial frequencies. These data differ in detail from those of Kulikowski and Tolhurst, but show a qualitatively similar pattern.

Breitmeyer and Julesz (1975) measured detection thresholds for gratings having either abrupt or gradual onsets and offsets. At low spatial frequencies (below 8 c/d for one observer, and 3 c/d for the other) thresholds were 50-100 percent lower for the abruptly (more transiently) presented stimuli.

ii. Adaptation Experiments. Tolhurst, Sharpe and Hart (1973) adapted subjects to moving gratings and measured the tuning (frequency specificity) of the two systems by testing thresholds for motion and form. Temporal tuning was only found when the temporal task (motion detection) was used. The spatial system therefore appears to have little or no tuning for motion. It would be useful to replicate this experiment using counterphase flickered gratings. This could be of value in investigating whether there are
differences in the processing of flicker and motion.

Panish, Swift and Smith (1980) corroborated this lack of temporal tuning of the sustained mechanism by using the magnitude of the spatial-frequency shift as a measure of the tuning of the temporal system. This experiment measured the perceived spatial frequency of a test grating following adaptation to a grating of similar but not identical spatial frequency. The test and adapt stimuli varied from 1 to 4 cycles/degree, and temporal velocities varied from -5 to 15 degrees/second (negative velocities indicate a reversal of the direction of motion of the test grating relative to the adapt grating). Because the task involves identification of stimulus spatial-frequency, irrespective of velocity, the experimenters assumed the spatial system was being tested.

The experiment used the method of constant stimuli in conjunction with a forced-choice double-staircase procedure. Following adaptation of an area in one side of the visual field, a frequency-shifted grating presented in that field was compared to a grating in the unadapted field. The staircase procedure altered the spatial-frequency of the grating in the unadapted field in order to match it to the apparent spatial frequency of the grating in the adapted field. Results were expressed as the ratio of the apparent frequency of the shifted grating to the actual frequency. Temporal tuning within a spatial mechanism was tested by varying test grating velocities while using the same spatial frequency. The adapt gratings had the same velocity and
spatial-frequency for all test combinations which were to be compared directly with one another. Tuning was to be manifested as a maximal spatial-frequency shift where adapt and test velocities were identical. Results clearly demonstrated the absence of tuning for either velocity or direction of movement: the magnitude of the spatial frequency shift was invariant with respect to different test velocities over the range of parameters tested. This range would be difficult to extend because of the difficulties inherent in using very low and very high spatial frequency gratings. These results would seem to indicate a rather dramatic separation of the spatial and velocity mechanisms. The separation could be particular to velocity mechanisms and not be descriptive of more general temporal mechanisms. It would be valuable to repeat this experiment with counterphase flickered gratings rather than moving gratings.

Green (1981) conducted an extensive series of adaptation experiments which compared the ability of uniform flickered fields and moving gratings to produce threshold elevation in the same two types of test stimuli. The intent was to investigate whether uniform field flicker and motion were detected by the same mechanisms. The results showed that each of the two forms of temporal variation had the ability to elevate the threshold for the other. Most of the experiments were devoted to demonstrating that sensitivity to drifting gratings is impaired by full-field flicker only at low spatial frequencies. The upper limit of the affected range is dependent on the particular paradigm and varies
between 1 and 4 c/d. Green interpreted these data to mean that detection of flicker and drift are performed by direction-selective temporal mechanisms active below 4 c/d. However, it is also possible that these low-frequency effects result from the spatial content of the full field display. The screen itself has a spatial-frequency which is directly related to its width, which in these experiments varied between 4 and 7 degrees. If the screen is considered to be a half-cycle, the effective spatial-frequency of the display is between 0.13 and 0.07 c/d. Spatial-frequency tuning has been found to broaden at low spatial-frequencies, and it is conceivable that Green's low spatial frequency threshold elevations result from spatial adaptation.

Green (1981) also attempted to use the two threshold technique to evaluate the sensation following adaptation. He reported that uniform spatial criteria could not be maintained and altered the procedure. The technique used was that of Watson and Nachmias (1977). In their procedure, the subject first set a detection threshold (detection criterion) and reported whether the percept was one of temporal modulation or unmoving form. If the latter, contrast was increased until motion was perceived (transient criterion). Green's results showed that when the (moving) test grating appeared stationary at threshold prior to flicker adaptation, no threshold elevation resulted when using a detection criterion. In all instances, the test grating was rated as stationary both before and after
adaptation. Using this detection criterion, no threshold elevation was observed at spatial-frequencies higher than 1 c/d. The transient criterion, in which motion was clearly perceived in the test stimulus, showed threshold elevation up to about 3 c/d. This latter figure is interpreted by Green as indicating the upper limit of the temporal system. This is a reasonable conclusion, except for the problems inherent in reliably setting the two criteria. Because it is also clear that we perceive motion at spatial-frequencies higher than this limit, Green also concluded that the spatial system is capable of signaling motion. It is unclear, however, why the two-criterion technique should ever work if the spatial system can itself signal motion or flicker. Thus, Green's logic is inconsistent unless a spatial mechanism is modeled which itself has separate temporal and spatial thresholds. Such a mechanism makes the dichotomy more difficult to test and less meaningful.

iii. Subthreshold Additivity Paradigms. Kingsmith and Kulikowski (1975) measured the temporal and spatial thresholds of a flickering line in the presence of subthreshold flickering lines and gratings. They found a spatial mechanism that showed linear spatial summation of contrast and a temporal mechanism that was non-linear. The inferred receptive fields of the temporal mechanism were broader than those of the spatial mechanism; and the dimensions of the former increased with temporal frequency, while the strength of lateral inhibition decreased. In the
case of broad stimuli modulated at high temporal frequency, no surround inhibition was found. At threshold, this stimulus appeared to flicker, but not move, as was common for stimuli of higher spatial-frequency and lower temporal frequency.

Tolhurst (1975) measured the additivity of 4 msec-flashes of a grating presented within an 800 msec. subthreshold presentation of a grating of the same spatial frequency. The time between the onsets were varied. It was assumed the long presentation would subliminally excite channels sensitive to the grating, and that the effectiveness of the additivity of the short presentation would vary with the level of subliminal stimulation in the channel. If the subliminal response was transient in nature, additivity of the short flash should be effective for only a short time about onset and offset of the long stimulus. If the subliminal stimulation was sustained in form, the short presentation should add throughout the duration of the long presentation (or subtract, if the gratings were out of phase, and the mechanism(s) phase sensitive). Results for 2 c/d gratings clearly showed a transient additivity for about 100 msec. following onset of the long flash when the gratings were in phase. Sensitivity to the 4 msec. flash was decreased for about 100 msec. following offset of the long flash. These data resemble transient on and off responses at onset and offset of the 800 msec. presentation. When the two gratings were presented out of phase, the above relationships were
reversed. Masking occurred at onset of the long presentation, and additivity at offset.

Results for the 7.6 and 15 c/d were less clear. In-phase gratings showed additivity throughout the long presentation, thus appearing to show sustained response within the 7.6 c/d mechanism(s). There was no additivity, and perhaps some slight elevation of threshold (referred to as masking) for 450 msec., following offset of the long grating presentation. However, the results of the out-of-phase gratings did not invert the form of the response. At onset there was a transient masking effect (250 msec. long) followed at offset by transient additivity of about 200 msec. The same pattern of response was reported as occurring at 15 c/d, although these data were not shown. Tolhurst interpreted these results as showing that channels involved in detection of low spatial-frequency gratings have transient response, while channels responding maximally to 7.6 c/d and higher frequencies show sustained response. Tolhurst noted that an experiment which used reaction times as a measure of channel sensitivity (Tolhurst, 1975b) showed different results. Gratings of 2 c/d were detected by mechanisms showing predominantly sustained response. He accounted for the discrepancy by claiming the existence of both sorts of channels at 2 c/d. The short flash would be detected by a transient responding channel as before. However, (although not explicitly stated) a long flash would be detected initially by a transient mechanism, and then by
a sustained channel which would respond for the duration of the stimulus presentation.

Arend and Lange (1977) used a subthreshold additivity procedure to measure channel bandwidths for steady and flickering sinusoidal gratings at three spatial-frequencies. It was expected that the stimuli in the range of a temporal mechanism (i.e., low spatial-frequency with flicker) would show different tunings than thresholds set using a steady grating. In addition, thresholds were set using both temporal and spatial criteria. No such differences were evident. Tuning curves were plotted for the three test frequencies and all revealed narrow bandwidths, including 1 c/d flickered gratings, which were clearly in the range usually considered to be covered by the temporal mechanisms. This contradicts data obtained with adaptation which showed broad tuning (Tolhurst, 1973). It is possible that the tuning curves of the low frequency/temporal mechanisms are narrow, and that the envelope of the functions is broad. However, to attribute essentially similar tuning curves to two different mechanisms would violate Occam's Razor. Arend and Lange concluded that they did not have evidence for separate mechanisms and cited other studies in which results obtained using subthreshold additivity were inconsistent with those of adaptation paradigms (Nachmias, Sansbury, Vassilev and Weber, 1973; Stecher, Siegel and Lange, 1973).
iv. Thresholds for Stimuli Presented for Different Temporal Durations, With and Without Masking. Legge (1978) and Breitmeyer and Ganz (1977) measured contrast thresholds for briefly presented sinusoidal gratings. As presentation time was lengthened, contrast thresholds decreased. In Legge's data, spatial-frequencies of 1.5 c/d and higher yielded a three-stage decline in threshold as stimulus duration was increased. The two lower spatial frequencies showed only a two-stage decline. The abrupt change from a two-stage to a three-stage decline was presented as evidence of separate spatial and temporal systems. However, the slope differences between stages are quite small. In spite of the remarkably clean data (which resulted from 270 trials per point), it is still difficult to determine whether the fits to the data were optimal. Data from Breitmeyer and Ganz (1977) were not as clean as Legge's and only two stages were observed in the threshold decline. However, as spatial-frequency was increased, the elbow points (at which thresholds ceased to decline with duration) gradually migrated to longer test durations. Both studies concluded that mechanisms detecting high spatial frequencies required a longer processing time than low spatial frequencies before threshold became independent of duration. In both studies, the authors concluded that these differences resulted from the existence of separate spatial and temporal mechanisms.

In a similar experiment, Legge (1978) preceded and followed the test grating with briefly presented masking gratings, so called because they were expected to elevate
the contrast thresholds. Because the masking presentations were brief (20 msec.), they were expected to interact with transient onset and offset responses more than with sustained responses. Legge predicted that the low spatial frequency threshold functions from the first experiment would be evenly raised by the presence of the mask stimuli, but the high frequency functions would reach the same asymptote as without masking stimuli. This effect was observed.

Breitmeyer and Ganz (1977) presented a grating preceded by a 10 msec. mask of the same spatial-frequency. Spatial frequencies of 1 and 10 c/d were used. Thresholds were plotted as a function of stimulus onset asynchrony (SOA). The effect of the mask varied from facilitation at short SOA to desensitization (masking) at longer SOA. The low spatial frequency test yielded a multiphasic decline in sensitivity with increasing SOA, while the high spatial-frequency test declined smoothly. The differences were very small. These results were interpreted to mean that the impulse response of transient channels consist of a damped period of excitation alternating with inhibition, while sustained channels are marked by prolonged excitation and inhibition.

v. Reaction-Time Studies. Breitmeyer (1975), Lupp, Hauske and Wolf (1976,1979), and Vassilev and Mitov (1976) measured changes in response latencies with spatial frequency. In all cases, a smooth increase in latency was observed with increasing spatial frequency. This was
interpreted in terms of the increased conduction times of x/sustained units reported in the neurophysiological literature.

Tolhurst (1975b) measured reaction times to sinusoidal gratings which were presented using either abrupt or gradual onsets and offsets. Very low (0.2 c/d) spatial frequency gratings produced reaction times that clustered shortly after onset or offset. This was not the case with gratings higher than 1 c/d.

C. Conclusion

Three explicit models of dichotomous systems have been proposed in the psychophysical literature. The earliest was that of Kulikowski and Tolhurst (1973). They proposed that a spatial system (collection of channels) was solely responsible for the sensation of form, and a temporal system was solely responsible for the perception of flicker/motion. The systems were proposed to have roughly the same ranges of sensitivity to spatial and temporal stimuli, although the peak sensitivities of each system were believed to differ. This model required very similar sensitivity ranges for the two systems, so as to account for the ability to see both form and flicker/motion over the whole range of human spatial and temporal sensitivity.

Legge (1978) proposed a system in which the temporal mechanism operates over a reduced range, having no sensitivity to stimuli having spatial frequencies higher
than 4 c/d. Although not discussed, this would imply that the spatial system has the ability to convey the sensation of motion/flicker at spatial-frequencies higher than this value. Green (1981) presented a model similar to that of Legge (1978), but he explicitly noted that it required the spatial system to be able to convey the sensation of flicker/motion.

The majority of the evidence indicates a broadly different pattern of response to stimuli having high spatial frequency/low temporal frequency and low spatial frequency/high temporal frequency. Results at intermediate spatial frequencies show different response forms with different experimental paradigms. Adaptation procedures can produce two different tuning curves for moving stimuli, which appear to separate sensitivity to motion and sensitivity to spatial properties of the grating. Purely spatial tasks appear to produce no tuning for motion, while such tuning does emerge when a motion sensitive task is used. However, the two-criterion threshold technique that is used to obtain these separate functions has proven difficult to employ. Panish, Swift and Smith's (1980) failure to find motion tuning in a spatial task (the spatial-frequency shift) is probably a more reliable indication of a failure to find motion tuning in a spatial task. Such results may be indicative of the involvement of different mechanisms in motion and spatial perception. The data do not yet allow a distinction to be made between alternate hypotheses of dichotomous spatial and temporal
mechanisms, or the existence of a continuum of channels with smoothly varying sensitivity and response characteristics.

If, in fact, separate mechanisms exist and are analogous to the x- and y-cells of the electrophysiologists, we might expect behavioral properties of the systems to differ in ways other than those which have been tested. If the temporal system is a faster conducting system than the spatial system, as implied by the reaction-time data (Lupp et al., 1976, 1979; Breitmeyer, 1975) and the electrophysiological data (Ikeda and Wright, 1972), temporal measures would be likely to discriminate between them. It is also possible that separate mechanisms will adapt and recover from adaptation at different rates.
III. STUDIES OF THE TIME-COURSE OF ADAPTATION

Few experimenters have specifically examined the time-course of adaptation effects beyond the level of the experiments described in the initial paper of Blakemore and Campbell (1969). These experiments examined the time-course of recovery from adaptation to spatial-frequency gratings, using the method of adjustment to study detection thresholds. Recovery over time was found to be roughly exponential, but the function was not analyzed in detail. Blakemore, Munsey and Ridley (1973) examined both the rise time and decay of adaptation to gratings. They again used the method of adjustment, but with a contrast matching procedure rather than contrast threshold. Using adapting gratings of 70 percent contrast and frequencies of 5 and 10 c/d, they found that sensitivity was maximally depressed after 45 seconds of adaptation (0.8 log units of contrast reduction was achieved). Adaptation times from five seconds to five minutes were used. However, the time constant of recovery continued to lengthen with adapting time, so that five minutes of adaptation required six minutes to return to baseline sensitivity. It was this finding of maximal contrast sensitivity reduction after 45 seconds ("complete adaptation") that has justified the familiar topping up procedure. In this paradigm, contrast reduction following one minute or so of adaptation is considered to be maintained at a peak by periodic readaptation of roughly 15
seconds preceding each psychophysical trial. This procedure has been used because the contrast reduction is assumed to remain independent of the duration of effect after the initial adaptation period. In fact, this procedure may ignore the underlying events which constitute adaptation.

Blakemore, Nachmias and Sutton (1970) studied the time course of the spatial-frequency shift. They found roughly 2 minutes of adaptation (at 8.4 c/d, 70% contrast) necessary to yield peak effect, but as with sensitivity measures, the decay time of the effect was prolonged by longer adaptation periods. One marathon 30 minute adaptation session resulted in a measurable shift after 180 minutes of recovery time.

Two studies have been aimed specifically at the time course of adaptation. Bodinger (1978) studied the decay of grating adaptation for two adaptation times, one and ten minutes, using the method of adjustment. In contrast to Blakemore and Campbell (1969), threshold elevation continued to increase beyond one minute of adaptation, with threshold elevation about 2 1/2 times higher following the 10 minute adapt period. Bodinger did not specifically state her adaptation contrast, but it appears to have been about 35 percent. This use of a lower contrast than Blakemore's may have caused her failure to find full adaptation in the one minute interval. She examined the form of the decay function more carefully than was done by Blakemore and Campbell, and it is clear that the simple exponential function proposed by the latter authors is a poor fit. Good fits could be obtained with one- and two- phase power
functions or a two-phase exponential.

Daugman (1980) has examined both rise and decay times using a forced-choice procedure to track changes in threshold. Both time-courses seemed to be well described by a simple exponential function, but the length of trials was limited to 60 seconds, avoiding the area of poor fit in Bodinger's study. Adaptation was limited to 30 seconds at 60 percent contrast, using six spatial-frequencies varying from 1.9 to 10.8 c/d. The lower spatial-frequencies appeared to show a faster recovery time, but the data were quite noisy.
Kulikowski and Tolhurst (1973) and Harris (1980) used the method of adjustment to measure separate thresholds for the sensation of pattern (spatial variation) and temporal change (motion and/or flicker) in temporally modulated spatial gratings. Both studies revealed substantial separation of the two thresholds which were interpreted in terms of separate spatial and temporal mechanisms.

Kulikowski and Tolhurst (1973) report their experiment as part of a larger body of work using a variety of procedures. In the case of concern here, only two spatial frequencies were used, 0.8 and 12 c/d. Eight rates of sinusoidal, on-off flicker were used, ranging from 0 to 15 Hz. At these spatial-frequencies, sensitivity profiles produced by the two thresholds were highly distinctive. The curves differed in shape, primarily in that the spatial thresholds had no low temporal-frequency falloff (low pass) while the temporal thresholds were clearly bandpass. The thresholds were typically separated by a factor of 2 or 3.

Harris (1980) was interested in explaining velocity perception as a function of relative excitation of separate form and flicker sensitive mechanisms. Since velocity is equivalent to the ratio of temporal and spatial-frequencies:

\[
\text{degree/sec} = \frac{(\text{cycles/second})}{(\text{cycles/degree})}
\]

he proposed that a linear relationship between the ratios of the activation of the two mechanisms with changes in velocity could code velocity. If the hypothesis is correct,
and if one assumes that the activation in the two mechanisms is represented by the separate pattern and form thresholds, the ratios of the thresholds should therefore vary linearly with velocity. Harris tested this by measuring the two thresholds over 16 spatial/temporal-frequency combinations (1, 2, 5 and 10 c/d and Hz). The primary experiment used drifting sinusoidal gratings, a secondary experiment used counterphase flickered gratings over a wider range of spatial and temporal-frequencies (0.9 to 20 c/d and Hz).

Harris did not present his threshold data. The ratios of the two thresholds were shown to increase approximately linearly with velocity, supporting the ratio-coding of velocity hypothesis. The ratios reveal that the separation between the two thresholds was comparable to that of Kulikowski and Tolhurst (1973). The maximum differences appear to be on the order of a factor of 2 (.3 log units). Because of the lack of actual threshold data, the shape of the pattern and flicker detection functions is unclear, and may have been different from those reported by Kulikowski and Tolhurst.

A. Experiment 1

The first experiment was designed to study the form and flicker threshold functions over a more complete set of stimulus values than was done by Kulikowski and Tolhurst (1973). Counterphase flickered gratings were chosen to minimize involuntary eye-tracking and afterimages.
Method

Stimuli  Counterphase-flickered, vertically oriented sinewave gratings were generated using a Xitan microprocessor equipped with an analog interface designed in this lab. The display was a Hewlett-Packard 1332A, mean luminance was 35 cd/m². The test grating occupied the center 2.5 degrees of a 10 degree wide display and had a 2 degree wide, mean luminance border on either side. The grating extended the full 8 degree vertical height of the display. Twenty-four combinations of spatial and temporal frequencies were used: 0.5, 1, 4, and 8 c/d, and 0.5, 1, 2, 4, 8, and 16 Hz counterphase.

Subjects  The author, a 29 year old corrected myope, and a 22 year old psychophysically naive female with normal acuity served as subjects.

Procedure  A dental chair with headrest assured a constant 30 inch viewing distance. The subject communicated with the computer via a movable keyboard. Trials were initiated by pressing a key. On each trial a short (6 second) blank field was presented, immediately followed by a 6 second test grating presentation. Contrast was adjusted by the subject using a potentiometer mounted on the keyboard. When setting a spatial threshold, the subject adjusted the contrast either until periodic bars or vertical spatial structure was visible. When setting a flicker threshold, contrast was adjusted until movement or flicker was observed. This
contrast setting was recorded by pressing a key, which also served to initiate the next 6 second trial. The experiment was terminated when seven thresholds had been set. Subject SP was tested over the entire range of conditions. Each condition was tested in three experimental sessions, yielding 21 threshold settings. The mean of the settings and a smoothed mean excluding the two extremes of each session were computed. The two rarely differed by more than .02% modulation. Plotted data are the smoothed means. Subject LM was tested at 1 and 4 c/d only.

Results

Thresholds are plotted in two and three dimensional form in Figures 1-4. The ratios (calculated as log threshold pattern - log threshold flicker) are plotted in three dimensional form in Figure 4 in a manner analogous to that of Harris, but with axes reversed.

Several striking differences are immediately apparent between these data and those of Kulikowski and Tolhurst (1973). Perhaps the most important is that the shapes of the temporal response functions are very similar for the pattern and flicker thresholds, even at very low and high spatial-frequencies. At .5 and 1 c/d both the pattern and flicker sensitivity functions are bandpass, while at 4 and 8 c/d the functions are low pass. It is also notable that these data show much less separation of the form and flicker curves.

Figure 1-A shows the temporal response functions at 0.5
c/d. Both pattern and flicker functions are bandpass, with peak sensitivity between 2 and 8 Hz. Flicker sensitivity was always greater than pattern sensitivity, with a fairly uniform separation of 2 db. Data from 1 c/d gratings (Figures 2 and 3) looks similar to that from .5 c/d, with a general increase in sensitivity but similar bandpass functions. In data from subject SP, flicker sensitivity exceeds pattern sensitivity at temporal-frequencies of 2 Hz and higher. Below 2 Hz pattern sensitivity is slightly greater. Data from subject LM (Figure 2) shows parallel bandpass functions at 1 c/d with highly uniform separation of the form and flicker curves. Flicker was always seen before form, with the form thresholds about 2 db higher than flicker thresholds.

At 4 c/d the curves become low-pass in data from both subjects. The crossover point for the flicker and pattern functions has migrated to between 4 and 8 Hz in data from subject SP, with pattern sensitivity higher at lower flicker rates. Separation of the functions is generally less than 2 db. Subject LM shows the same basic pattern, with location of a crossover point below 2 Hz.

At 8 c/d, data from subject SP shows quite distinct flicker and pattern curves below 8 Hz. Pattern thresholds are lower than flicker thresholds at all temporal frequencies except the highest, 16 Hz. Separation of the flicker and form functions below 8 Hz reaches 6 db, while at 16 Hz no clear difference is apparent between pattern and
flicker thresholds.

The overall picture which emerges from these data is quite different from that of the previous experimenters. Although flicker and pattern thresholds appear to be reliably separable, the form of their temporal response functions are quite similar rather than separate as was the case in data from Kulikowski and Tolhurst (1973). Interpretation in the present case is ambiguous, since parallel curves can be interpreted as criterion shifts rather than evidence of separate mechanisms. At 1 and 4 c/d, data from subject SP does qualitatively appear similar to that of Kulikowski and Tolhurst, in that flicker is seen before form at high rates of flicker, and form before flicker at low rates of flicker. The systematic shift in the crossover point of the functions suggests separate mechanisms. However, the separation between the curves is very small and could also be due to a criteria shift.

These data for subject SP are plotted as surfaces in Figure 3. Figure 4 plots threshold ratios for data from subject SP. There is no trend in the threshold ratios, which would be discernable as an inclined surface. Harris' ratio hypothesis predicts a planar surface, which he clearly found using moving gratings, and somewhat less clearly found for counterphase flickered gratings. The discrepancy between data in the present study and Harris' data is difficult to assess because he did not present threshold data. However, it seems unlikely that the discrepancy is due to error. The present study shows no linear trend in
Figure 1-A. Two-criterion contrast thresholds obtained using separate temporal and spatial criteria. Gratings were counterphase-flickered, with a spatial frequency of .5 c/d. Subject SP.
Figure 1-B. As 1-A, except spatial frequency was 1 c/d.
Figure 1-C. As 1-A, except spatial frequency was 4 c/d.
Figure 1-D. As 1-A, except spatial frequency was 8 c/d.
Figure 2-A. Two-criterion contrast thresholds obtained using separate temporal and spatial criteria. Gratings were counterphase-flickered, with a spatial frequency of 1 c/d. Subject LM.
Figure 2-B. As 2-A, except spatial frequency was 4 c/d.
Figure 3-A. A three-dimensional perspective plot of temporal thresholds for counterphase flickered gratings. Subject SP.
Figure 3-B. Spatial thresholds from the same conditions as 3-A.
Figure 4. The ratio of the temporal and spatial sensitivities to counterphase flickered gratings. The ratios were calculated as log temporal sensitivity minus log spatial sensitivity. Subject SP.
the ratios.

B. Experiment 2

Because of the failure to replicate the findings of previous investigators using counterphase flicker, the experiment was repeated using moving gratings. This tested the possibility that the type of temporal modulation employed could affect the threshold functions.

Method

Experiment 2 was identical to Experiment 1 except that gratings were swept across the test field rather than modulated by sinusoidal counterphase flicker.

Results

Notable differences exist between the temporal response functions for moving gratings and those generated by counterphase flickering gratings. Results also differed between subjects. Results are plotted in Figures 5-8. Data from subject SP closely resemble those obtained by Kulikowski and Tolhurst (1973) at .8 and 12 c/d respectively.

In data from subject SP, pattern thresholds yielded similar results for the counterphase flicker and moving conditions. The pattern threshold temporal response function gradually changed in form from bandpass at .5 c/d to low pass at 8 c/d. The corresponding motion threshold functions retained their bandpass character over the range of spatial
frequencies tested. Data from subject LM is similar to the counterphase flicker data in that the form of both pattern and motion thresholds changed from bandpass to low pass with the increase from 1 to 4 c/d.

Subject SP produced bandpass motion thresholds in each of the 4 spatial-frequency conditions tested. The lowest thresholds centered about 4 Hz. The .5 c/d functions are similar to their counterphase counterparts, with temporal thresholds always lower than spatial. This similarity may in part be due to artifacts caused by the limited number of cycles present in the test field. Only one full cycle was present within the 2.8 degree field, effectively removing spatial periodicity as a cue to the presence of a grating. This cognitive factor should not have affected the motion threshold, but the presence of only a limited number of cycles can reduce the visibility of a grating (Hoekstra, Van der Goot, Van der Brink, and Bilsen, 1974; Estevez and Cavonius, 1976; McCann, Savoy and Hall 1978). This effect is much reduced or eliminated by use of a mean luminance surround about the grating (Panish, Swift and Smith, 1979) as used in the present study.

Pattern thresholds were highly similar in form at 1, 4 and 8 c/d. The functions are low-pass, with an area of approximately equal sensitivity extending from .5 to 4 Hz, followed by a fourfold increase in threshold by 16 Hz. At low frequency there is some bandpass character to the curve, marked by a peak sensitivity at 4 Hz. As spatial-frequency
Figure 5-A. Two-criterion contrast thresholds obtained using moving gratings. Spatial frequency was .5 c/d. Subject SP.
Figure 5-B. As 5-A, except spatial frequency was 1 c/d
Figure 5-C. As 5-A, except spatial frequency was 4 c/d.
Figure 5-D. As 5-A, except spatial frequency was 8 c/d.
Figure 6-A. Two criterion contrast thresholds obtained using moving gratings. Spatial frequency was 1 c/d. Subject LM.
Figure 6-B. As 6-A, except spatial frequency was 4 c/d.
Figure 7-A. A three-dimensional perspective plot of temporal thresholds for moving gratings. Subject SP.
Figure 7-B. Spatial thresholds from the same conditions as 7-A.
Figure 8. The ratio of the temporal and spatial sensitivities. Moving gratings, subject SP.
Fig. 7. The sensitivity for flicker detection and pattern recognition as functions of the frequency of sinusoidal modulation. The spatial frequency of all the gratings was 12 c/deg. The continuous line was drawn by eye through the points for pattern recognition (●); and the dashed curve was drawn by eye through the points for flicker detection (○). Mean luminance 100 cd/m². Subject D.J.T.

Fig. 8. As for Fig. 7, except that the spatial frequency of all the sinusoidal gratings was 0.8 c/deg. The data for the recognition task (●) are reasonably well fitted by the continuous curve of the previous Figure; the curve has been shifted up the sensitivity axis to fit the points. The flicker detection data (○) are reasonably fitted by the dashed curve of the previous Figure; again the curve has been shifted up the sensitivity axis, but by a larger factor. Mean luminance 100 cd/m². Subject D.J.T.

Figure 9. Two-criterion threshold data from Kulikowski and Tolhurst, 1973. Their original figure numbers and captions are presented.
increases, this peak becomes less salient by virtue of the relative increase in sensitivity at the low temporal frequencies. These functions are very similar to corresponding pattern thresholds generated using counterphase flickered gratings.

Over this same range of 1 to 4 c/d, the motion threshold functions retained their bandpass character. Peak sensitivity was always at 4 Hz. These data are similar in form to those of Kulikowski and Tolhurst (1973), shown for comparison in Figure 9. They used the temporal response curve fit to the flicker thresholds at 12 c/d to also fit flicker data from .8 c/d. In spite of the similarity of data from the present experiment to those of Kulikowski and Tolhurst, ratios of the spatial and temporal thresholds did not vary linearly with velocity, again failing to replicate Harris (1980).

Discussion

It is clear that subjects can set different thresholds for the perception of temporal and spatial modulation, and that there is general correspondence between data from different subjects. Unfortunately the data does not allow firm conclusions to be drawn concerning mechanisms underlying the percepts.

The two-criterion task is inherently fraught with problems of interpretation. These experiments have compared data generated from both moving and counterphased flickering gratings. The comparison is difficult because the
perception of motion in a moving grating is phenomenally very different from the perception of flicker generated by counterphase flicker.

Even within each of these conditions the subject is in fact responsible for establishing a variety of criteria over the range of spatial- and temporal-frequencies tested. For instance, the appearance of low frequency counterphase flicker is very different from high frequency flicker. As a result, the criterion for flicker thresholds differs with frequency. The experimenter may carefully define the perception of flicker, a simple enough concept, as a response to a change in luminance at a point over time but to the subject, a low (temporal) frequency counterphase flickering grating may have the appearance of spatial undulation rather than pure flicker. Consequently the setting of a criterion for the two conditions is quite different. The perception of movement involves similar problems. At low velocities, wherever a spatial percept is present, movement is visible as the vertical structure of the grating drifts past a visible point of reference. The purely temporal judgement of moving vs not moving, which is the temporal criterion for moving gratings, must therefore be made without reference to the spatial contamination of a fixation point. In both the counterphase flicker and drifting grating conditions, essentially spatial properties of the stimulus are confounded with the perception of temporal change. Even a spatial system which can only signal sensation of unmoving pattern and not the sensation
of temporal modulation may thereby allow inference of temporal change. Setting a criterion involves ignoring these interwoven cues and attending to the elusive sensation of temporal change in some pure sense.

A similar problem exists for the perception of pattern, which for grating stimuli may be parsed into the separate categories of periodicity and orientation. These are perceptual dimensions which (phenomenally) seem to vary independently of spatial-frequency, although no systematic study has been conducted to examine the relationship. In this study, at low spatial-frequencies, orientation seemed to be visible at lower contrast than was periodic structure. At high spatial frequencies the two became visible simultaneously.

The procedure of interpreting distinguishable sensations as different mechanisms also has theoretical problems, for it has no strong empirical or theoretical basis. With reference to the case above, are we to infer the existence of separate orientation-sensitive and periodicity-sensitive mechanisms? Such a supposition may be no less reasonable than that of the existence of separate flicker and pattern mechanisms. A more satisfactory model would avoid the implicit reductio-ad-absurdum of infinite mechanisms for infinite sensations by proposing a single mechanism capable of simultaneously encoding both sensations. With respect to the present study, it should be noted that the subject is performing different tasks in
setting pattern thresholds over varying spatial frequencies. This makes valid interpretation in terms of a single spatial mechanism difficult in light of the underlying assumption that separate sensations imply separate mechanisms.

Derrington and Henning (1981) found that orientation threshold functions closely match detection threshold functions from low spatial frequency, counterphase flickering gratings. If we consider orientation to be purely a parameter of form (and not flicker) this experiment weighs heavily against the hypothesis of a spatial-temporal dichotomy. It is possible, however, that orientation can be coded by direction-sensitive mechanisms in cases where movement is at right angles to the orientation of the grating. This follows because the direction of movement and the orientation of the grating are perfectly negatively correlated. A perfect negative correlation should be able to function as well as a positive correlation in unambiguously signaling a dimension such as orientation. Orientation discrimination should parallel direction discrimination, or exceed it if there is any sort of summation between oppositely-tuned, direction-sensitive mechanisms. Counterphase flickered gratings, such as those used by Derrington and Henning (1981) should also yield orientation specificity, because counterphase flickered gratings may be decomposed into two half-amplitude gratings moving in opposite directions. If direction selective mechanisms such as those proposed by Levinson and Sekuler (1975) are operative at low spatial-frequencies, we would
expect orientation sensitivity to parallel direction sensitivity, which is most likely temporal sensitivity.

Several studies have failed to replicate results from Kulikowski and Tolhurst (1973). Green (1981) noted that his subjects were unable to maintain a stable spatial criterion. Burbeck (1981) attempted to replicate their results using counterphase flickering gratings after obtaining quite different thresholds using a modified yes-no procedure. Her method of adjustment data at .75 c/d and 12 c/d shows a marked similarity to .5 c/d and 8 c/d counterphase data from the present. Both spatial-frequencies yield nonoverlapping pattern and flicker temporal-sensitivity functions. At .75 c/d flicker was always seen before pattern, the converse being true at 8 c/d. Both functions are low pass at 8 c/d, with extremely similar pattern and flicker thresholds at 15 Hz, and greater separation at low flicker rates. At .75 c/d, her data are unlike those of the .5 c/d condition of the present study in that only the flicker response function is bandpass, while the spatial function is low pass. The present study found nearly parallel bandpass functions at .5 c/d, and the spatial function retained a good deal of bandpass character at 1 c/d. The temporal curve was still clearly bandpass. Subject LM produced two parallel bandpass functions at 1 c/d, although both had become essentially low pass at 4 c/d.

Two general problems emerge from these data: (1) accounting for the different forms of the temporal response
functions generated by counterphase flickering and drifting gratings; (2) determining whether the data support the hypothesis of a dichotomy of sustained and transient mechanisms.

An answer to the first problem is speculative. The counterphase data are more trustworthy both because the counterphase presentation is less prone to afterimages and tracking and because it is in fair agreement with data from Burbeck (1981). Given this assumption, the differences in the data from drifting gratings may be interpreted as resulting from artifacts produced by the drift.

If one does not postulate that different detectors are involved in the two tasks, the most obvious difference between the two conditions is the tendency to track a drifting grating. Since tracking affects the temporal parameters of the retinal image, it is an important factor in the measurement of thresholds (Arend, 1976). This change in temporal parameters will be particularly great at high spatial frequencies where relatively small eye movements are responsible for a greater change in temporal frequency on the retina.

The tendency to track the drifting grating was obvious to the subject during the experiment. Drifting gratings were compelling targets and, even with a fixation point, the elimination of tracking was almost certainly not accomplished.

The net effect of the tracking is to reduce the effective temporal-frequency of the stimulus. At higher
spatial frequencies, such as 4 and 8 c/d, tracking would have the effect of decreasing the high-temporal-frequency sensitivity decline that is evident in the counterphase data. This effect will probably vary with subject fatigue and individual differences in ability to hold fixation. This predicted retention of high temporal-frequency sensitivity is evident in the 8 c/d and 4 c/d spatial threshold functions, but not in the motion criterion functions.

The motion-identification curves seem to retain virtually the same bandpass shape over all spatial frequencies tested in the drifting grating experiment. The major difference between the curves is a uniform change in sensitivity varying with spatial-frequency. Relative to the corresponding flicker threshold functions in the counterphase conditions, the principle difference is the retention of bandpass character at all spatial frequencies tested. The difference between drifting and counterphase presentations is probably again related to eye movements, in this case specific to the moving identification task. An explanation follows.

It seems probable that the two-threshold technique results in different patterns of eye movements as the subject adopts different strategies to seek each of the two percepts. The purpose of each strategy would be to optimize the desired percept. This is particularly true at very low drift rates, where the sensation of tracking is not so apparent as at higher drift rates. The combination of slow
drift rates and high spatial-frequency makes identification of motion particularly difficult because the fixation point is in danger of becoming a spatial reference for movement. There is thus a tendency to set a very high criterion for motion seen without spatial reference, because it is unclear when the motion is globally perceived and when it is seen relative to a local point of reference. This criterion shift is probably responsible for the sensitivity decline (and resultant bandpass shape) in the motion detection task at low temporal-frequencies at 4 c/d and 8 c/d. A true test of these speculations would unfortunately require the two threshold experiments to be carried out with an image stabilizer controlling the velocity of the image on the retina. The decline in sensitivity at low temporal frequencies would be expected to disappear under stabilization.

Kelly (1975) has shown that unstabilized gratings, flickered in counterphase at temporal-frequencies of 0.1 Hz and higher, yield essentially the same thresholds as stabilized gratings. The data from the counterphase conditions in the present study therefore offer a stronger basis for evaluating the two-mechanism hypothesis than does the drifting grating condition or Kulikowski's and Tolhurst's in-phase flicker.

A decision concerning the existence of separate pattern and flicker mechanisms rests in this case upon the presupposition that separate mechanisms will result in qualitatively distinguishable percepts. Data from the
counterphase-flicker condition indicates that it is possible for an observer to set separate pattern and flicker thresholds over a wide range of spatial and temporal frequencies. The naive subject in this study reported seeing flicker before pattern while being trained in the method of adjustment, prior to being told that her next task would be to set separate thresholds for pattern and flicker. However, this distinction probably depends to a large degree on the observer's conception of what constitutes a grating. A periodicity criterion is much more stringent than merely seeing vertical structure, especially at low spatial frequencies where only a few cycles are present on the display. In this study, vertical structure constituted the spatial criterion, while any perceived temporal variation defined flicker. Kulikowski and Tolhurst (1973) referred to "flicker detection" and "pattern recognition", the latter being the point at which individual bars could be "readily" discriminated. Harris (1980) instructed his subjects to adjust the contrast until "he or she could just detect either its spatial or its temporal structure." These more stringent pattern criteria would tend to bias the subject to higher thresholds for pattern, where the stimulus was clearly recognizable as a grating. Kulikowski's and Tolhurst's comparison of flicker detection and pattern recognition represent the comparison of a detection task with an identification task. Because of these criterion problems, and the use of drifting gratings, neither of the
previous studies constitutes strong evidence for a sustained-transient dichotomy. Data from the present study, collected under more carefully defined procedures and using counterphase flickered gratings, utilizes the separate perceptions assumption in a less clearcut, but more trustworthy manner. Although this assumption is not of proven validity, it is of sufficient interest that it warrants further testing. The best support for such an assumption would come about through correlation with evidence less prone to observer bias. This will be one goal of the remaining experiments in this study.
V. ADAPTATION EXPERIMENTS

The second section of this study used adaptation paradigms to further examine the proposed sustained/transient dichotomy. The primary thrust of the project was an examination of the time-course of adaptation to counterphase flickering gratings. It was hoped that adaptation time-course could provide a fingerprint characteristic of the visual mechanisms being tested. The first experiment measures the change in contrast threshold which occurred during adaptation rise-time and decay. A second experiment examined the appearance of near threshold flickering gratings over the same adaptation time-course as the previous experiment. A control experiment, described in Appendix I, examined whether the test procedure used in these experiments affected contrast threshold.

A. Experiment 1. Time-Course Thresholds

A variety of procedures have been used to demonstrate differences in the processing of stimuli having widely separated spatial and/or temporal frequencies. It has also been noted that separate thresholds may be set for the perception of spatial form and the perception of flicker (Keesey, 1971; Kulikowski and Tolhurst, 1973) and for spatial form and motion (Harris, 1980). These experiments have generally been interpreted as evidence for the existence of separate mechanisms for the processing of
spatial and temporal variation. Although details differ, this body of work portrays a spatial mechanism as being composed of a variety of psychophysically defined spatial channels, with peak sensitivity to stimuli of high spatial frequency and low temporal frequency. The temporal mechanism shows the reverse pattern, having peak sensitivity to stimuli of low spatial frequency and high temporal frequency. It is not clear to what degree the temporal variation which results from the drift of gratings can be equated with the temporal variation which results from flicker. Results from Harris (1980) suggest that motion may be coded as the ratio of the activation of temporal and spatial mechanisms. Experiments by Green (1981) showed that adaptation to flickering or moving gratings could each raise the threshold of the other type of stimulus. The temporal tuning revealed by these data were interpreted as showing the existence of broadly tuned temporal channels sensitive to both flicker and motion.

Other studies have interpreted changes occurring with spatial frequency as resulting from separate spatial and temporal systems. For instance, response time latencies increase with spatial frequency (Lupp, Hauske and Wolf 1976; 1978). Tolhurst (1975a) found differences in the temporal summation properties of high and low spatial-frequency gratings. Legge (1978) and Breitmeyer and Ganz (1977) found differences in the decrease of threshold with test stimulus presentation time when using different spatial frequencies.
However, some experimenters have obtained results which do not support the two-mechanism hypothesis. Arend and Lange (1977) used a subthreshold additivity paradigm to measure channel bandwidths at several spatial frequencies, using both flickering and steady gratings. It was expected that stimuli in the range of a temporal system (e.g. flickering gratings of low spatial frequency) would show different tunings than thresholds set using a steady grating. No such differences were evident, even when thresholds were set using spatial and temporal criteria. Derrington and Henning (1981) found that a 2AFC discrimination of grating orientation showed the same dependence on spatial and temporal frequency as a 2AFC detection task. The two-mechanism hypothesis would predict that the orientation discrimination, a spatial task, would yield a higher contrast threshold than would the 2AFC detection task where the temporal system had higher sensitivity than the spatial system. Earlier in this study it was reported that contrast thresholds obtained using separate flicker and form criteria were very similar, and did not vary independently.

The nature of the proposed spatial and temporal mechanisms has not been carefully elaborated in the psychophysical literature. In this paper, a mechanism will be considered to be an independent psychophysically definable entity. Spatial and temporal mechanisms would therefore function independently in the processing of
spatial and temporal variation. If these two mechanisms exist, it is likely that they are composed of other mechanisms, usually referred to as channels. Various paradigms, such as adaptation, have been used to demonstrate the existence of channels tuned for spatial and temporal frequency (Blakemore and Campbell, 1969; Smith, 1971; Swift and Smith, 1981).

Figure 10-A illustrates how different channel configurations might underly general models of separate spatial and temporal mechanisms. The first case illustrates the simplest sort of two-mechanism model, in which each mechanism is composed of a single channel. The temporal mechanism is composed of a single channel tuned to high temporal frequency and low spatial frequency. The spatial mechanism is composed of a single channel tuned to low temporal frequency and high spatial frequency.

The second case is more realistic (Figure 10-B). Each mechanism is composed of many channels, and the sensitivities of these subpopulations of channels overlap extensively. However, each mechanism has a preferred range of spatio-temporal sensitivity which is related to its population of channels. The presence of more channels sensitive to a given spatio-temporal frequency range results in greater likelihood of the detection of a stimulus falling within that range. The temporal mechanism possesses more channels at high temporal frequency and low spatial frequency, while the spatial mechanism possesses more channels at low temporal frequency and high spatial
Figure 10. Three examples of hypothetical channel distributions which could form the basis for two-mechanism and continuum models of spatial and temporal vision. The stipled areas within A and B represent the spatio-temporal tunings of channels within a temporal mechanism. The hatched areas of A and B represent a spatial mechanism. C is a continuum model, in which the underlying channels are not segregated into temporal and spatial mechanisms.
frequency. This model is similar to those proposed by Kulikowski and Tolhurst (1973), Legge (1978) and Green (1981). It is clear that there can be a wide variety of similar models in which the distributions of the channel populations differ while preserving the differential sensitivities of the proposed mechanisms.

The last case (Figure 10-C) illustrates a model which does not have separate spatial and temporal mechanisms. As in the previous models, the overall distribution of channels shows an inverse relationship between sensitivity to spatial and temporal frequency. However, the channels form a continuum within this range, with no spatial or temporal subdivisions. Such a continuum model assumes that spatial and temporal variations are processed in common. The sensations of form and temporal variation represent at most separate outputs from this common analyzer.

It is extremely difficult to experimentally differentiate between two mechanism models and continuum models which propose a similar overall distribution of channels. Differences (such as thresholds) found through the use of stimuli which are widely separated in spatial and/or temporal frequency may be due solely to different characteristics of such widely spaced channels. There is no need to postulate separate spatial and temporal mechanisms to account for the observed differences. This problem would not arise if evidence for separate mechanisms was found at the same test parameters. However, it is difficult to separate mechanisms that are active at the same
test parameters. When using a sensitivity measure such as contrast threshold, it is difficult to determine whether a threshold results from the more sensitive of two mechanisms active at the test parameters, or a single system active at those parameters. If one accepts the hypothesis that the percept (pattern or flicker) identifies the mechanism performing the detection, it should be possible to separate the two mechanisms, as was done by Kulikowski and Tolhurst (1973). However, as noted earlier, the two-criterion threshold technique has proven difficult to employ. Furthermore, Green (1981) has presented evidence that the perception of flicker may be produced by the spatial system.

Better evidence for the two mechanism hypothesis would result from a paradigm that differentially altered the sensitivities of the two hypothetical mechanisms, such that each could be observed in isolation. If there was instead a continuum of channels, this would be impossible. Adaptation is one clearly applicable technique, because it has the ability to selectively desensitize spatial and temporal frequency channels (Blakemore and Campbell, 1969; Smith, 1971). Adaptation studies such as Blakemore and Campbell (1969) have provided the basis for contemporary spatial-channel models of the visual system. In their procedure, the decrease in contrast sensitivity to a test grating of fixed spatial frequency was measured following presentation of high-contrast adaptation gratings of
various spatial frequencies. The resulting pattern of sensitivity losses was interpreted to represent the spatial tuning characteristics of the channel defined by the test frequency. Analogous experiments have studied temporal frequency tuning, with results showing very broad adaptation profiles (Smith, 1971).

This selectivity of adaptation is the basis for its utility in the present study. The hypothetical spatial and temporal mechanisms are proposed to differ in their general spatial and temporal tunings. The temporal mechanism is primarily sensitive to low spatial and high temporal frequencies. The spatial mechanism has the reverse profile, with high spatial frequency sensitivity and low temporal frequency sensitivity. These systems may be conceptualized as being located at opposite poles of a distribution of spatio-temporally tuned channels, as illustrated in Figure 10-B. If two such mechanisms exist, it should be possible to selectively adapt them by placing the adaptation parameters closer to the peak sensitivity range of one or the other mechanism. Because the adaptation grating is biased towards one of the two mechanisms, this procedure will be referred to as the biased adaptation procedure.

Suppose that the spatial and temporal frequencies of the test grating are chosen at which the two proposed mechanisms possess equal sensitivity. Suppose also that detection within each mechanism proceeds by the activation of a sub-population of channels within that mechanism.
Gratings having spatial and temporal parameters offset from those of the test grating would favor the mechanism more sensitive to those parameters, by affecting more channels within that mechanism than the other. Therefore, an adaptation grating that is biased toward the temporal pole of the channel population (lower spatial frequency, higher temporal frequency) will be more likely to depress the sensitivity of the temporal channels operative at the test parameters than the spatial channels. Threshold tests following adaptation will then reveal the sensitivity of the system which is currently the more sensitive at the test parameters - in this case, the spatial system, which is less adapted. It is important to note that because the preadaptation sensitivities of the two systems are equal, the most sensitive mechanism following adaptation will be that which is least adapted. If we were to accept the assumption that the percept of the stimulus at detection threshold identifies the most sensitive system, the two-mechanism hypothesis would predict the nature of the sensation at threshold. However, in view of the difficulties inherent in the two criterion procedure, it is preferable to use a criterion-free paradigm to separate the proposed mechanisms.

The paradigm used in this experiment measures the time-course of the changes in contrast sensitivity which occur with the buildup and decay of adaptation. It is possible that independent mechanisms which perform
different functions will adapt and/or recover from adaptation at different rates. Daugman (1980) investigated adaptation time-course and found that the rate of recovery of contrast sensitivity was correlated with spatial frequency. Higher spatial frequencies yielded longer recovery times. His rise-time and decay time data were satisfactorily fit with exponential functions. Bodinger (1978) fit rise-time and decay-time threshold elevations with exponential and power functions. The best fits were obtained using a multi-stage model rather than single functions of either type.

In the present experiment, adaptation time-course was measured with the use of a biased adaptation procedure. If separate spatial and temporal mechanisms exist, each possessing characteristic time-course parameters, this procedure should allow independent observation of the two adaptation time-courses at both widely separate and at identical test parameters. The time-course of each hypothetical mechanism will be isolated within two experimental conditions.

First, each system can be revealed by using extreme spatio-temporal test and adaptation parameters at which one mechanism is significantly more sensitive than the other. For instance, the spatial system would be tested by using adaptation and test gratings of high spatial and low temporal frequency. However, even if clearly different time-courses are found for the two conditions, the differences could be attributed to the properties of widely
separated channels rather than the existence of separate spatial and temporal mechanisms.

The biased adaptation procedure can avoid this problem by testing for the separate mechanisms with the same test grating. The test grating parameters are selected such that detection by either mechanism is equally likely. Adaptation grating parameters are chosen so as to unequally adapt the two systems. With increasing adaptation time, the sensitivity of the less adapted mechanism will exceed that of the other. The adaptation time-course of the less adapted mechanism will be revealed by successive threshold tests throughout the adaptation procedure.

The simplest outcome of these two procedures would be a clear correspondence between results from the two conditions designed to show the time-course of the same mechanism. However, if the two mechanisms possess very different adaptation time-courses, threshold measurements from a single adaptation condition may reflect both mechanisms. Significant adaptation time may be required to depress the sensitivity of one system sufficiently to reveal the other. The resultant sensitivity over time curve would have two branches, one for each mechanism. This is analogous to the dark adaptation curve, which shows separate branches for the rod and cone systems.

This analysis has presumed the existence of separate spatial and temporal mechanisms. However, if a continuum model is correct, there is little reason to expect
substantial differences in time-course under the biased adaptation conditions. As in the two-mechanism case, differences found would reflect the channels involved in the detection. However, rather than forcing the channel population involved in the detection from one mechanism to the other as in the two mechanism case, there would only be a shift between contiguous channels within the single mechanism illustrated in Figure 10-C.

Method

This experiment uses a forced-choice test probe insertion technique to measure the time course of adaptation to temporally modulated spatial-frequency gratings. High contrast adaptation gratings were used to maximize adaptation. A short test probe was selected, 1 second in duration, in order to prevent sensitivity changes from occurring during the time covered by the test probe. Because changes in threshold are rapid at the beginning of both the rise and decay of adaptation, test probes were spaced at equal log time intervals beginning with each of the two phases of the experiment (rise and decay). The procedure is outlined in Figure 11. A control experiment described in Appendix I examined the effects of temporal transients introduced by the test probe procedure.

A simplified conceptual diagram of the design is presented in Figure 12. A more accurate depiction would portray the sensitivities of the hypothetical mechanisms as spatio-temporal surfaces. Four conditions were used (Table
1). Two were extreme conditions in which the test stimuli had parameters which should have made them more detectable to one of the two proposed systems, 8 c/d at 1 Hz counterphase flicker for the spatial mechanism, and .5 c/d at 8 Hz for the temporal mechanism. The remaining two conditions used a central stimulus of 2 c/d at 2 Hz, to which the two hypothetical systems should have been equally sensitive (Section IV).

All four conditions used biased adaptation stimuli. The spatial frequency of each adaptation stimulus differed from that of the test grating by +/- .5 octave. The adaptation stimuli thus allowed significant adaptation to occur at the test spatial frequency. Temporal frequencies of the adaptation gratings were offset from those of the test by a full octave, as temporal tuning is much broader than spatial tuning (Smith, 1971; Nilsson, 1975; Green, 1981). The adaptation and test parameters are listed in Table 2, with the mechanisms which should be revealed.

**Stimuli** All stimuli were vertical sinusoidal gratings flickered in counterphase, with a mean luminance of 35 cd/m². Adaptation gratings were of 80% modulation and entirely covered the screen, which occupied a visual angle of 10 degrees horizontally and 8 degrees vertically at the 30" viewing distance. Test stimuli were 2.8 degrees wide and located on either the left or the right side of the display. The remainder of the display contained a mean luminance blank field. The centermost edge of the test
Figure 11. A diagram of a single trial within the adaptation time-course procedure. Time proceeds from left to right. Tall blocks show adaptation grating presentation, short blocks containing diagonal slashes represent the test probes.
Figure 12. A conceptual diagram of the biased adaptation procedure. The sensitivities proposed for the hypothetical spatial and temporal mechanisms are shown in relation to the spatial and temporal parameters of the adaptation and test stimuli.
<table>
<thead>
<tr>
<th>Condition Name</th>
<th>Adaptation Stimulus</th>
<th>Test Stimulus</th>
<th>Mechanism Shown</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extreme Temporal</td>
<td>c/d</td>
<td>c/d</td>
<td>temporal</td>
</tr>
<tr>
<td></td>
<td>Hz</td>
<td>Hz</td>
<td></td>
</tr>
<tr>
<td>Central test</td>
<td>3 c/d 1 Hz</td>
<td>2 c/d 2 Hz</td>
<td>temporal</td>
</tr>
<tr>
<td>spatial adapt</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central test</td>
<td>1.5 c/d 4 Hz</td>
<td>2 c/d 2 Hz</td>
<td>spatial</td>
</tr>
<tr>
<td>temporal adapt</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Extreme Spatial</td>
<td>6 c/d 2 Hz</td>
<td>8 c/d 1 Hz</td>
<td>spatial</td>
</tr>
</tbody>
</table>

Table 1. The experimental parameters and the mechanisms which should be revealed in isolation.
gratings began 0.06 degrees from the center of the display. The test field used the full height of the display. Test gratings began at 0 degrees phase angle (mean luminance) at their leftmost edge. The sinusoidal contour at the right edge was multiplied by a linear ramp which decreased the modulation to 0 over a distance corresponding to 1/4 cycle. This eliminated the possibility of detecting the grating by the high contrast edge resulting from a chopped cycle at the border of the field.

**Subjects** The author, a 29 year old corrected myope, and a psychophysically naive 22 year old woman with normal acuity served as subjects.

**Procedure** The subject was seated in a dental chair, with head position maintained by the headrest. Experiments were conducted in the dark. The stimuli were generated by a TDL Xitan microprocessor equipped with a specially designed interface. The CRT display was a Hewlet-Packard 1332A. Communication with the computer proceeded via a small handheld keyboard. The psychophysical method used an interwoven double staircase to present test stimuli (probes) in a simultaneous forced-choice procedure. Thirteen probes were used during each adaptation cycle. Each cycle consisted of:

1. A 15-second mean-luminance blank field.
2. A 60-second adaptation presentation, with test probes inserted at 0, 2, 4, 8, 16, and 60 seconds. The first probe preceded the adaptation grating, the last probe
marked termination of the adaptation presentation.

3. A recovery period, 131 seconds long, during which the screen was at mean luminance except during the presentation of test probes. These probes were presented at 2, 4, 8, 16, 32, 64 and 128 seconds. The final 3 seconds allowed response to the final test probe.

4. An additional 3 minutes recovery time, during which the screen was dark and the subject free to move about and do as he pleased. At the end of this period the computer sounded a tone from the console, indicating that a new cycle could be initiated. Preliminary experiments demonstrated that full sensitivity had been regained within 90 seconds of the offset of the adaptation grating. The additional time ensured the absence of residual adaptation in the following trial.

The entire cycle therefore consisted of 60 seconds of adaptation and a 5 minute recovery. The adaptation stimuli and the blank recovery field contained a flickering vertical line at the center of the screen to aid fixation. Test probes were of 1 second duration, and did not contain the fixation line. The beginning of each test probe was marked by a tone from the console. The task was a simultaneous forced-choice, in which the observer had to determine which side of the CRT (left or right) contained the test grating. The subject could respond at any time from the end of the test probe until the beginning of the next probe.

Contrasts of the probe stimuli were determined by use
of two concurrent, independent (interwoven) staircases at each test interval. Effectively, therefore, 26 separate experiments were being conducted during each session, two at each of the 13 test periods. Selection of each staircase was semi-random. The probability of using a staircase was weighted inversely by the number of reversals on each staircase, so that the total number of reversals was equal for the two staircases. The randomization insured that the contrast of a test presentation at a given test time could not be predicted. The initial contrast of each staircase was set to a contrast well above threshold. Contrast was initially decreased by 25 percent with each correct response. This rate was changed to 5 percent following either the first mistake or a response from the subject which informed the computer that the stimulus was near threshold. The subject could keep track of the rate of descent of each staircase via a status line on the console. Incorrect answers resulted in contrast being raised by a factor of 5 percent. These staircase parameters made it improbable that a series of fortuitous correct responses would drop the test contrast to a level significantly below threshold, since a single error raised test contrast as much as 5 correct responses decreased it. Each reversal of the direction of the staircase was noted, and a run was terminated when a minimum of 8 reversals had been achieved at each delay time.

Each run was typically conducted over 2 or 3 sessions lasting 1 to 3 hours apiece. A single run of each condition
typically required 5 hours. Several practice sessions were run for each subject before the experiment(s) proper were begun. Subjects were free to stop at any time, and were instructed to do so if overly fatigued. Each condition was run 3 times, making a total of 12 runs requiring roughly 60 hours to complete. The order in which the conditions were run was randomized. Subject LM was run 6 times on the extreme spatial condition, due to very high variability in her thresholds.

Results and Data Analysis

Two data analyses were performed. In the first, the mean of the reversals from both staircases at each test time was taken as threshold. In the second a probit analysis fit the data points with a psychometric function. This analysis (adapted from a program written by R. Lange) derived the 75% threshold and its error, and the width and error of the ogive underlying the psychometric function. The agreement between the two analyses was very good for data of low variability, such as that of subject SP. Further discussion will only use thresholds from the probit analysis. These thresholds were transformed to threshold elevation, and the resultant rise-time and decay-time thresholds were fit with exponential functions using a non-linear regression least squares estimate.

Threshold elevations and their exponential fits are presented in Figures 13 and 14. The central test conditions
showed the greatest threshold elevation. The form of the rise-time functions appear to have two stages. An initially steep increase of threshold over the first two or three test probes is followed by a plateau at the next two or three probes, and then a rise to the peak threshold. More data would be needed to verify a two stage model. The decay functions appear to have only a single stage. For purposes of comparison, all the threshold elevation curves were fit with the exponential model proposed by Daugman (1980). The fits are shown in Table 2. The functions used were:

\[ Y = A (1 - e^{-Bt}) \] for rise-time, and

\[ Y = A e^{-Bt} \] for decay.

\( Y \) is threshold elevation at time \( t \). The free parameters \( A \) and \( B \) are measures of the peak threshold elevation and of the time constant of the functions respectively. Stable data, such as those from subject SP, allowed fits of the rise and decay functions which showed good agreement between the maximal predicted threshold elevation of both the rise-time and decay functions. This point, the 60 second probe, was common to both curves. Poor correspondence between values derived from the fits is an indicator of poor accuracy of the fit. The ratio of these values for each condition is therefore a quality index for the fits. These values are also given in Table 2. Data from subject SP showed poor fit correspondence only in the extreme spatial condition, but data from subject LM had high variability and could not be fit with confidence. Her extreme spatial data had no apparent pattern.
Psychometric functions were derived from the probit analysis. The parameters of the function (ogive width and error) were too variable to demonstrate any trends. The error was typically one-third to one-half the ogive width. The exception was the extreme temporal data of subject SP. Although the error/ogive width ratio was roughly similar to the other cases, the widths showed a widening trend as threshold elevation increased. The errors of the ogive as well as the standard error of the threshold followed this trend. The ogive widths at each test probe time showed the same trend when averaged across all four conditions (Table 3).

Discussion

The principle comparisons to be made are between the two rate constants which were predicted to represent each system (Table 2). Subject LM did not produce enough usable data to make a full set of comparisons, so data from subject SP will be emphasized. For subject SP, the extreme temporal rise-time constant was 3.6 times that of the extreme spatial rise-time. The rise-time constants from the corresponding central conditions showed the reverse trend. The rate constant of the central test, spatial adapt condition should also have revealed the time-course of the temporal mechanism, since it would be the less-adapted and therefore more sensitive mechanism. However it's time constant was only 0.23 that of the central test, temporal adapt
Figure 13-A. Elevation of contrast threshold measured over the time-course of adaptation. Extreme temporal condition, Subject SP.
Figure 13-B. As 13-A, except central test, spatial adaptation condition.
Figure 13-C. As 13-A, except central test, temporal adaptation condition.
Figure 13-D. As 13-A, except extreme spatial condition.
Figure 14-A. Elevation of contrast threshold measured over the time-course of adaptation. Extreme temporal condition, subject LM.
Figure 14-B. As 14-A, except central test, spatial adaptation condition.
Figure 14-C. As 14-A, except central test, temporal adaptation condition.
Figure 14-D. Contrast thresholds for subject LM obtained over the time-course of adaptation during the extreme spatial condition. Because the data had no apparent pattern, no stable threshold could be found with which to calculate threshold elevation.
<table>
<thead>
<tr>
<th>Condition</th>
<th>Rise-time ( F(t) = A(1 - e^{-t/B}) )</th>
<th>Decay ( F(t) = A(e^{-t/B}) )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(seconds)</td>
<td>(seconds)</td>
</tr>
<tr>
<td></td>
<td>( A )</td>
<td>( B )</td>
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<tr>
<td>Adapt 75 c/d, 4Hz test 5 c/d, 8Hz extreme temporal</td>
<td>1.46 7.42</td>
<td>1.60 5.7</td>
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<tr>
<td>Adapt 3 c/d, 1Hz test 2 c/d, 2Hz central test, spatial adapt</td>
<td>2.13 2.86</td>
<td>2.14 5.3</td>
</tr>
<tr>
<td>Adapt 1.5 c/d, 4Hz test 2 c/d, 2Hz central test, temporal adapt</td>
<td>3.25 12.60</td>
<td>3.72 3.44</td>
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<tr>
<td>Adapt 6 c/d, 4Hz test 8 c/d, 1Hz extreme spatial</td>
<td>0.68 2.05</td>
<td>1.48 .86</td>
</tr>
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</table>

Subject SP

<table>
<thead>
<tr>
<th>Condition</th>
<th>Rise-time ( F(t) = A(1 - e^{-t/B}) )</th>
<th>Decay ( F(t) = A(e^{-t/B}) )</th>
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<tr>
<td></td>
<td>(seconds)</td>
<td>(seconds)</td>
</tr>
<tr>
<td></td>
<td>( A )</td>
<td>( B )</td>
</tr>
<tr>
<td>Adapt 75 c/d, 4Hz test 5 c/d, 8Hz extreme temporal</td>
<td>1.43 39.36</td>
<td>1.65 1.28</td>
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<td>(simplex did not converge)</td>
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<tr>
<td>Adapt 3 c/d, 1Hz test 5 c/d, 8Hz central test, spatial adapt</td>
<td>0.81 0.96</td>
<td>1.54 0.96</td>
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<td>Adapt 1.5 c/d, 4Hz test 2 c/d, 2Hz central test, temporal adapt</td>
<td>1.17 18.79</td>
<td>2.34 1.02</td>
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<tr>
<td>Adapt 6 c/d, 2Hz test 8 c/d, 1Hz extreme spatial</td>
<td>excessive variability</td>
<td>excessive variability</td>
</tr>
</tbody>
</table>

Subject LM

Table 2. Curve fits to force-choice threshold elevations adaptation time course.
<table>
<thead>
<tr>
<th>Test time seconds</th>
<th>Mean Ogive width</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>.17</td>
</tr>
<tr>
<td>2</td>
<td>.24</td>
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<tr>
<td>4</td>
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<td>64</td>
<td>.12</td>
</tr>
<tr>
<td>128</td>
<td>.15</td>
</tr>
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</table>

Table 3. The mean estimated ogive widths for the four test conditions.
condition. Subject LM's data from the extreme conditions was not usable, but her results from the central conditions showed the same trend as those from subject SP. The results from the extreme conditions clearly failed to predict the results from the central conditions.

The decay constant of the extreme temporal condition was 6 times that of the extreme spatial condition (Subject SP). The same direction was observed between the corresponding central conditions, but the difference was only a factor of 1.56. Subject LM had essentially identical decay constants for the central conditions. The decay constants of the extreme conditions are poor predictors of the rate constants in the central test conditions.

These results do not show a pattern of characteristic rate constants which could be associated with the proposed spatial and temporal systems. However, it is not clear that a continuum model will be better able to unambiguously explain the data.

A continuum model is essentially a description of the distribution of spatial and temporal channels which underly the spatial and temporal modulation transfer functions. This distribution is itself in dispute. Some researchers propose the existence of a small number of broad bandwidth channels (Wilson, 1979). Other researchers propose the existence of a large number of narrow bandwidth channels (Swift and Smith, 1982; Watson, 1982).

If the continuum consists of many narrow band-channels, the biased adaptation procedure would produce local shifts
in the population of channels performing the detection. The two groups of channels tested by the two central conditions will be similar to one another, since they do not perform specialized spatial or temporal tasks. Their time-courses should therefore be similar. However, this was not observed, the central conditions yielded large differences in rise constants.

These data may indicate the existence of different mechanisms which are being tapped by the biased adaptation procedure. However, these mechanisms do not appear to be the spatial and temporal mechanisms which this study attempted to find. There seem to be at least four of these mechanisms/channels, one shown by each of the test conditions.

This experiment used the minimal set of conditions necessary to test the two-mechanism hypothesis. The experiment did not use a sufficient number of conditions to investigate models having more than two mechanisms. It appears that the temporal fingerprint of the adaptation time-course may be suitable for identifying these mechanisms. Further testing, at conditions between the extreme and central conditions would be valuable in the search for a pattern of time constants which could be related to a multi-channel model.
R. Experiment 2

The second experiment of this series examines whether the appearance of a near-threshold grating is altered by adaptation. The experimental procedure corresponds to that of the previous experiment in all respects save for the task. A change in the appearance of gratings in the central spatial/temporal frequency ranges would be indicative of a spatial-temporal dichotomy.

Method

Subjects  The same subjects were used as in the previous experiments.

Stimuli  Stimuli were generated as in the previous experiments. The same spatial and temporal stimuli were used, except that each test probe was presented at one of seven fixed test contrasts, one of these being a 0 contrast catch trial. The six non-zero test contrasts were determined by different procedures for the two subjects. For subject SP, the contrasts were varied in increments which were the mean ogive width from the 13 psychometric functions of the corresponding conditions in the previous experiment. The mean of the ogive widths was used because the individual psychometric functions had high errors, and individual width values were not trustworthy. The intent was to evenly distribute the six non-zero test contrasts over the psychometric functions, while avoiding the tails. The
Figure 15. A conceptual diagram of the five-choice procedure.
contrasts and raw data are listed in Appendix II.

This same procedure was initially used to determine test contrasts for subject LM. However, it became apparent after a very few sessions that the resultant contrast increments had been too large (typically 2-3 times those of SP). This was due to the instability of LM's threshold data, which had considerable inter- and intra-session variability. New test contrasts were then calculated using contrast increments of .1%. This value was chosen because the slightly larger values used by subject SP had proven wider than was optimal.

Field sizes were the same as in the previous experiment. Test gratings were randomly alternated between the left and right sides of the screen, although the experiment did not use a 2AFC task. This was done in order to equate present test conditions with those of the previous task.

Procedure A diagram of the five-choice procedure is presented in Figure 15. The stimulus presentation sequence was the same as in the 2AFC experiment. However, the response to be entered did not serve to identify the side of the display that had contained the grating. Instead, the subject responded by pressing one of five buttons on the keyboard, indicating that he had seen:

1. nothing
2. flicker alone
3. form alone
4. both flicker and form
5. other

The "other" response was to be used if the subject felt that the stimulus had been detected but did not appear to flicker or have any structure which was identifiable as part of a grating. Because of the complexity of this task, each subject was run on several full practice sessions before the experiment proper was initiated.

A session consisted of seven adapt-test sequences, each containing 13 test probes as in the previous experiment. Within a session, each of the appropriate seven test contrasts (including the catch trial) for each of the 13 test probes was presented once. The distribution of the various test contrasts within the seven sequences was randomized at the start of each session. Each session, if completed, lasted approximately 45 minutes. This time was dependent on whether the subject made mistakes. At the end of each adapt-test sequence, the subject was queried (by the computer) as to whether any mistakes had been made. If the subject answered affirmatively, the results of the entire 13 test sequence were discarded. Discarded sequences were repeated.

As many sessions as desired could be run, and any session could be terminated at any time. Subject SP ran the central conditions 12 times apiece, and the extreme conditions 5 times apiece. Subject LM was only tested using the central conditions, which she ran seven times each. The order in which the conditions were run was alternated. Two
sessions were run in a typical setting.

Data Analysis  Data from corresponding conditions were combined. For each condition, and each test probe, the number of times that each of the five percepts had been chosen was expressed as a percentage of the total number of trials completed on that condition and test-probe. The result is a matrix for each adapt/test condition which expresses the percentage with which each of the five perceptual categories was used at each test probe time and test contrast (Appendix II). Ratings from 0-contrast test stimuli (catch trials) produced false-alarm rates for each perceptual category. Corrected scores for each perceptual category were produced by subtracting the appropriate catch trial score from the category rating score.

Another measure was produced in order to compare the contrasts at which flicker seeing and form seeing reached the 50% seeing threshold. The "flicker" and "form" scores at each contrast and test-time were combined with the "both" scores. Two frequency of seeing curves were thus produced for each test-time, one for "flicker", the other for "form". The 50% seeing contrast of each curve was derived by graphic interpolation. The difference of the two scores, which will be called the 50% difference scores, express the perceptual predominance of flicker or form at each test time within each test condition. These difference scores were derived for both uncorrected and corrected data (Figure 17).
Results

Results from each of the four conditions (for subject SP) and the two central conditions (for subject LM) are presented in Appendix II. Representative results from the central conditions (subject SP) are graphed in Figure 16. Unless otherwise stated, the results referred to will be those of subject SP.

The extreme conditions gave results which were predictable from the method-of-adjustment studies. The extreme temporal condition was rated as "flicker" more often than "form" at low test contrasts, and the extreme spatial stimulus was rated as "form" more often than "flicker". The corresponding catch trials showed the same pattern, blank fields presented within the extreme temporal condition were more likely to be rated as "flicker" than "form", and catch trials presented during the extreme spatial condition were more likely to be rated as "form" than "flicker". The extreme conditions were run a minimal number of trials, as the results were not critical to the outcome of the study as a whole. The trends were clear in spite of the small number of trials.

In both central conditions, the most prominent feature in the data is the curve for seeing both flicker and form. These curves have the typical shape of a probability of seeing curve (psychometric function), starting at a level of 0% seeing, and rising to 100% at the highest contrasts tested. The spatial seeing functions are the next most
Figure 16. Representative raw data from the five-choice experiment. The three curves in each panel show flicker ratings (x), form ratings (●) and both ratings (□). The false alarm rates for each category are shown by their respective symbols at 0 modulation, and a horizontal line where the false alarm rate exceeded zero.
prominent. These data have the form of inverted U shaped curves, which rise very closely with the previously described functions, but reach a peak of about 50% seeing and then decline to 0% as the perception of both form and flicker becomes predominant. These patterns are more difficult to see in data from subject LM because of the smaller sample size and high variability relative to data from subject SP.

Flicker responses were made the least of the three categories. The "flicker" rating curve typically is highest at the lowest contrast tested, declining quickly as contrast rises. In the central test, spatial adaptation condition, "flicker" scores increase steadily into the adaptation period, and then decline in the decay period. The peak value attained was 50% seeing, which occurred at the 60 second test (peak adaptation). Flicker scores were less well represented following the temporal adaptation stimulus, with a peak seeing score of only about 17%.

When "flicker" false alarms are subtracted from "flicker" scores, the corrected scores rarely rise above 10% seeing in either condition. These decreases result from the high number of "flicker" responses which were made to the catch trials. Flicker false-alarm rate is correlated with the occurrence of "flicker" ratings. Following the central-test, spatial-adaptation condition, the percentage of "flicker" false alarms rose steadily with time into the adaptation period, as did the "flicker" ratings of the test gratings. Flicker false alarms, and "flicker" ratings of
test stimuli then decreased sharply during the decay period. The remaining categories ("form", "both", "other") accounted for far fewer of the false alarms. This pattern was less clear in the central test, temporal adapt conditions.

Subject LM showed a generally similar pattern of results. Both conditions had much higher false-alarm rates than those from subject SP. The overall false-alarm rate was higher following the more spatial adaptation, having a 0% correct rejection rate during the adaptation period. Within this condition, all the rating categories had substantial false-alarm rates, "flicker" having the highest. Both ratings were also high, with "form" the least common. There was no apparent pattern in the false alarm rates following the spatial adaptation. After the more temporal adaptation stimulus, LM's "flicker" false-alarm rate was clearly the highest of the three response types. The "form" and "both" ratings were present at much lower levels than after the more spatial adaptation stimulus. Flicker false-alarm rate increased during adaptation, and decreased in the decay period.

The predominant sensation at threshold can be seen in the 50% difference scores (Figure 17). Because this score was calculated as the 50% "flicker" seeing contrast minus the 50% "form" seeing contrast, a positive difference score indicates a predominant perception of flicker, and a negative score a predominant perception of form. Uncorrected scores show form to predominate following the more temporal adaptation stimulus, and flicker to
Figure 17. Fifty-percent difference scores. The difference of the contrasts at which 50% of the rating scores were "flicker" or "both" and 50% were "form" or "both". A positive value indicates that flicker was seen at lower contrast than form. Both corrected and uncorrected scores were calculated.
predominate following the more spatial adaptation stimulus. Difference scores calculated from the corrected data show little change for the temporal adaptation condition. However, the corrected difference scores from the more spatial adaptation condition show virtually no predominance of a flicker percept. The subtraction of the "flicker" false alarm rates actually overcompensates the "flicker" ratings, and the corrected difference scores shows a predominance of "form" ratings as time into adaptation increases.

In general, the contrast increments were too coarse to allow good resolution of the psychometric functions. It appears that these functions were quite narrow. Percent seeing rises from 0 to 100% over a contrast range of .5% or less for subject SP. The range of contrasts were in most cases centered about threshold. The few exceptions were in the probes which occurred at or near the peak of adaptation, which tended to be centered about too high a threshold. Data from subject LM are difficult to evaluate in detail because of high variability.

Discussion

This study is in essence similar to the two-criterion threshold experiments in the first section. Both procedures produce a description of the percepts of the observer. However, in a method-of-adjustment study, it is not possible to assess observer bias. The five-choice experiment allows the effects of bias to be approximated through the use of
catch trials and subtracted from the final scores to give a bias-corrected estimate of the appearance of the gratings. While this procedure does not take the probability of each response type simultaneously into account, an elaborate analysis is unwarranted in view of the low probability resolution permitted by the small number of trials which were used.

The most significant result of this experiment is the demonstration that the elevation of "flicker" ratings following adaptation appears to result from an increase in the false-alarm rate. The uncorrected results would have supported the two-mechanism hypothesis. At the 50% seeing threshold in the central conditions, the appearance of flicker predominated following the more spatial adaptation stimulus. The appearance of form predominated following the more temporal adaptation stimulus. However, the bias-correction procedure removed the predominance of flicker. Form is the dominant sensation under criterion corrected conditions. It is interesting to note in this context that Burbeck (1981), in a recent study of criterion-free form and flicker judgements, found form to be the predominant sensation at low contrasts. The data from the present study support this finding.

The original intent of this experiment was to determine the nature of the percepts at the thresholds obtained using forced choice procedures in the previous experiment. If the two mechanisms were both involved in the time-course curves,
the percepts at threshold would have allowed separation of
the curves into the separate underlying functions. The
extreme conditions showed results similar to the method of
adjustment at comparable parameters, as expected. The
central conditions were critical to the differentiation of a
continuum model and a dichotomy model of spatial/temporal
mechanisms. The results at these conditions showed that the
sensation of temporal modulation without spatial modulation
does not occur at a level which can reliably be
distinguished from the response to a blank catch trial. The
plots of the perceptual ratings show that as test contrast
was decreased, flicker seeing rose. Given no variability,
this trend would presumably continue until flicker seeing
approached the false-alarm rate at 0 test contrast. This
flicker seeing is occurring at contrasts for which the
summed percentage of stimuli seen minus the false-alarm rate
is below 50%. As might be expected, these contrasts are
also below the contrast thresholds of the corresponding test
probes from the previous experiment.

Although the original hypothesis of the time-course
experiment does not demonstrate the presence of dichotomous
mechanisms, new problems have been raised. The most
interesting of these concern the increased "flicker" false
alarm rate. Firstly, why did it occur? Second, why was it
selectively raised above the false-alarm rates of the other
response categories?

The appearance of the test probes suggest that the
elevation of "flicker" false-alarm rates resulted from a
temporal afterimage. This afterimage had the appearance of swirling or pulsating motion without apparent direction. The pulsation resembled that which is seen in a counterphase flickered grating which is well fixated. The author noted a spatial afterimage early in the experiment, but this effect seemed to disappear following the first few time-course runs. The spatial afterimage was therefore presumed to result from improper fixation. Subject LM complained of prominent, patterned afterimages. If the interpretation of her method-of-adjustment data within the first section was correct, she was not maintaining fixation. This would account for her results having substantial elevation of response categories other than "flicker", as she would be unevenly (spatially) adapting her retina.

The use of counterphase flickering gratings can be expected (given perfect fixation) to eliminate spatial afterimages. If all temporal information is initially coded by direction-selective mechanisms, a counterphase flickering grating will also eliminate temporal afterimages, since a counterphase-flickering grating may be decomposed into two half-amplitude gratings moving in opposite directions. However, if temporal information was coded (at least in part) by direction independent mechanisms, counterphase flicker could produce temporal afterimages.
VI. DISCUSSION AND CONCLUSION

Psychophysical experiments show major differences in the processing of visual stimuli that are widely separated in spatial and/or temporal frequency. Much of the work which examines these different properties has attributed them to the existence of two classes of processing mechanisms. These hypothetical psychophysically defined mechanisms have been related to the x/y and sustained/transient classifications proposed in the neurophysiological literature. Some researchers claim that the two classes play separate roles in the perception of time-varying and time-stable aspects of the stimulus. One mechanism is proposed to have greater sensitivity to low spatial-frequency, high temporal-frequency stimuli, and be responsible for the perception of flicker/motion. The other is proposed to have greater sensitivity to high spatial-frequency, low temporal frequency stimuli, and be responsible for the perception of form. However, relatively few experiments require a two-mechanism model. Much of the work merely shows differences of some sort (sensitivity bandwidths, period of temporal integration, reaction time, etc) in the processing of stimuli which are widely separated along spatial and temporal dimensions. Such differences do not rule out alternative hypotheses, such as a single mechanism composed of a continuum of channels possessing widely varying response properties. These experiments do
not demonstrate convincingly that specific mechanisms tested play a role in evoking a particular sort of percept - a spatial percept or a temporal percept.

Ideally, different mechanisms would be revealed by the presence of individual sensitivity functions for the isolated mechanisms, measurable over a common range of test parameters. In human psychophysics, the mechanisms can seldom be isolated. Many experiments attempt to show the boundary or transition point between proposed mechanisms by following the change in a measure (such as threshold contrast) over a dimension (such as spatial frequency). Figure 18 illustrates the problem of deciding whether the single resultant curve is produced by one or more underlying mechanisms, each having its own sensitivity function. Ignoring the effects of probability summation, at each point along the curve only the most sensitive mechanism contributes to the visible profile. Whenever a mechanism becomes less sensitive than another, it becomes invisible to the threshold measure. It does not appear possible to objectivly determine whether the sensitivity profile represents a single function, or the envelope of underlying functions. Carried to its logical extreme, the problem becomes circular, because the shape of the underlying curves must be known (or assumed) in order to find them within the envelope.

Even if the presence of underlying mechanisms cannot be proven in the strict sense, in practice multiple mechanisms
Figure 18. The problem of identifying multiple mechanisms underlying the curve of a single sensitivity measure is shown in hypothetical form. This is the problem presented by the hypothesis proposing separate spatial and temporal mechanisms.
have been satisfactorily (in terms of acceptance by the scientific community) derived from single curves. Ultimately, science is empirical, and evaluation of single curves as revealing multiple underlying processes is not uncommon. This approach is justifiable when supported by evidence from other experiments, although any claims of inferred mechanisms should be carefully qualified. One example is the resolution of the dark adaptation function into the two underlying sensitivity functions corresponding to the rods and cones. The two-limbed dark adaptation function was resolved into two underlying sensitivity profiles by interpreting the family of curves resulting from varying the visual angle of the stimuli. The assumption involved is that the sensitivity profile of the underlying mechanism(s) are smooth and unimodal. Although it cannot be proven by inspection that the profile of the thresholds represents multiple underlying mechanisms, a clear change in direction greatly increases the likelihood. The 'elbow' marking the sensitivity of the photopic mechanism in the dark adaptation function is a good example of a feature which is readily interpreted as the sensitivity profile of a mechanism underlying the overall curve. By contrast, a smooth, monotonically changing sensitivity profile is poor evidence of multiple mechanisms. A bi-modal curve is the best evidence of dichotomous underlying mechanisms that a single sensitivity profile can produce.

A variation of this approach uses adaptation to
selectively depress the sensitivity of one of the proposed mechanisms, so as to leave the other more sensitive. Threshold tests should then reveal the sensitivity of the less adapted mechanism. The principal problems involved in interpreting the results are: 1) it is not assured that one mechanism has been sufficiently depressed so that the other(s) are revealed. 2) The adaptation parameters (such as spatial and temporal frequency) may not be representative of the dimensions along which the perceptual mechanisms are tuned. It is therefore unclear what an altered sensitivity profile means. This problem is unavoidable and is common to all adaptation procedures. It illustrates the difficulties involved in drawing together the empirical and theoretical content of a scientific investigation. The empirical work should not be regarded as invalid, but interpretation should be pursued with care.

The two-criterion threshold technique is an example of a procedure potentially capable of finding separable response properties at common test parameters. Unfortunately, it has proven extremely difficult to employ. Although the x/y and sustained/transient categories were developed to explain the perception of form and motion/flicker, it is not clear that the connection between analyzer and percept is as simple as was stated by Kulikowski and Tolhurst (1973). For instance, it is unclear that the x/y systems are completely independent. The degree of segregation maintained by x/y units has not been extensively investigated. If these units converge, the
psychophysical analogy of independent systems would be inaccurate.

At this point it seems that all psychophysical procedures applicable to the spatial/temporal dichotomy involve logical shortcomings. A proof of either the dichotomy or continuum hypotheses is probably not possible using these, or perhaps any psychophysical procedures. This is a ubiquitous problem in experimental design. The best approach to resolving the issue may be to correlate the results from several approaches, and seek a systematic pattern (if one exists) in the data. An example would be to correlate a change in the appearance of a grating with a change in slope or otherwise prominent feature in the threshold curve. This general approach has been used by several experimenters, and was also used in the present study. It is important to press such an approach as far as possible, because it is unclear that any other route exists to resolve the dichotomy/continuum issue.

The majority of psychophysical experiments investigating the proposed dichotomy use one or more of the procedures which were described in the introduction to this paper. Virtually all of these experiments find differences between results from test conditions that are widely separated in spatial and temporal frequency. It is valuable to briefly review examples of these procedures in light of the requirements for revealing separate mechanisms.

1. Separate identification thresholds for flicker and
form. If one accepts the assumption that the two thresholds define different systems, this technique would allow the mapping of the sensitivities of the individual systems. Keesey (1971) and Tolhurst (1973) have used this technique alone and in conjunction with other procedures. However, their results have proven difficult to replicate in the present study and by Green (1981) and Burbeck (1981).

2. Change in contrast threshold with stimulus duration. Legge (1978) and Breitmeyer and Ganz (1977) showed changes in threshold with duration of stimulus presentation. These experiments attempt to reveal a transition between dichotomous mechanisms. In both cases the differences which were described as representing the transition were quite small and do not constitute strong evidence of separate mechanisms.

3. Adaptation procedures. Tolhurst, Sharpe and Hart (1973) and Green (1981) measured form and flicker thresholds following adaptation at different parameters. The inferred transition point between mechanisms was correlated with a change in the appearance of the test grating. These experiments strongly support the existence of separate mechanisms.

4. Additivity paradigms. Subthreshold additivity techniques have been used to show changes in linearity of the spatial summation of contrast with changes in spatial frequency of the test stimuli (Kingsmith and Kulikowski, 1975; Watson and Nachmias, 1977). Used without a two-criterion paradigm, these procedures can only seek a
transition point between the two mechanisms. If the two
criterion threshold procedure is used in conjunction with
the additivity paradigm, separation of mechanisms at common
test parameters should be possible. The latter approach did
not yield evidence of separate mechanisms (Watson and
Nachmias, 1977). Subthreshold additivity combined with a
two threshold procedure also failed to reveal changes in
channel bandwidth for flickering and steady gratings. (Arend
and Lange, 1977).

5. Reaction-time measures. Changes in RT with spatial
frequency, stimulus duration, and/or rapidity of onset offer
the possibility of revealing a transition point between the
proposed mechanisms (Lupp et al, 1976, 1978; Tolhurst,
1975b; Breitmeyer and Julesz, 1975). However, these
experiments did not reveal any obvious transition point,
either because the measures tested yielded smooth curves, or
because the test parameters were so widely spaced that clear
functions of any sort could not be produced.

The strongest evidence for the existence of dichotomous
mechanisms makes use of the two-criterion threshold
 technique. It thus seemed important to further test this
technique by using it to separate the two systems in a
manner less prone to response bias than the existing
procedures. The experiments of the present study have
resulted from this conceptual approach.

The present study, like other recent experiments
dealing with the two mechanism issue, has served to
demonstrate the complexity of the issue rather than resolve it. The evidence presented in the experimental sections of this paper provide, at most, marginal evidence in favor of a dichotomy. Attempts to replicate early method of adjustment studies revealed only minor differences between the two threshold criteria, and proved quite difficult as a task, casting doubt on the earlier work. Parameters of curves tracing sensitivity over adaptation time-course showed no clear similarities between conditions which should have tapped the same systems, although at different spatial and temporal parameters. Most importantly, these thresholds were not associated with reliably separable sensations of flicker and form as measured by the bias-corrected procedure of the last experiment. This last experiment demonstrated that the predominant sensation measured in a bias-corrected procedure was form. These results would seem strange were they not similar to those from a different criterion-free procedure by Burbeck (1981). Her study showed that the spatial-frequency contrast-sensitivity surface was essentially identical to the surface revealed by the spatial thresholds.

Clearly there exists some unknown factor which results in such different patterns of response under bias corrected and uncorrected conditions. Other experimenters have actually given different names to the flicker and pattern tasks, calling the former "detection" and the latter "recognition" (Kulikowski and Tolhurst, 1973; Harris, 1981). It is unclear what the difference between the two
tasks is, other than criterion. Their difficulty in defining their criteria could well account for the discrepancy between their results and those from criterion-correcting procedures.

Within the current study, the strongest evidence produced for the existence of a dichotomy was the selective elevation of the flicker false-alarm rate with adaptation. This could be interpreted in two ways. The elevation could result entirely from a response bias. If a subject was seeking flicker, some cognitive process might well result in his seeing flicker more often than when seeking another percept. However, no corresponding major elevation of form false alarms occurred when the task was form detection. The elevated flicker false alarm rate may indicate different noise levels in neural systems playing separate roles in the perception of flicker and form. These data do not allow a decision between the two hypotheses. However, the high elevation of the flicker false alarm rate in both the experienced and the naive subject is difficult to attribute solely to response bias. The use of bias-corrected procedures should be continued, since it appears to be a promising approach to resolving the issue of the existence of separate sustained and transient mechanisms in human vision.
REFERENCES


Ikeda, H. & Wright, M. Receptive field organization of "sustained" and "transient" retinal ganglion cells which subserve different functional roles. *Journal of Physiology*, 1976, 227, 769-800.


APPENDIX I. THE EFFECTS OF TEMPORAL TRANSIENTS ON GRATING DETECTION: A CONTROL EXPERIMENT

This experiment determined whether transients arising from a briefly presented conditioning grating will affect the contrast threshold of a subsequently presented test grating. The test grating parameters were identical to those to be used in the preceding adaptation time course experiments, so as to determine whether the insertion of probe stimuli would alter threshold.

Method

Subjects The author served as the subject.

Procedure Stimuli were generated as for the previous experiments. All stimuli were vertically oriented spatially sinusoidal gratings. Test gratings were counterphase flickered. The conditioning gratings were stationary and unflickered in the usual sense, but the temporal envelope assumed one of three forms:

1. The contrast came on abruptly at 50% modulation, remained on for 1/4 second, and was then linearly decreased to 0 over the next 1/4 second. (end ramped condition)

2. Contrast was linearly ramped from 0 to 50% modulation over the first 1/4 second of presentation, remained at 50% for 1/4 second and was abruptly decreased to 0. (beginning ramped condition)
3. The grating was both turned on and off with no ramp. In this condition the presentation was shortened to 3/8 second to keep time averaged contrast the same as in the previous two conditions. (square wave presentation)

Differential effects of the conditioning stimuli should come about in the following manner. The stimulus that is ramped on and turned abruptly off should produce a small on transient, but a large off-response which immediately precedes the test presentation. If the test stimulus is being detected at threshold by transient mechanisms, masking would be expected to occur. If the conditioning stimulus is ramped off, but not on, the on-transient will be large relative to the off-transient, but the displacement of the transient in time should result in relatively little masking by comparison to the previous case. The "square wave" presentation, with no ramping, would be expected to produce masking equal to or exceeding that from the "ramped on" condition.

The spatial frequencies of the adapt and test gratings (.5, 2, and 8 c/d) were always identical in order to maximize sensitivity changes. The test gratings were counterphase flickered at 8, 2, and 1 Hz respectively. These stimulus parameters placed the first test stimulus in the range of the proposed temporal system (.5 c/d, 8 Hz). The second condition (2 c/d, 2 Hz) was at the point of equal sensitivity of the two systems, as measured by the method of adjustment experiments in Section IV. The third condition (8 c/d, 1 Hz) was within the range of the proposed spatial
system.

The conditioning prefIELDS occupied the entire 10 degree wide by 8 degree high screen. Test stimuli were 2.8 degrees wide and located on either the left or the right side of the display. The remainder of the CRT was a mean luminance blank field. The centermost edge of the grating began 0.06 degrees from the center of the display. The test field utilized the full height of the display. Test gratings began at 0 degrees phase angle (mean luminance) at their leftmost edge. The sinusoidal contrast at the right edge was multiplied by a linear ramp which decreased the modulation to 0 over a distance corresponding to 1/4 cycle, eliminating the possibility of detecting the grating by the high contrast edge resulting from a chopped cycle at the border of the field.

The subject was seated in a dental chair. The screen was viewed from 30 inches, with head position maintained by the headrest. Experiments were conducted in the dark. After entering the relevant starting parameters, communication between the subject and the computer proceeded via a small, handheld keyboard. Each trial was initiated by the subject and consisted of:

1. A mean luminance blank field was presented for 15 seconds. A flickering line bisected the midpoint of the screen to aid fixation.

2. A conditioning prefIELD grating, presented at 50% modulation for either 1/2 or 3/8 second. The central
flickering line remained to aid fixation.

3. A test grating, presented for one second on either the left or right side of the display. No line was present.

4. A 3 second blank, mean luminance field.

5. A dark field, terminated when the subject responded.

The rather short duration of the test presentation (1 second) was chosen to correspond to that used in the time-course experiments. This duration is the maximal temporal resolution of the time course experiments.

The subject's task was to determine which side of the display contained the test grating. The 2AFC procedure utilized 2 independent but interwoven staircases which were randomly selected to make the progression of test contrasts unpredictable by the subject. The position of the test grating was randomly determined for each trial. Test contrast was decreased in two stages. Prior to the first reversal, a correct response decreased the contrast of the next trial on that staircase by 25%. After the first error, all subsequent correct responses reduced contrast by 5%. In both stages, an incorrect response increased contrast by 25%. Correct responses were followed immediately by a feedback tone. The experiment continued until 8 errors had occurred. Threshold was defined as the mean of the reversals, excluding the first from each staircase. Each threshold therefore was the mean of 14 reversals. All 2 c/d conditions were run three times. This condition was of primary interest because it corresponded to the 'central'
conditions of the time course experiments. Each conditioning pref/field/spatial frequency condition constituted a block of trials, the order of which was randomized. The .5 c/d and 8 c/d conditions were each run once.

**Results**

Results are shown in Table 4. None of the conditions revealed any significant trends resulting from the temporal profile of the conditioning pref/field. However, in the 2 c/d, 2 Hz condition a uniform increase in threshold was noted for all experimental conditions, relative to a control condition (blank conditioning pref/field). The increase was roughly a factor of 2. No such threshold elevation was obtained at the other spatial/temporal frequency combinations. Thresholds of the .5 c/d and 8 c/d stimuli were approximately the same 80% modulation. At 2 c/d the control threshold was .38%, the mean of the conditioned thresholds was .65%. Standard deviations for each block of 14 reversals were typically about .17%, yielding a within session standard error of .05%. Intersession errors are given in Table 4.

**Discussion**

The conditioning pref/field used in this experiment is a novel variation of the adaptation paradigm. The correspondence between the behavioral effects and the
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Table 4. The effect of varying the temporal taper of a conditioning prefield on contrast threshold.
underlying physiological mechanization of the two procedures is unclear. For instance, it is unclear that the threshold elevation produced would reveal the same tuning characteristics of underlying channels shown by a full scale adaptation procedure. The technique may be suitable for producing an action spectrum of channel sensitivity analogous to that produced with adaptation procedures by Swift and Smith (1982). The present study was a very limited exploration of the technique.

In this experiment, the conditioning stimulus was of very short duration in order to avoid adaptation in the usual sense. The aspect of the conditioning stimulus of primary interest was the production of a transient of somewhat variable parameters. Effects of this transient upon grating detection would not necessarily be deleterious. Facilitation might be expected when the conditioning field was subthreshold and the activated channel was capable of summing response over interval containing the conditioning and test fields. In this case, however, the conditioning stimulus contrast was quite high, and the expected effect would be masking. Since the conditioning grating occupied the entire screen, residual channel activation would be expected to interfere with localization of the test grating, thereby raising the 2AFC threshold.

In a temporal system, channel activation would be confined to the time at and shortly following onset and/or offset. Interactive effects such as masking would be expected to occur within this limited period of activation.
In a spatial system, the duration of channel activation is relatively long, and the period over which two stimuli could interact is lengthened.

Because this experiment served primarily as a control for the probe insertion technique used in the time-course experiments, the major transient of interest is that produced by the offset of the conditioning stimulus. The primary concern was that this offset not raise the threshold unequally when transient and sustained units are expected to both be operating at the test parameters. Were this the case, thresholds derived from a probe technique would be difficult to evaluate, because offset transients from the adaption grating offset would differentially affect the two mechanisms. In the present experiment, the various temporal envelopes of the adaptation stimuli served to modify and delay the temporal nature of the presentation. This altered the likelihood of its interaction with subsequent activation of the test channel(s) by the test stimuli.

No differential masking effects were observed. Several interpretations are possible. The simplest is that the parameters of the conditioning field were inadequately explored, and that different temporal envelopes would yield different results. This is certainly a possibility, and the technique should be more thoroughly explored as a tool for investigating the two mechanism hypothesis. Assuming, however, that the parameters were adequate to differentiate
the two mechanisms if they exist, differential effects should have been noted at least at the low spatial frequency condition, which would maximize the chances of observing a temporal channel. No effect would have been expected at high spatial frequency, where (presumably) spatial mechanisms are primarily operative.

Accepted at face value, these results indicate that there is no undue effect of offset transients upon test gratings which will be used in subsequent adaptation experiments. The technique of inserting probe stimuli within a high contrast adaptation presentation should not yield artifacts across the spatio-temporal frequency range employed here. This range extends across the proposed ranges of the spatial and temporal systems.

The failure to obtain any threshold increase in the two extreme conditions could be interpreted as revealing the use of inadequate contrast in the conditioning stimulus. Certainly the reduced effectiveness of the 50% conditioning modulation at these spatial frequency extremes was responsible for the absence of any threshold elevation. Yet the effects of the transient will be less than those of adaptation, and care must be taken to keep the effects of the conditioning field from becoming adaptation effects in the usual (sustained) sense. It is possible that the threshold elevation obtained in the central spatial frequency condition was itself an adaptation effect of sustained duration. Alternatively, this distinction may itself be fallacious. The problem clearly warrants further
research, unfortunately along time-consuming parametric lines. The effects of varied adapt contrast as well as form and duration of the temporal envelope should be explored.
### APPENDIX II

**RAW DATA, FIVE-CHOICE EXPERIMENT**

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Extreme temporal condition, subject SP.
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Central test, temporal adaptation. Subject SP.
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Central test, temporal adaptation. Subject LM.