Vision Res. Vol. 33, No. 7, pp. 959–980, 1993
Printed in Great Britain. All rights reserved

0042-6989/93 $6.00 + 0.00

Forward Pattern Masking and Adaptation: Effects of Duration, Interstimulus Interval, Contrast, and Spatial and Temporal Frequency*

JOHN M. FOLEY,† GEOFFREY M. BOYNTON†

Received 27 November 1991; in revised form 15 September 1992

Eight experiments are described that compare pattern adaptation and forward pattern masking by examining the effects of five variables on the contrast threshold of a target presented after an adapter or masker. The target is a Gabor pattern with a center frequency of 2 c/deg and a duration of 33 msec. Thresholds are determined using an adaptive spatial forced-choice method. Principal results are as follows. (1) An adapt-refresh regime with a 2 sec refresh and a 2 sec recovery period on each trial is shown to maintain constant performance. (2) Desensitization is very rapid, reaching near maximum in < 200 msec. (3) Recovery is very rapid during the first 100–200 msec and then very slow with the rate of slow recovery decreasing as adapter/masker duration increases. (4) Threshold vs contrast functions are step-like for certain frequency pairs. (5) Sensitivity vs frequency functions derived from adapting and masking are similar in form. (6) Masker temporal frequency (0–15 Hz) has very little effect. These results are described by a theory that postulates that the target is detected by a few mechanisms that are differentially tuned to spatial frequency. The effect of both a forward masker and an adapter is to desensitize the mechanisms that respond to it. Recovery is a weighted sum of two decay processes, one fast and one slow. The theory fits the data from both paradigms well with some differences in parameters.

Pattern vision Adaptation Masking Spatial frequency Temporal frequency Contrast Theory

INTRODUCTION

After a luminance grating has been viewed for a few seconds, several aftereffects occur. Most studied among them is an increase in the contrast threshold of gratings that are similar to the first grating in spatial frequency and orientation (Pantle & Sekuler, 1968; Blakemore & Campbell, 1969; Braddick, Campbell & Atkinson, 1978). This occurs even when the eyes scan back and forth across the grating during the initial presentation or the grating repeatedly reverses phase so that retinal illuminance averaged over time is approximately the same at each point on the retina. This and other aftereffects are thought to be manifestations of a pattern adaptation process which is distinct from adaptation to light. This distinction was strongly reinforced by an experiment by Kelly and Burbeck (1980) using controlled retinal motion. They showed that pattern adaptation occurs at adapting velocities that are too high to produce local sensitivity changes. Although there are a large number of studies of pattern adaptation, there is not yet a generally accepted theory of pattern adaptation phenomena or even agreement about their description. Some of the empirical differences may be a consequence of variations in method, particularly the temporal aspects of the adapting stimulus, including those produced by voluntary and involuntary eye movements, and the methods used to measure thresholds. Control of the temporal aspects of the retinal stimulus has been by either voluntary scanning movements, fixation while the stimulus undergoes counterphase contrast modulation, or controlled, constant velocity, retinal motion. Thresholds in adaptation tasks have usually been measured by the method of adjustment, but yes–no and forced-choice methods have also been used.

Interest in pattern adaptation has recently been stimulated by new ideas concerning the nature and function of this process. Barlow and Földiák (1989) have proposed that adaptation corresponds to the gradual decorrelation of cortical neurons by anti-Hebbian mutual interaction (i.e. an increase in mutual inhibition among neurons whose responses are correlated). Its proposed function is the acquisition and storage of past associations among stimuli and the detection of

---

*A preliminary report of this work was given at the European Conference on Visual Perception, Paris, August 1990.

†Department of Psychology, University of California—Santa Barbara, Santa Barbara, CA 93110, U.S.A.

new associations (Barlow & Foldiak, 1989; Barlow, 1990). Although the present study does not test this hypothesis, it does further clarify the properties of pattern adaptation.

Forward pattern masking refers to an increase in the threshold for one pattern (target) produced by another pattern that precedes it in time (masker). Forward pattern masking and pattern adaptation have not been sharply distinguished. Both terms have been used to refer both to experimental paradigms and to visual processes. As experimental paradigms, they differ primarily in the duration of the first pattern (adapter/masker). As processes they have not been clearly defined or distinguished, and there may be several types of each. Although Breitmeyer (1984) has proposed a distinct process for forward masking that can be effective only at short stimulus onset asynchronies (SOAs), Georgeson and Georgeson (1987, p. 378) suggest that "masking and adaptation studies not only reveal the same spatially tuned channels, but also reflect to a large extent a common mechanism of desensitization differing only in time–course according to the temporal regime of the experiment". The present study examines this possibility by measuring the effects of several variables on the target threshold in the two paradigms. For the purposes of this study adapting and masking paradigms are defined as follows: an *adapting paradigm* is one in which a pattern (adapter) is presented for at least several seconds before trials begin and re-presented (refreshed) briefly on each trial. A *masking paradigm* is one in which a pattern (masker) is presented for a short interval on each trial. We will consider the distinction between adapting and masking as visual processes in the Discussion.

The present study compares adapting and forward masking by examining the effects of adapter/masker duration, interstimulus interval (ISI), adapter/masker contrast, adapter/masker spatial frequency, adapter/masker temporal frequency and interactions among these variables on threshold elevation. Across experiments, it also examines the effect of the spatial phase of the adapter at offset. The study uses a spatial forced-choice method to determine the threshold for a Gaussian windowed patch of grating presented after the offset of an adapter or masker. In the adapting conditions a refresh regime was used that had been demonstrated in Expt 1 to maintain constant performance. Seven other experiments are described that examine the effects of various combinations of the variables in the two paradigms. A theory is proposed which describes the results of both masking and adapting experiments. The theory is an extension of the theory of forward masking proposed by Foley and Yang (1991). The same pattern vision mechanisms are assumed to mediate both classes of phenomena. Some of the parameters are the same for masking and adapting and some are different. Although the theory assumes two processes of desensitization, both of these may be involved in both paradigms.

Before describing the experiments, we will briefly review the literature on the effects of the variables that are examined in the present study. Most of the studies have employed an adapting paradigm, i.e. they have used a first stimulus of at least several seconds duration. Blakemore and Campbell (1969) found that desensitization reached a plateau after about 1 min of adapting, and that recovery after 1 min of adapting also took about 1 min. Using a contrast matching task Blakemore, Muncey and Ridley (1973) showed, however, that if the duration of the adapting stimulus is several minutes, recovery also takes several minutes. This has been confirmed using detection tasks by Heggelund and Hohmann (1976), Bodinger (1978), and Rose and Lowe (1982). Recent studies have shown that desensitization may have also have a long time–course (Rose & Lowe, 1982; Rose & Evans, 1983; Magnussen & Greenlee, 1985). Magnussen and Greenlee tracked thresholds over 3 hr of exposure to an adapting stimulus and a comparable period of recovery. They found that desensitization increased for 30–60 min and that recovery took approximately the same amount of time. More recently Greenlee, Georgeson, Magnussen and Harris (1991) reported a more extensive study in which targets were presented at known times after the offset of the adapter and a "seen/not seen" single presentation method was used. There were four adapter durations (1–1000 sec) and 4 adapter contrasts (-31 to -1 dB re 1). For the longer adapter durations, recovery duration was again approximately the same as adapter duration, but for short adapter durations, the ratio of recovery duration to adapter duration increased. This suggests that there may be two components to recovery, a constant component and a component that is proportional to adapter duration.

Studies in the literature differ not only over the durations of desensitization and recovery, but also over the form of the functions that describe the time–course of desensitization and recovery. Most of the research focuses on the recovery function. Blakemore and Campbell (1969) found that threshold elevation was a negative exponential of recovery time with a time constant of about 20 sec. Bodinger (1978) fitted her data with two exponential decay functions. An exponential function with a short time constant described the first few seconds of recovery and an exponential with a long time constant described the later stage. Several more recent studies have found that in log–log coordinates the threshold varies linearly with time during both desensitization and recovery (Rose & Lowe, 1982; Rose & Evans, 1983; Magnussen & Greenlee, 1985; Greenlee *et al*., 1991). This means that power functions of time may be used to describe both desensitization and recovery. It seems unlikely that this function is correct for very short recovery times, because it implies that the threshold will be infinite at adapter offset.

Georgeson and Georgeson (1987) have pointed out that there is a methodological weakness in all of the experiments that attempt to show the time–course of desensitization. All of them measured sensitivity at least several hundred milliseconds after the offset of the adapter. This means that the different thresholds obtained after different durations of adapting may be a consequence of different rates of recovery rather than different levels of initial desensitization. The present study shows that differences in initial desensitization are at most small.

Masker duration effects have not been studied in forward pattern masking. The time-course of recovery has been studied somewhat (Breitmeyer, 1984; Gorea, 1987) and the general finding is that it takes several hundred milliseconds to recover from a masker whose duration is only a few milliseconds.

The present study examines desensitization and recovery over shorter durations than those examined by earlier studies. One of its findings is that the power function does not hold for either adaptation or recovery when adapting and recovery durations are short. Recovery seems to follow the weighted average of two negative exponentials with different time constants.

Studies that have examined the relation between target contrast threshold and adapter/masker contrast (TvC functions) have yielded quite varied results. Blakemore and Campbell (1969) obtained TvC functions that were approximately linear on log–log coordinates. They used a range of spatial frequencies, but the adapter and target frequencies were equal in each condition. Slopes were about 0.4, except at the highest spatial frequencies, where they were higher. Blakemore and Nachmias (1971) used a temporal regime that consisted of 3 min of initial adaptation, followed by an adjustment trial of variable duration. The other trials were preceded by 13 sec re-adaptation. They plotted their data on log–log coordinates and fitted them with straight lines which had slopes in the vicinity of 0.2 Stecher, Sigel and Lange (1973), using a yes–no method with readaptation between trials, also found TvC functions that were linear on log–log coordinates with still lower slopes, especially when target and adapter frequencies were different. Tolhurst (1972) found that the threshold, increased with adapter contrast for contrasts up to about 0.1 and became approximately constant at higher adapter contrasts. Swift and Smith (1982) obtained TvC functions that consisted of a horizontal segment at low contrasts and a rising segment at higher contrasts that was linear on log–log coordinates with slopes of 0.3–0.4. Ross and Speed (1991) obtained the same form with slopes of about 0.25. Most of the functions obtained by Georgeson and Harris (1984) were slightly concave downward. Greenlee *et al.* (1991) obtained TvC functions of two forms: concave downward and increasing in two steps with a horizontal segment in between. Thus we find in the literature almost all the principal types of increasing function. In a forward masking task Foley and Yang (1991) found step-like TvC functions containing, one, two or three steps depending on the target and masker frequencies. The rising segments are approximately linear on log–log coordinates with slopes of about 0.4 for an ISI of 33 msec. Georgeson (1988) showed that the slope decreases as ISI increases, reaching 0 at an ISI of about 130 msec.

Several studies have examined the effect of the relation between target spatial frequency and adapter spatial frequency in the adapting paradigm. The usual finding has been that desensitization is greatest when the adapter frequency equals the target frequency and decreases as the separation between the frequencies increases. This is different than the finding in both simultaneous masking (Legge & Foley, 1980; Wilson, McFarlane & Phillips, 1983) and forward masking (Foley & Yang, 1991) in which maximum desensitization may occur at a frequency that is somewhat different than the target frequency.

The spatial frequency bandwidth over which threshold elevation occurs is usually taken to be the range between the frequencies at which threshold elevation is one-half its maximum value and is measured in octaves (full bandwidth at half maximum). Blakemore and Campbell (1969) found this to be about 1 octave for adapting frequencies of 3–14 c/deg and to become narrower at higher spatial frequencies. Several other investigators have found threshold elevation bandwidths in the vicinity of 1 octave, but the typical bandwidth is closer to 1.5 octaves, especially for low target frequencies (Graham, 1972; DeValois, 1977; Kelly & Burbeck, 1980; Swift & Smith, 1982; Georgeson & Harris, 1984). Some studies have found that when target and adapter are separated by about 2 octaves, the adapter has the effect of decreasing the target threshold (facilitation) (DeValois, 1977; Tolhurst & Barfield, 1978; Kelly & Burbeck, 1980). Bandwidths for threshold elevation produced by simultaneous masking (Wilson *et al.*, 1983) are somewhat wider than those produced by adapting, especially at low target frequencies, where simultaneous masking bandwidths tend to be three octaves or more. Foley and Yang (1991) obtained similar threshold elevation bandwidths at low masker contrasts, but these tended to become narrower as masker contrast increased. Threshold elevation bandwidth may also depend on ISI.

It is clear that several questions about these threshold elevation functions have not been definitely answered. These include: what is their mathematical form? Do the functions always peak at the target frequency? How do they depend on masker contrast, ISI and target frequency? These threshold elevation functions have sometimes been taken to correspond to relative sensitivity functions of pattern mechanisms in the visual system. This cannot be done except in the context of a theory that links threshold measurements with structures in the system. Theories of pattern adaptation have generally not identified threshold elevation functions with sensitivity functions of the pattern vision mechanisms (Swift & Smith, 1982; Georgeson & Harris, 1984; Graham, 1989).

Does adapter contrast interact with adapter spatial frequency to determine threshold elevation and, if so, what is the nature of this interaction? Again the results are inconsistent. Swift and Smith (1982) found that the rising segments of their TvC functions were linear and parallel on log–log coordinates. This means that changing the adapter frequency has the same multiplicative effect on the target threshold at all adapter contrasts. On the other hand, Stecher *et al.* (1973) and Georgeson and Harris (1984), found that the slope of the TvC function on log–log coordinates varied with the adapter frequency being greatest when the adapter frequency and the target frequency are the same. This implies a more complex interaction between the two variables in which the relative sensitivity to different adapter frequencies depends on their contrast.

This brief review shows that there is inconsistency in the literature concerning the effects of several variables on threshold elevation. Our general rationale in this study was to use a method that seems to offer some advantages over those used in the past and to reexamine these relations. It seemed to us that a good method would (1) provide a known time between adapter/masker offset and target (ISI) and control of this interval by the experimenter, (2) be relatively free of criterion effects, and (3) yield relatively fast threshold determinations. (Our threshold determinations were slow relative to method of adjustment, but fast relative to a forced-choice paradigm in which complete recovery is allowed between trials.) We used a spatial forced-choice paradigm and the QUEST procedure (Watson & Pelli, 1983) to determine target contrast thresholds. In adapting conditions the adapter was presented prior to the trial sequence and re-presented (refreshed) at the start of each trial. The ISI, target duration and intertrial interval were all under experimenter control. Our first step was to find a temporal regime which maintained constant sensitivity to the target throughout the trial sequence. Experiment 1 accomplished this. The method for forward pattern masking conditions was the same, except that there was no presentation of the masker prior to the trial sequence and the intertrial interval of 2 sec was long enough to allow complete recovery from the masker between trials. That 2 sec was sufficient had been established in a pilot study.

METHOD

Equipment

The stimuli were generated using a computer graphics system that consisted of an AST 386/20 computer, a Truevision ATVISTA graphics board with 2 Mbyte video memory, a contrast mixer and attenuator circuit, and two video monitors (Sony, model CPD-1304 in Expt 1–4, 7, and 8 and NEC, multisync II in Expts 5 and 6). Truevision Stage graphics software was used for image generation and control. In seven of the eight experiments, the masker was generated on one monitor and the target on the other, and they were combined by a beam splitter. In Expt 5 target and masker were presented on a single monitor. Images of the fixation field, the masker field and the target field were computed and stored on the graphics board. Each of these images was 512×400 pixels and its intensity was specified by an 8-bit number. The frame rate was 60 Hz. The methods of contrast control described by Watson, Nielson, Poirson, Fitzhugh, Bilson, Nguyen and Ahumada (1986) were adapted to our system and to the adapting and forward masking paradigms. The contrast of the masker was controlled by the green segment of the lookup table and was output on the green line. The contrast of the target was controlled by the red segment of the lookup table and was output on the red line. An external analog circuit attenuated one or both of these signals. Each was then directed to the green input jack of one of the monitors, so that all the stimuli were monochrome green. The lookup tables had the dual role of controlling contrast and correcting for the nonlinear relation between voltage and screen intensity. As a consequence the number of possible intensities was approx. 180; it varied somewhat between conditions. The attenuator circuit made possible two ranges of contrast so that low contrast patterns could be presented without loss of waveform definition.

Stimuli

The fixation field was uniform except for a small dark fixation point at the center. Adapter/maskers were vertical sine-wave gratings that filled the entire screen and were in cosine phase with the fixation point. A single target waveform was used throughout the study. It was a Gaussian windowed sine-wave grating (Gabor pattern) with a center frequency of 2 c/deg that was in cosine phase with the fixation point. The Gaussian window was centered on the fixation point and had a 1/e half-width of 0.47 deg in both vertical and horizontal directions. Thus, the target was a circular patch of sine-wave grating which faded in both vertical and horizontal directions. The target was kept relatively small so that it would stimulate a region of the retina that is relatively homogeneous with respect to spatial properties. The target had a rectangular temporal waveform and a duration of 33 msec. Maskers filled the screen so as to minimize their bandwidth. The space average luminance of the target was, at maximum, 0.5% higher than the background. This small zero spatial frequency component of the target is likely to have had a negligible effect on the target threshold. Contrast for both patterns was defined as (peak luminance − background luminance)/background luminance. For the sine-wave maskers, this is equivalent to Michelson contrast. Contrast is specified in decibels re 1, where 1 dB corresponds to $\frac{1}{20}$ of a log unit of contrast (i.e. No. dB re $1 = 20 \log C$, where C is contrast). In some conditions the adapter was modulated in counterphase with a square-wave temporal waveform. The background luminance varied from 19 to 33 cd/m^2 across the eight experiments. Viewing distance was 162 cm and the visual angle subtended by the stimulus field was 7 deg horizontal × 5 deg vertical. The adapter/masker parameters varied from experiment to experiment and are stated in the tables that describe the individual experiments.

Procedure

The observer fixated on the fixation point during the adapter presentation (if any) and throughout each trial sequence. A two-position spatial forced-choice method was used to determine target contrast thresholds. On each trial the target was presented either 0.8 deg above the fixation point or 0.8 deg below the fixation point. The position was determined randomly with the probability of each position being 0.5. The time when the target came on was marked by a tone. The observer responded by pushing a lever forward or back to indicate target "above" or "below". The response was followed by a high or a low tone indicating correct or incorrect. The QUEST procedure was used to adjust the contrast so as to seek the contrast corresponding to a probability correct of 0.92. We refer to this contrast as the *target contrast threshold.* The QUEST sequence was terminated after 40 trials, or 50 trials if there were no errors on the last 20 trials.

In the adapting conditions, the adapter was presented for 2 or 3 min prior to the start of the trial sequence. The adapter was either steady or phase-shifted by 180 deg (counterphase flicker) with a square-wave form and frequencies of 1–15 Hz. The adapter was always offset at the end of a half-cycle. The spatial phase of the adapter at offset varied from experiment to experiment. The trials began immediately after the offset of the adapter. Each trial consisted of a short re-presentation of the adapter (refresh), followed by an ISI, the target interval and an intertrial interval. The recovery interval (interstimulus interval + target interval + intertrial interval) was determined in Expt 1 and thereafter set at 2 sec. Note that here recovery interval refers to the total time between presentations of the adapter. The time between the adapter and the target is referred to as the ISI.

In the masking conditions each trial began with a premasker interval of 1 sec. The masker was then presented with a rectangular temporal waveform. Its offset was followed by an ISI, the target interval, and an intertrial interval. Timing diagrams of both paradigms are shown in Fig. 1.

In both paradigms the durations of the stimuli and timing intervals varied from experiment to experiment and sometimes within an experiment. The specific values will be given in the descriptions of the individual experiments.

EXPERIMENT 1: ADAPTING REGIME THAT MAINTAINS CONSTANT DETECTION PERFORMANCE

Pattern adaptation is a dynamic phenomenon. Desensitization increases over time after adapter onset and eventually reaches a maximum. Recovery begins after offset and proceeds rapidly at first and then more slowly. To examine the dynamics of adaptation it is necessary to measure sensitivity at specific known times during this process. The spatial forced-choice method allows for threshold measurement at specific known times. However, this method requires many trials to measure a threshold. If the observer fully recovered between trials and then readapted, the experiments would take almost forever. A common solution to this problem is to allow only partial recovery between trials and to re-present the adapter on each trial for a duration that will restore the previous state of adaptation. In practice the recovery periods have been 3–10 sec (sometimes the time required to make a threshold adjustment and not always controlled) and they have been followed by 10–30 sec of re-presentation of the adapter. The rationale for such regimes may have been based on the hypothesis that desensitization reaches a maximum after 1–3 min of adaptation and that after the few seconds interruption required to measure a threshold, re-presentation of the adapter for a few seconds will restore maximum desensitization.

Although the adapt and refresh paradigm has been used frequently there is very little published evidence that these regimes do maintain constant performance. Rose and Lowe (1982) studied temporal regimes in which adapt and test intervals were equal. During each test interval the observer continuously tracked her or his threshold. The period of the adapt–test cycle ranged from 2 sec to 12 min. Although most of the threshold increase occurred early in the sequence, it continued over the 12 min duration of sequence. Recovery periods five times longer than the adapt periods were not sufficient for complete recovery to occur. This surprising result may depend on the use of a continuous threshold tracking method. However, it does show that many refresh regimes do not maintain constant performance. Further, the finding that at least one aspect of the adapting process continues to increase over several minutes casts doubt on the rationale for the refresh paradigms that have been used in the past.

Experiment 1 examines several adapting regimes to determine which, if any, maintain constant thresholds. The experiment used spatial forced-choice trials with short recovery and re-presentation times, since this is the type of regime that we planned to use in the other experiments. Short trials were a necessity in a study involving several experiments with 5000–8000 trials per observer per experiment.

Method

Table 1 summarizes the design of the experiment. There were four conditions. The conditions differ in the adapting, refresh and recovery regime used, including the temporal frequency of the adapter, initial adapt duration, refresh duration, spatial phase at offset, and recovery duration. Condition (a) used a regime of 3 sec refresh and 1.5 sec recovery (ISI + target duration + intertrial interval). Conditions (b), (c) and (d) used a regime of 2 sec refresh and 2 sec recovery. In conditions (a) and (b) adapter temporal frequency was 1 Hz; in condition (c) it was 15 Hz and in (d) 0 Hz. The observer maintained fixation throughout the adaptation and trial sequence. Each trial consisted of a re-presentation of the adapter, an ISI, a target interval, and an intertrial interval. The target contrast was kept constant at a contrast chosen so that the proportion correct was between 0.5 and 1. There were 100 trials in each trial sequence, and 3–10 sequences were run per condition. The dependent variable was the percent correct over

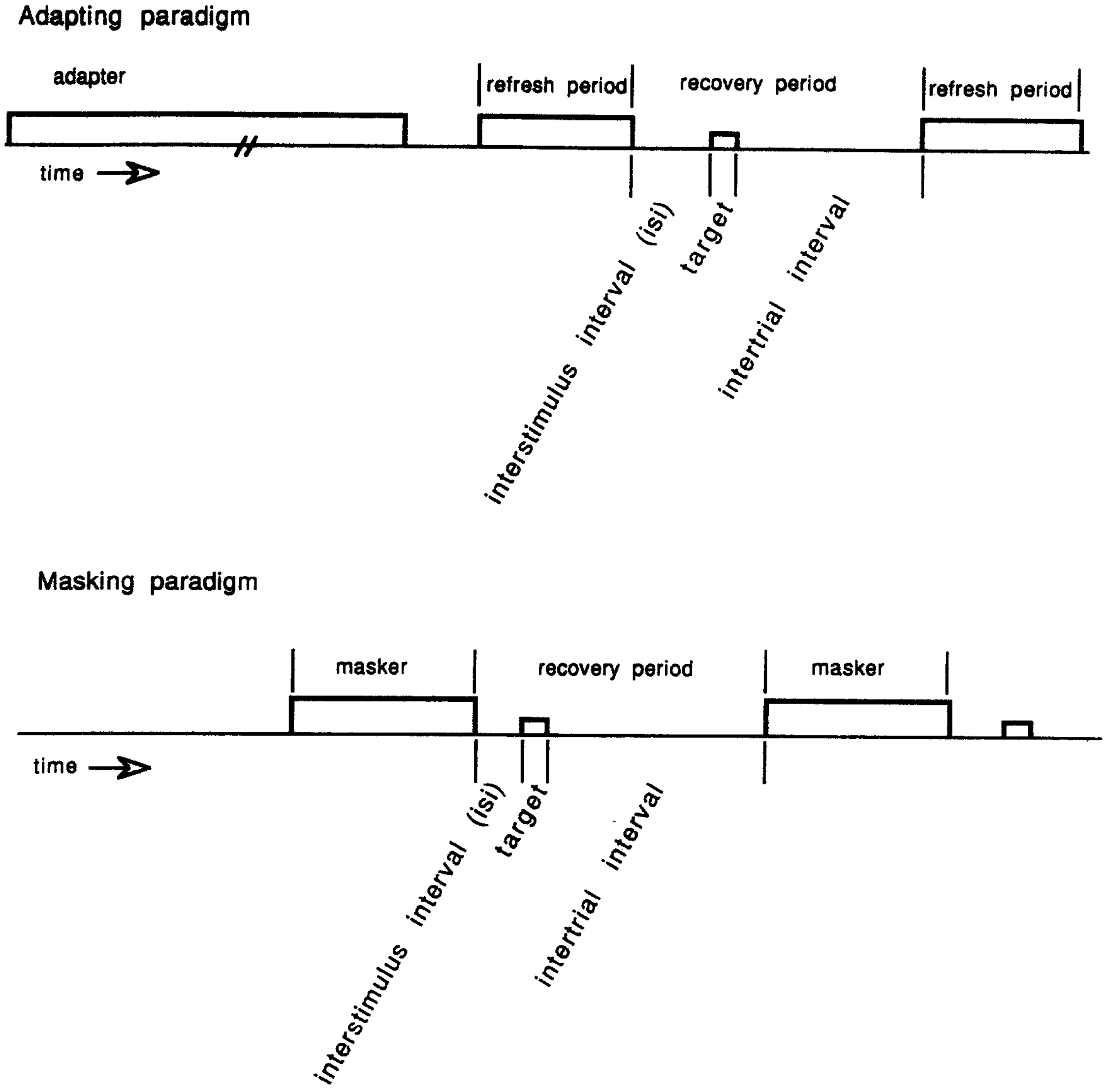

FIGURE 1. Timing diagram for the adapting and masking paradigms. The paradigms have the same basic structure except that, in the adapting paradigm, the adapter is presented once for a relatively long duration before the trials begin.

blocks of 10 trials. The observers and the target contrasts were different in the three conditions. The results are shown in Fig. 2.

Figure 2(a) shows the effect of a regime in which refresh duration was 3 sec and recovery time was 1.5 sec. The three functions correspond to three target contrasts. A downward trend is evident in all three functions, although it is not statistically significant. The result suggests that in this regime desensitization continues to increase over the trial sequence.

Figure 2(b) illustrates the effect of a regime in which refresh duration was 2 sec and recovery time was 2 sec.

TABLE 1. Experiment 1

	Condition			
Experimental variables	1a	1b	1c	1d
Mean luminance (cd/m^2)	28	28	19	22
Target contrast (dB re 1)	−26, −24, −22	−24, −20	−21	−22
Adapter spatial frequency (c/deg)	2	2	2	2
Adapter temporal frequency (Hz)	1	1	15	0
Adapter temporal phase at offset (deg)	180	180	0	0
Adapter contrast (dB re 1)	−2	−2	−2	−2
Adapter duration (min)	3	3	2	3
Refresh duration (msec)	3000	2000	2000	2000
Interstimulus interval (msec)	133	133	133	133
Intertrial interval (msec)	1333	1833	1833	1833
Recovery time (msec)	1500	2000	2000	2000
Number of measurements/data point	30	70	100	100

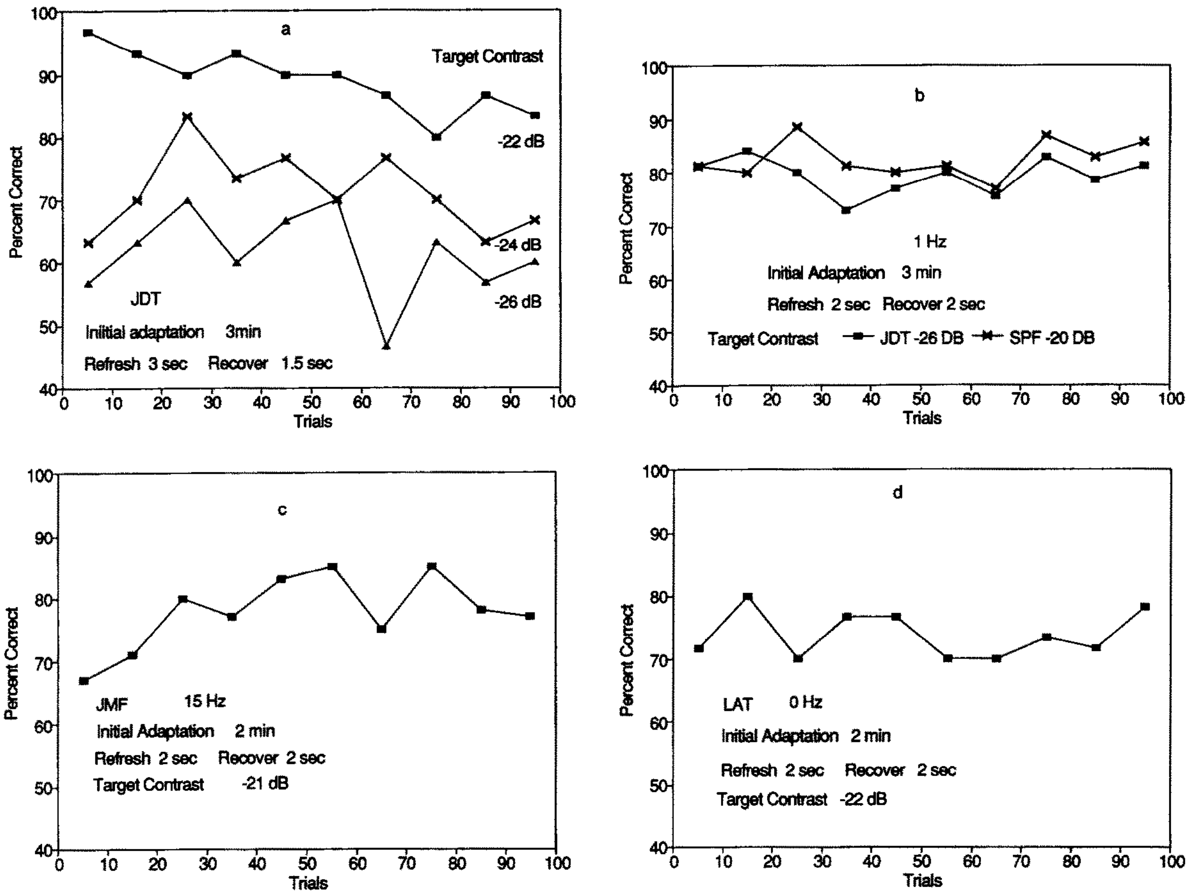

FIGURE 2. Experiment 1. Adapter contrast and target contrast held constant. Percent correct over blocks of 10 trials as a function of the mean trial number of the block. (a) Condition (a): 1 Hz adapter, refresh 3 sec and recover 1–5 sec, $n = 30$. (b) Condition (b): 1 Hz adapter, refresh 2 sec and recover 1–5 sec $n = 70$. (c) Condition (c): 15 Hz adapter, refresh 2 sec and recover 2 sec, $n = 100$. (d) Condition (d) 0 Hz adapter, refresh 2 sec and recover 2 sec, $n = 100$. The value of n is the number of trials on which each data point is based.

The two functions are for two observers. No trend is evident in performance indicating that this regime maintains a constant level of performance.

Figure 2(c) illustrates the effect of the same regime when the temporal frequency of the adapter was 15 Hz. There is a suggestion of an upward trend in the early trials, but it is not statistically significant by a χ^2 test (d.f. $= 9$, $P > 0.05$).

Figure 2(d) illustrates the effect of the same regime when the adapter was steady (0 Hz). Again no trend is evident. In all adapting conditions in Expts 2–8 we used a refresh duration of 2 sec and a recovery interval of 2 sec.

EXPERIMENT 2: EFFECT OF ADAPTER/MASKER DURATION ON TARGET CONTRAST THRESHOLD

This experiment examined the time–course of desensitization by varying the duration of the adapter/masker and measuring the target contrast threshold 50 msec after adapter offset. Two other features of the adapter/masker were varied: contrast (-2 and -14 dB re 1) and temporal waveform (0 and 15 Hz square-wave). Contrast is known to affect the magnitude of desensitization, but there is evidence that it does not affect the time–course of desensitization (Blakemore & Campbell, 1969, Fig. 3). This experiment will further test that finding. The temporal waveform variable reflects one of the main differences between the adapting and masking paradigms. In forward masking a rectangular waveform has usually been used, while pattern adaptation studies have employed time varying adapters. This experiment examines the effect of two temporal frequencies and a range of durations on the target contrast threshold after the offset of the adapter/masker.

Values of the experimental variables are given in Table 2. Both target center spatial frequency and masker spatial frequency were 2 c/deg. Mean luminance was 22 cd/m^2. There were two observers, both of whom had experience in pattern detection experiments. The design was as follows. For durations in the range of 16.67–2133 msec for the steady masker and 66.67–2133 msec for the 15 Hz masker (66.67 msec = 1 period at 15 Hz) a masking paradigm was used. An adapting paradigm was used for one duration, 2 min, with the adapter re-presented for 2 sec and a 2 sec recovery period on each trial. Three measurements were made in each condition.

The results for both observers are shown in Fig. 3. The data points at duration = 120,000 msec correspond to the adapting condition and those for the shorter durations, to the masking conditions. Target contrast

TABLE 2. Experiment 2

Experimental variables	
Mean luminance	22 cd/m^2
Adapter/masker spatial frequency	2 c/deg
Adapter/masker temporal frequency	0, 15 Hz
Adapter/masker temporal phase at offset	0 deg
Adapter/masker contrast	−14, −2 dB re 1
Adapter duration	2 min (2 sec refresh)
Masker duration	16.7 – 2133 msec
Interstimulus interval	50 msec
Measurements per condition	3

Theoretical analysis	JMF	KMF	Mean
Number of data points	23	19	21
Mean standard deviation (dB)	0.91	0.92	0.92
Mean standard error (dB)	0.53	0.53	0.53
Free parameters	4	4	4
Sum of square error (dB)	14.67	9.23	11.95
Mean square error (dB/data pt)	0.64	0.49	0.57
Parameter values			
s_{lt} (dB re 1)	31.50	28.83	30.17
s_{ll} (dB re 1)	35.86	31.88	33.87
v	0.45	0.47	0.46
d_a (msec)	16.62	10.82	13.72

threshold increases rapidly over the first 67 msec and then more slowly. Increasing the duration beyond 1 sec produces little further increase. Temporal frequency, 0 vs 15 Hz, has essentially no effect. Increasing the adapter/masker contrast by 12 dB increases the asymptotic threshold by about 6 dB. There is good agreement between the two observers. The results are consistent with the hypothesis that the time–course of desensitization is very short. They are also consistent with the hypothesis that differential local adaptation does not affect the target contrast threshold (Kelly & Burbeck, 1980). In this and all the succeeding figures the continuous lines correspond to a theory that will be described in the Discussion.

EXPERIMENT 3: EFFECT OF ISI ON TARGET CONTRAST THRESHOLD FOR THREE ADAPTER/MASKER DURATIONS

This experiment examined the time–course of recovery by varying the ISI. Adapter/masker contrast was −2 dB re 1. There were two masker durations, 200 and 2000 msec, and one adapter duration, 2 min. In the

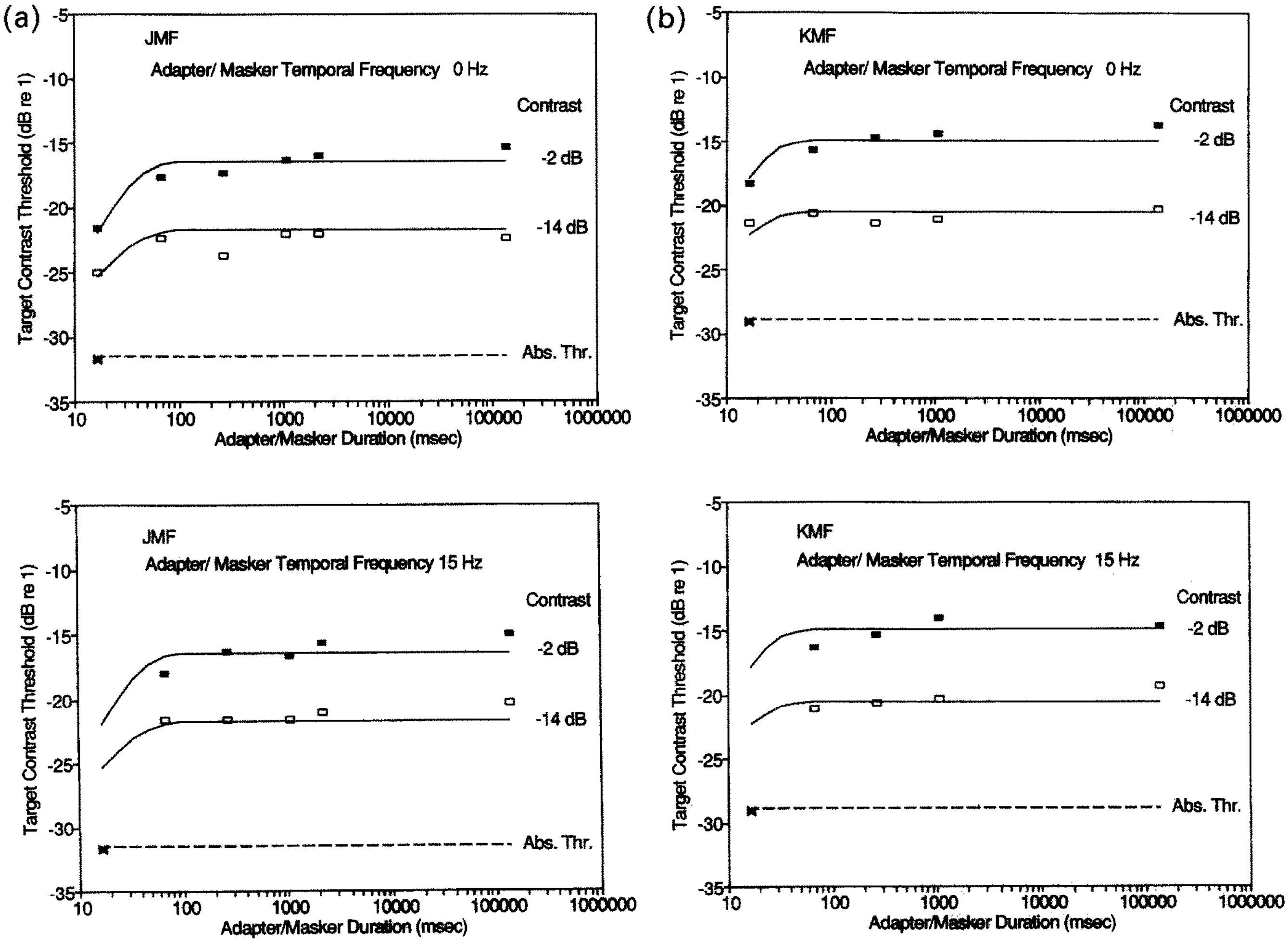

FIGURE 3. Experiment 2. Target contrast threshold in dB as a function of adapter/masker duration for two values of adapter/masker contrast. Continuous lines correspond to theoretical predictions. Dashed line corresponds to the predicted absolute threshold. The × symbol corresponds to the measured absolute threshold. Top, adapter/masker temporal frequency, 0 Hz; bottom, 15 Hz. (a) JMF, (b) KMF.

TABLE 3. Experiment 3

Experiment variables			
Mean luminance	22 cd/m^2		
Adapter/masker spatial frequency	2 c/deg		
Adapter/masker temporal frequency	15 Hz sq		
Adapter/masker temporal phase at offset	0 deg		
Adapter/masker contrast	−2 d B re 1		
Adapter duration	2 min (2 sec refresh)		
Masker duration	200, 2000 msec		
Interstimulus interval	0–2133 msec		
Measurements per condition	3		
Theoretical analysis	**JMF**	**KMF**	**Mean**
Number of data points	30	29	29.5
Mean standard deviation (dB)	0.47	0.94	0.71
Mean standard error (dB)	0.27	0.54	0.41
Free parameters	7	7	7
Sum of square error (dB)	30.78	26.71	28.75
Mean square error (dB/data pt)	1.03	0.92	0.98
Parameter values			
s_{lt} (dB re 1)	30.16	28.89	29.53
f_{lmin}	0.19	0.24	0.22
w	0.81	0.78	0.80
d_{r1} (msec)	76	98	87
d_{r2}, 200 msec (msec)	937	310	624
d_{r2}, 2 sec (sec)	25	2	13
d_{r2}, 2 min + 2 sec (sec)	25,900	2	12,951

adapting condition the full duration was presented only at the start of the QUEST sequence; the adapter was re-presented for 2 sec on each trial and the recovery duration was also 2 sec. Only one temporal waveform was used: a 15 Hz square-wave. Otherwise the stimuli were the same as in Expt 2. Values of the experimental variables are given in Table 3.

TABLE 4. Experiment 4

Experimental variables			
Mean luminance	19 cd/m^2		
Adapter/masker spatial frequency	2 c/deg		
Adapter/masker temporal frequency	0, 15 Hz sq		
Adapter/masker contrast	−2 dB re 1		
Masker duration	267 msec		
Interstimulus interval	0–1076 msec		
Measurements per condition	5		
Theoretical analysis	**LAT**	**JYS**	**Mean**
Number of data points	16	16	16
Mean standard deviation (dB)	1.35	1.00	1.18
Mean standard error (dB)	0.60	0.45	0.53
Free parameters	7	7	7
Sum of square error (dB)	9.97	2.32	6.15
Mean square error (dB/data pt)	0.62	0.15	0.39
Parameter values			
s_{lt} (dB re 1)	29.28	26.94	28.11
f_{lmin} (0 Hz)	0.127	0.147	0.137
(15 Hz, LAT; 7.5 Hz, JYS)	0.184	0.226	0.205
w	0.85	0.80	0.83
d_{r1} (0 Hz) (msec)	50	50	50
(15 Hz, LAT; 7.5 Hz, JYS)	82	58	70
d_{r2} (sec)	4011	462	2237

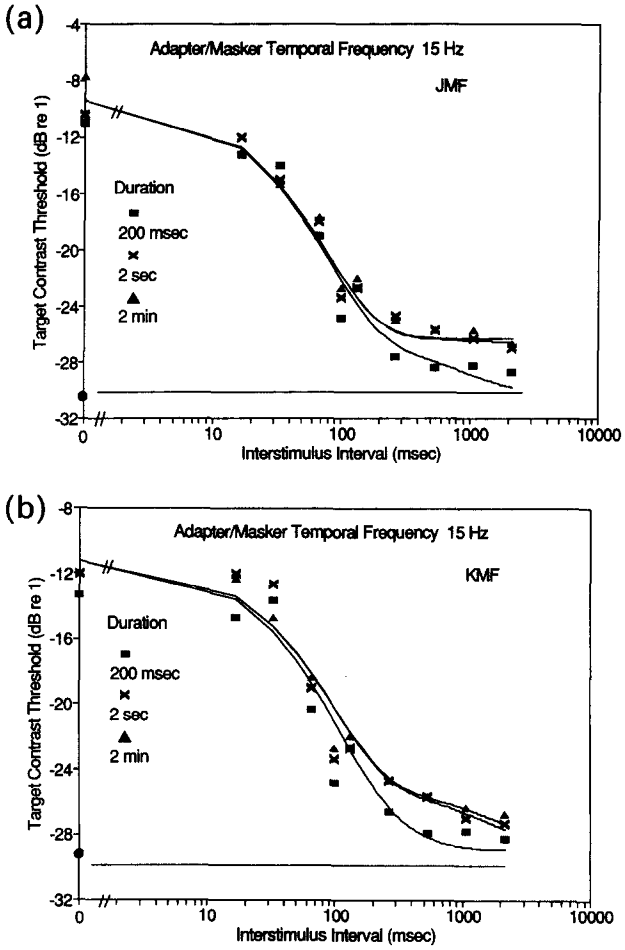

FIGURE 4. Experiment 3. Target contrast threshold in dB as, a function of ISI for three values of adapter/masker duration. Adapter/masker temporal frequency: 15 Hz. Continuous curves correspond to the best version of the theory. The solid circle corresponds to the measured absolute threshold. The horizontal line corresponds to the absolute threshold estimated from the theory. (a) JMF, (b) KMF.

The results for the two observers are shown in Fig. 4. Thresholds decrease rapidly for 100–200 msec and then more slowly. Target contrast thresholds are essentially the same for the three conditions for ISI = 0–33 msec. Two-way analyses of variance on this subset of the data done separately for each observer show no statistically significant effect of adapter/masker duration and no significant interaction between adapter/masker duration and ISI ($P > 0.05$). This result is consistent with Expt 2 in which, at an ISI of 50 msec, adapter/masker durations > 200 msec produced essentially the same thresholds. At long ISIs thresholds are higher for longer masker and adapter durations. This means that duration has an effect on the rate of recovery and does not have an effect on the maximum magnitude of desensitization. This is in agreement with what Georgeson and Georgeson (1987) had conjectured, but in disagreement with what many other researchers had concluded. There are two other remarkable aspects of these results. First, 1000 msec after the offset of a 200 msec masker, there is still about 2 dB threshold elevation. So for this short adapter duration, recovery time is more than 5 times longer than adapter duration. Second, after an ISI of 500 msec, a

2 min adapter produces a threshold elevation of only about 5 dB. This is less than has been found in other studies. This difference may be related to our use of a spatial forced-choice paradigm in which the targets were centered 0.8 deg from the fovea center. We do not yet know whether the difference is due to the paradigm, the eccentricity of the targets, both, or neither.

In addition to the detection responses, one of the observers, JMF, made judgments of whether the adapter appeared to be successive or simultaneous. There was very little variability in these judgments. When the adapter was 2 sec in duration or was refreshed for 2 sec on each trial, the stimuli were always judged to be successive, even when the ISI was 0. When adapter duration was 200 msec, the stimuli were judged to appear simultaneous for ISIs < 133 msec and successive for ISIs > 133 msec. At 133 msec both responses occurred with approximately equal frequency. This result implies that the percept evoked by the 200 msec masker persists for about 133 msec longer than the percept evoked by the 2000 msec masker, which has very little persistence. This result is consistent with results on the persistence of steady uniform lights (Breitmeyer, 1984). This differential persistence appears to have no effect on the thresholds in the two conditions, which are essentially the same at short ISIs.

EXPERIMENT 4: EFFECT OF ISI ON TARGET CONTRAST THRESHOLD FOR STEADY AND FLUCTUATING MASKERS

Like Expt 3 this experiment studied the time–course of recovery. Here a masking paradigm was used and masker duration was fixed at 267 msec. The masker was either steady (0 Hz) or modulated in counter-phase at 7.5 Hz (JYS) or 15 Hz (LAT). Masker contrast was −2 dB re 1. Target and masker spatial frequencies were both 2 c/deg. ISI varied from 0 to 1067 msec. The absolute threshold of the target was also measured. Values of the experimental variables are given in Table 4.

The results are shown in Fig. 5. For JYS the thresholds for the 0 Hz masker are higher than those for the 7.5 Hz masker, but the difference decreases with ISI. For LAT the threshold for the 0 Hz masker is initially higher than that for the 15 Hz masker, but as ISI increases it decreases faster at first and then more slowly.

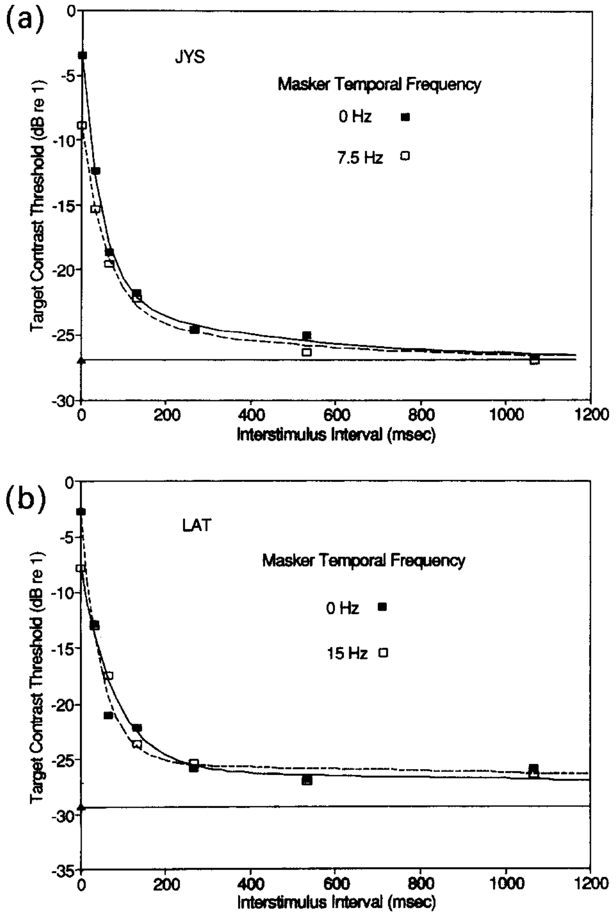

FIGURE 5. Experiment 4. Target contrast threshold in dB as a function of ISI for two values of masker temporal frequency. Continuous curves correspond to the best version of the theory. The triangle corresponds to the measured absolute threshold. The horizontal line corresponds to the absolute threshold estimated from the theory. (a) JYS, (b) LAT.

TABLE 5. Experiment 5

Experimental variables			
Mean luminance	27 cd/m^2		
Adapter/masker spatial frequency	2 c/deg		
Adapter temporal frequency	1 Hz sq		
Adapter temporal phase at offset	180 deg		
Adapter/masker contrast	−46 to −2 dB re 1		
Adapter duration	3 min (2 sec refresh)		
Masker duration	33.3 msec		
Interstimulus interval			
(adapting)	33, 133, 533 msec		
(masking)	33, 67, 133 msec		
Measurements per condition	2		
Theoretical analysis	**PCL**	**SSF**	**Mean**
Number of data points	78	78	78
Mean standard deviation (dB)	1.05	0.86	0.96
Mean standard error (dB)	0.74	0.61	0.68
Free parameters	11	11	11
Sum of square error (dB)	61.54	73.82	67.88
Mean square error (dB/data pt)	0.79	0.95	0.87
Parameter values			
s_{1t} (dB re 1)	31.11	22.89	27.00
s_{2t} (dB re 1)	28.18	18.76	23.47
s_{11} (adapting) (dB re 1)	31.39	28.56	29.98
s_{21} (masking) (dB re 1)	52.72	36.02	44.37
z*	0.27	0.12	0.20
u	0.8	1.94	1.37
d_a (msec)	36	0	18.00
w (adapting)	0.64	0.91	0.78
(masking)	1.00	1.00	1.00
d_{r1} (msec)	67	42	54.50
d_{r2} (sec)	1	7022	3512
q	3.71	1.31	2.51

*In this version of the theory it was assumed that $z = s_{21}/s_{11}$ was constant for adapting and masking. Thus z appears in the table instead of s_{21}. This assumption is equivalent to assuming that the ratio of adapting to masking sensitivity is constant.

The form of all the functions is very similar to that in Expt 3. What is remarkable about this result is that the effect of a large difference in temporal frequency is relatively small.

LAT made judgments of whether the stimuli appeared simultaneous or successive. For the steady masker, they were consistently reported to appear simultaneous for ISIs of 0–133 msec, uncertain at 267 msec, and successive for longer ISIs. For the fluctuating masker, they were consistently reported to appear simultaneous for ISIs of 0–67 msec, uncertain at 133 msec, and successive for longer ISIs. This suggests that the persistence of the steady masker was longer than the modulated one. Again thresholds do not seem to be closely related to this differential persistence.

EXPERIMENT 5: EFFECT OF ADAPTER/MASKER CONTRAST AND ISI ON TARGET CONTRAST THRESHOLD

Up to this point the experiments have employed one or two contrasts. The purpose of this experiment is to examine the function that relates target contrast threshold to adapter/masker contrast (TvC function). As noted in the Introduction, studies of adaptation have not given consistent results as to the form of this function. In forward masking Foley and Yang found functions that may be described as step-like or made up of two or three upward steps with flat segments in between, at least for some target-masker pairs. Three values of ISI were also employed in this study to determine the effect of ISI on the TvC function. Adapter/masker contrasts ranged from −46 to −2 dB in 4 dB steps. The three ISIs were different for adapting and masking since recovery time is greatly different in the two paradigms. For adapting they were 33, 133, and 533 msec; for masking they were 33, 67, and 133 msec. The adapting regime was 3 min of pretrial presentation of the adapter in counterphase square-wave modulation at 1 Hz and 2 sec refresh of the adapter on each trial followed by a 2 sec recovery period (ISI + target duration + intertrial duration). Maskers had a duration of 33 msec. Values of the experimental variables are given in Table 5.

The results for the two observers are shown in Fig. 6. The adapting results are shown in the upper panels and the masking results in the lower panels. The functions are essentially flat at the lower adapter/masker contrasts with the exception that facilitation is apparent after

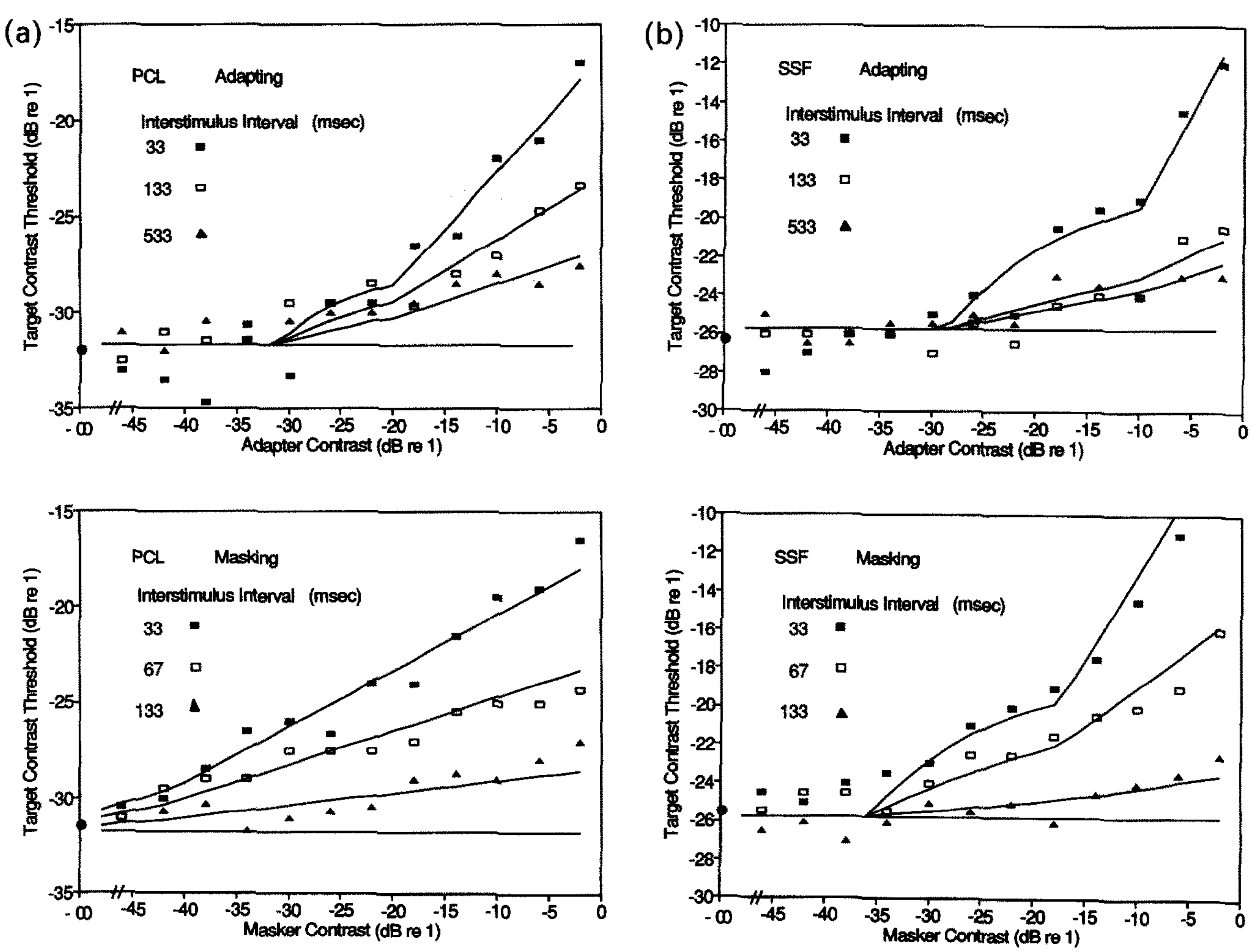

FIGURE 6. Experiment 5. Target contrast threshold in dB as a function of adapter or masker contrast for three values of ISI. Continuous curves correspond to the best version of the theory. The solid circle corresponds to the measured absolute threshold. Note that ISIs are different for adapting and masking. Top, adapting; bottom, masking. (a) PCL, (b) SSF.

adapting at the shortest ISI. The threshold begins to rise at lower contrasts for masking than for adapting. At the shortest ISI the threshold increase appears not to be linear, but to rise, level off, and then rise again. The step-like functions are not as evident here as they were in some of the conditions of the Foley and Yang (1991) study. This may be a consequence of the particular frequency used here or the fact that in the spatial forced-choice paradigm used here, the targets were imaged on different retinal areas. At longer ISIs the rise seems to be approximately linear. The effect of increasing ISI is to decrease the slope of the rising segments of the functions. In the case where the ISI is the same (33 msec), slopes are greater for adapting than for masking. However, threshold elevation begins at a lower contrast for masking so that at intermediate adapter/masker contrasts, the masker produces a greater threshold increase than the adapter. At the highest adapter/masker contrast the two effects are about equal. In Expt 7 it will be shown that a short masker sometimes produces a greater threshold elevation than a long adapter. These results show that the monotonic relation between duration and threshold elevation found in Expt 2 does not hold when the adapter is modulated at 1 Hz.

EXPERIMENT 6: EFFECT OF ADAPTER/MASKER SPATIAL FREQUENCY AND CONTRAST ON TARGET CONTRAST THRESHOLD AT ISI = 50 MSEC

One of the first facts discovered about pattern adaptation is that threshold elevation depends on the relation between the target frequency and the adapter frequency with the greatest elevation occurring when the frequencies are similar. The same is true of forward masking. In forward masking the relative effectiveness of the different maskers, however, depends on the masker contrast (Foley & Yang, 1991), a result was interpreted as indicating that different pattern vision mechanisms mediate target detection in different parts of the contrast range. This suggests that to describe adapting and masking, it is necessary to measure TvC functions for different target-masker pairs. TvC functions have not been studied much for adapting and there is disagreement about their form. The present study measures TvC functions for the same three frequency pairs in adapting and masking.

Mean luminance was 33 cd/m^2. The range of adapter/masker contrasts was −46 to −2 dB with 4 dB steps (−38 to −2 dB for LAT in the adapting paradigm). The initial adapter duration was 2 min during

TABLE 6. Experiment 6

Experimental variables						
Mean luminance	33 cd/m^2					
Adapter/masker spatial frequency						
(LAT)	0.71, 2, 5.66 c/deg					
(JMF)	0.83, 2, 4.76 c/deg					
Adapter temporal frequency	1 Hz sq					
Adapter temporal phase at offset	180 deg					
Adapter/masker contrast	−46 to −2 dB re 1					
Adapter duration	2 min (2 sec refresh)					
Masker duration	33.3 msec					
Interstimulus interval						
(adapting)	50 msec					
(masking)	50 msec					
Measurements per condition	2					
Theoretical analysis	JMF		LAT		Mean	
Number of data points	78		72		75	
Mean standard deviation (dB)	1.69		1.34		1.52	
Mean standard error (dB)	1.20		0.95		1.07	
Free parameters	18		16		17	
Sum of square error (dB)	36.48		60.48		48.48	
Mean square error (dB/data pt)	0.47		0.84		0.66	
Parameter values						
s_{1t} (dB re 1)	30.27		29.13		29.70	
s_{2t} (dB re 1)	26.35		25.82		26.09	
	Adapt	*Mask*	*Adapt*	*Mask*	*Adapt*	*Mask*
s_{11} (dB re 1)	28.96	32.88	27.63	42.46	28.30	37.67
s_{12} (dB re 1)	37.46	47.34	37.99	42.72	37.73	45.03
s_{13} (dB re 1)	34.53	27.71	20.08	21.26	27.31	24.49
s_{21} (dB re 1)	15.01	7.88	12.75	21.68	13.88	14.78
s_{22} (dB re 1)	20.88	19.60	20.48	35.68	20.68	27.64
s_{23} (dB re 1)	14.17	13.59	5.57		9.87	13.59
v	0.61		0.52		0.57	
d_a (msec)	25		47		36	
q	1.67	2.47	7.58	7.58	4.63	5.03

which the adapter was modulated in counterphase at 1 Hz; on each trial the adapter was re-presented for 2 sec and there were 2 sec of recovery (ISI + target duration + intertrial interval). ISI was 50 msec. The three adapter/masker frequencies were slightly different for the two observers. Values of the experimental variables are given in Table 6.

The results for the two observers are shown in Fig. 7. The adapting results are shown in the upper panels and the masking results in the lower panels. The functions appear to be less regular than in the other experiments, and as a consequence, it is more difficult to draw general conclusions about their form from these data. Many of the functions for both adapting and masking have rising segments that are clearly not a single straight line. As in Expt 5 the threshold begins to rise at lower contrasts for masking than for adapting, but the rising segments are steeper for adapting than for masking. When the adapter/masker frequency is different than the target frequency, the threshold increase is less. At high contrast the relative sensitivity to the three adapter/masker spatial frequencies changes. Figure 8 shows the masking and adapting sensitivities as a function of spatial frequency (SvF functions) derived from the data using the theory described in the Discussion. Although relative sensitivity to the adapter/masker frequencies has the same general form for adapting and masking and for the two observers, the actual functions differ quite a bit. JMF shows broader functions for adapting than for masking; LAT shows no low frequency falloff in one of the masking functions. In those cases where bandwidths can be measured, they are in the vicinity of 2 octaves at half maximum.

EXPERIMENT 7: COMPARISON OF ADAPTING AND MASKING WHEN ADAPTER ENDS IN-PHASE WITH TARGET

In Expts 5 and 6 a briefly pulsed masker was more effective in raising the target threshold than a much longer adapter except at the highest contrasts. At low contrasts only the masker raised thresholds. In these experiments the adapter was a 1 Hz square-wave which was 180 deg out of phase with the target during its last half cycle. Could the difference between adapting and masking in these experiments be a consequence of adapter spatial phase at offset? Jones and Tulunay-Keesey (1980) found that threshold elevations following adaptation were independent of the phase shift between the test and adapting gratings. Their ISI was 2 sec.

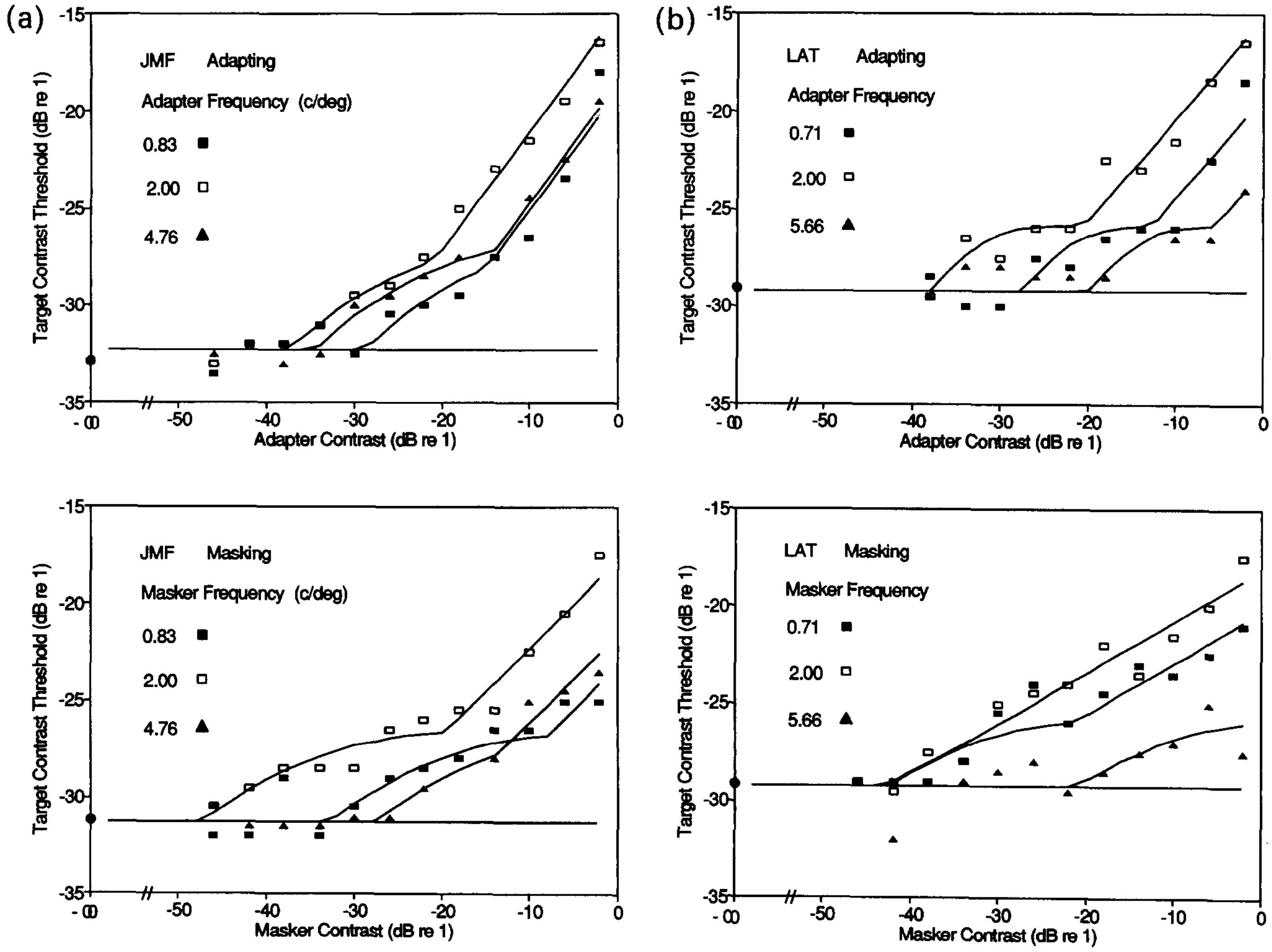

FIGURE 7. Experiment 6. Target contrast threshold in dB as a function of adapter or masker contrast for three values of adapter or masker frequency. Continuous curves correspond to the best version of the theory. The solid circle corresponds to the measured absolute threshold. Top, adapting; bottom, masking. (a) JMF, (b) LAT.

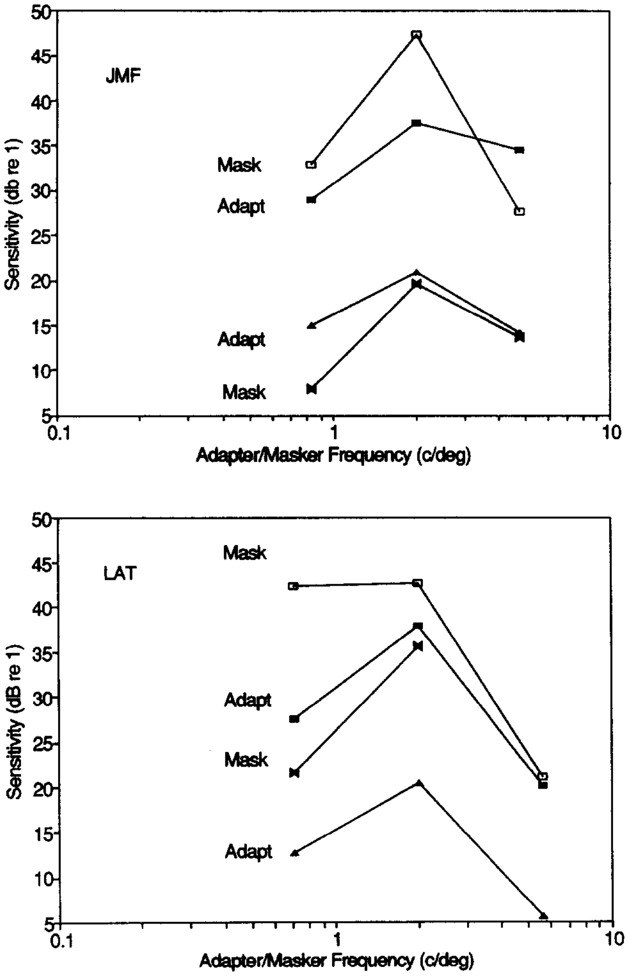

FIGURE 8. Experiment 6. Adapting and masking sensitivity estimated by the theory from the data of Expt 6. Two mechanisms are required for the best version of the theory for each data set. The most sensitive mechanism is more sensitive to masking than to adapting for both observers. Top, JMF; bottom, LAT.

Georgeson (1988) found that forward masking with short ISIs is phase dependent. In Expts 5 and 6 the ISIs were 33 and 50 msec, respectively, so the phase difference at adapter offset could be responsible for the difference between adapting and masking. Experiment 7 tested for this possibility. Experiment 7 was like Expt 6, except for these differences: the adapter ended in spatial phase with the target, the initial adapter duration was 30 sec, and only one adapter/masker spatial frequency was used. The experimental parameters are given in Table 7 and the results are shown in Fig. 9. As in the other experiments, the TvC functions for both masking and adapting are step-like and show transitions at approximately the same target contrasts. For JMF the adapting function is shifted to the right of the masking function by an approximately constant factor; for KMF the functions are more separated for adapter/masker contrasts in the middle of the range. In the functions for adapting, but not those for masking, there is a tendency for the threshold to decrease slightly after each increase. This suggests facilitation, which we have not previously seen at an ISI as long as 50 msec. Experiment 3 found no difference between adapting and masking when the adapter/masker contrast was high and the ISI was short. In Expt 7 a difference was found. This difference seems likely to be related to the difference in maskers; in Expt 2 it was a 200 msec, 15 Hz square-wave; in Expt 7 it was a 33 msec rectangular pulse. A supplementary experiment was done to examine the threshold vs duration (TvD) function for maskers of 1 Hz. At durations < 500 msec these are rectangular pulses in spatial phase with the target. The result was that in this condition the TvD function is non-monotonic, rising to a peak for durations < 1 sec and then decreasing about 3 dB at longer durations. For longer durations a 15 Hz adapter is more effective than a 1 Hz adapter when the target is a rectangular pulse.

In addition to the detection responses KMF reported the appearance of the target at threshold. The appearance varied somewhat from trial to trial, so the observer reported the dominant percept in each condition. In the forward masking condition, the masker percept persisted long enough for the target to appear superimposed on it. In the adapting condition, the adapter disappeared before the target appeared. In the forward masking condition KMF reported five percepts. As the masker contrast increased, the target percepts reported were: flicker with unidentifiable contrast polarity, dark vertical line or lines, dark blob, light blob, and light vertical line. In the adapting condition, only flicker, light blob, and light vertical line were reported. Flicker was reported only for no adapter and the lowest contrast adapter. A light blob was the predominant report over the next range of contrast until the target threshold began to rise. A light vertical line was reported over the rising segment of the function. If we make the assumption that each mechanism is associated with a single percept, five mechanisms are implicated here. However, there is not a very close association between the different reported percepts and the transitions inferred from the theoretical analysis.

EXPERIMENT 8: EFFECT OF ADAPTER FREQUENCY AND CONTRAST ON TARGET CONTRAST THRESHOLD AT AN ISI OF 100 MSEC

In Expt 6 we compared masking and adapting sensitivities at different adapter/masker frequencies with an ISI of 50 msec. The conclusion was that although masking sensitivity is higher, relative sensitivity to different spatial frequencies is similar. SvF functions were mostly bandpass with bandwidths at half maximum of about 2 octaves. In Expt 8 we reexamined the effect of spatial frequency for adapting only, with some modifications to improve the experiment. Here adapting frequency was 5 Hz, the adapter ended in phase with the target, pretrial adapting duration was 30 sec with a 2 sec refresh on each trial and the ISI was 100 msec. We went to the longer ISI to allow the neural response to the adapter to end or at least greatly diminish before the target was presented. The cost of this is a smaller effect. The parameters are given in Table 8 and the results are shown in Fig. 10. We also used more experienced observers and did more replications, three in each condition.

There is good agreement between the two observers and the measurements are less variable than in Expt 6. TvC functions are distinctively step-like for all three adapter frequencies. Four steps appear to be present in each data set. Figure 11 shows the adapting sensitivity functions derived from these data using the theory to be described below. The most sensitive mechanism is approximately low pass and the next most sensitive mechanism is bandpass with a bandwidth of about 2.5 octaves.

In this experiment we obtained phenomenological reports of the appearance of the target at threshold from both observers. JYS described most targets as a flicker of uncertain shape and contrast polarity or a light blob. The flicker percept predominated at low adapter contrasts and the blob percept at high contrasts. Some of the blobs had a roughly vertical orientation. For KMF the reports changed from flicker to light blob to light vertical line as contrast increased. KMF made some reports of dark blobs and dark lines at intermediate contrasts.

DISCUSSION

When the results of the present study are compared with those in the literature, it is seen that the present study gives different answers to two of the fundamental questions about pattern adaptation.

As to how long an exposure to the adapting stimulus is required to produce maximum desensitization, it is neither 1–2 min (Blakemore & Campbell, 1969) nor 30–60 min (Magnussen & Greenlee, 1985). It is < 100 msec. The reason that other studies did not find this is that they measured thresholds too long after the offset of the adapter. This weakness in experimental design did not allow their experiments to distinguish different levels of desensitization from different rates of recovery. Rapid desensitization means that pattern adaptation is like light adaptation in this respect. Most of the desensitization in light adaptation also takes place within the first 100 msec (Hood & Finkelstein, 1986).

As to the form of the TvC function for pattern adaptation, it depends on the spatial frequency of adapter and target, and it is often steplike. It is different from any of the several forms proposed in the literature and like the form found for forward masking by Foley and Yang (1991). The simplest form is a flat segment at low values of adapter contrast and a rising segment at higher adapter contrasts. This rising segment is approximately linear on log–log coordinates with a slope that decreases as ISI increases. For certain frequency pairs there are two or more flat segments interspersed with rising segments, so that the function has a scalloped appearance much like Stiles' threshold vs intensity functions for light increment thresholds (Stiles, 1978).

THEORY

Foley and Yang (1991) developed a theory of forward pattern masking to describe the form of TvC functions

TABLE 7. Experiment 7

Experimental variables						
Mean luminance			19 cd/m^2			
Adapter/masker spatial frequency			2 c/deg			
Adapter temporal frequency			1 Hz sq			
Adapter temporal phase at offset			0 deg			
Adapter/masker contrast			−46 to −2 dB re 1			
Adapter duration			30 sec (2 sec refresh)			
Masker duration			33.3 msec			
Interstimulus interval			50 msec			
Measurements per condition			3			
Theoretical analysis	JMF		KMF		Mean	
Number of data points	26		26		26	
Mean standard deviation (dB)	0.99		1.08		1.04	
Mean standard error (dB)	0.57		0.62		0.60	
Free parameters	11		8		9.50	
Sum of square error (dB)	3.66		6.06		4.86	
Mean square error (dB/data pt)	0.14		0.23		0.19	
Parameter values						
s_{1t} (dB re 1)	28.47		31.29		29.88	
s_{2t} (dB re 1)	28.41				28.41	
s_{3t} (dB re 1)	25.06		26.29		25.68	
s_{4t} (dB re 1)			23.20		23.20	
	Adapt	*Mask*	*Adapt*	*Mask*	*Adapt*	*Mask*
s_{11} (dB re 1)	45.98	61.74			45.98	61.74
s_{21} (dB re 1)	27.74	39.16	23.04	43.30	25.39	41.23
s_{31} (dB re 1)	10.78	18.97	10.14		10.46	18.97
y	0.57	0.37	1.65	0.28	1.11	0.33
q (fixed)	4.00	4.00	4.00	4.00	4.00	4.00

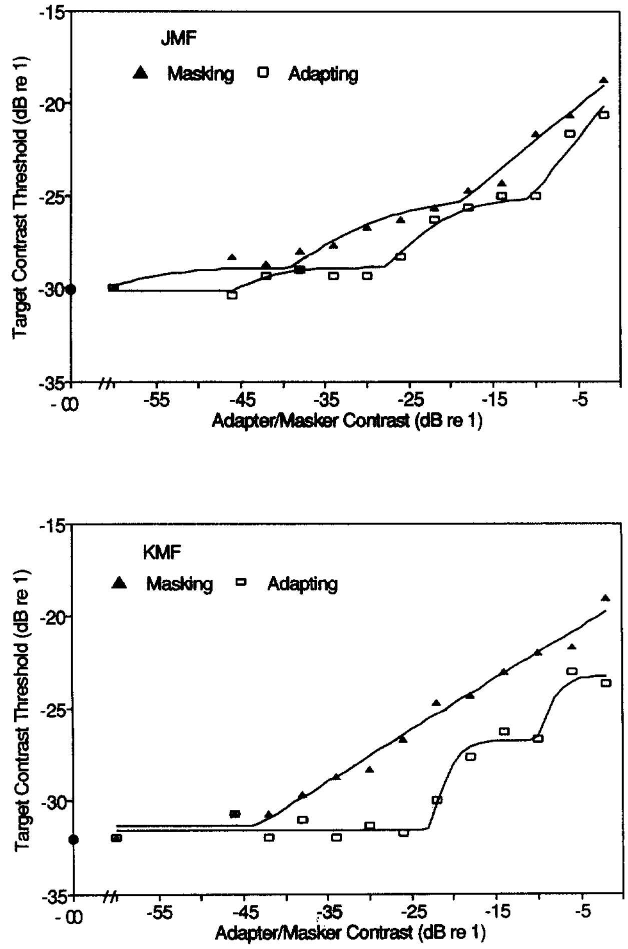

FIGURE 9. Experiment 7. Target contrast threshold in dB as a function of adapter or masker contrast for an adapter and masker of 2 c/deg. Adapter had a temporal frequency of 1 Hz, a duration of 30 sec with 2 sec refresh, and ended in-phase with the target. Continuous curves correspond to the best version of the theory. The solid circle corresponds to the measured absolute threshold. Masker was a 33 msec pulse, $n = 3$. Mean standard errors were: JMF, 0.57 dB; KMF, 0.62 dB. Top, JMF; bottom, KMF.

and their dependence on masker frequency. This theory is formally closely related to Stiles' theory of color mechanisms (Stiles, 1978; Graham, 1989). Here we further develop this theory to take account of adapter/masker duration and ISI. We then fit it to the data of the present study and estimate its parameters. This theory gives a good fit to both masking and adapting data with some systematic differences in parameter values.

The basic ideas of the theory are the following.

(1) Detection of our Gabor targets is mediated by a few mechanisms that are differentially sensitive to spatial patterns.

(2) Adapters and forward maskers have the effect of temporarily desensitizing those mechanisms that respond to them. Desensitization acts in a multiplicative manner on the spatial frequency sensitivity function of the mechanism.

(3) There is a mechanism response below which no desensitization occurs (mechanism desensitization threshold). When the mechanism response exceeds this threshold, the mechanism sensitivity is reduced by a multiplicative factor that is a negative power function of mechanism response. The power increases with adapter/masker duration and decreases with ISI (recovery time prior to target).

(4) Mechanism responses are combined non-linearly to yield a combined response. A constant level of this combined response corresponds to the performance threshold.

We normalize the theory by setting both the mechanism desensitization threshold and the combined response that corresponds to the detection threshold equal to 1.

Table 9 defines the symbols used in this section. The theory may be expressed mathematically as follows. When an adapter/masker, a, is presented, the response of any mechanism, i, is:

$$r_{ia} = C_a s_{ia}. \tag{1}$$

[There is much evidence that this function is quite non-linear, having an S-shaped form (Foley & Legge, 1981; Legge & Foley, 1980; Nachmias & Sansbury, 1974; Wilson, 1980). However, for the data of this study we have found that equation (1) is adequate to provide a good fit.]

Desensitization is described by f_i, the desensitization factor, which is related to the mechanism's response as

TABLE 8. Experiment 8

Experimental variables			
Mean luminance	19 cd/m^2		
Adapter spatial frequency	0.71, 2, 5.66 c/deg		
Adapter temporal frequency	5 Hz sq		
Adapter temporal phase at offset	0 deg		
Adapter contrast	−46 to −2 dB re 1		
Adapter duration	0.5 min (2 sec refresh)		
Interstimulus interval	100 msec		
Measurements per condition	3		
Theoretical analysis	**JYS**	**KMF**	**Mean**
Number of data points	39	39	39
Mean standard deviation	0.91	0.90	0.91
Mean standard error	0.53	0.52	0.52
Free parameters	14	14	14
Sum of square error (dB)	9.56	7.35	8.46
Mean square error (dB/data pt)	0.25	0.19	0.22
Parameter values			
s_{1t} (dB re 1)	28.49	30.59	29.54
s_{2t} (dB re 1)	25.76	28.08	26.92
s_{3t} (dB re 1)	23.37	26.89	25.23
s_{4t} (dB re 1)	22.76	24.50	23.63
s_{11} (dB re 1)	47.00	46.00	46.50
s_{12} (dB re 1)	47.59	51.82	49.71
s_{13} (dB re 1)	29.15	26.96	28.06
s_{21} (dB re 1)	26.87	26.37	26.62
s_{22} (dB re 1)	34.94	39.36	37.15
s_{23} (dB re 1)	9.99	6.74	8.37
s_{31} (dB re 1)	6.00	7.19	6.60
s_{32} (dB re 1)	23.11	25.26	24.19
s_{33} (dB re 1)			
s_{42} (dB re 1)	6.37	7.35	6.86
y	0.61	0.70	0.66
q (fixed)	4.00	4.00	4.00

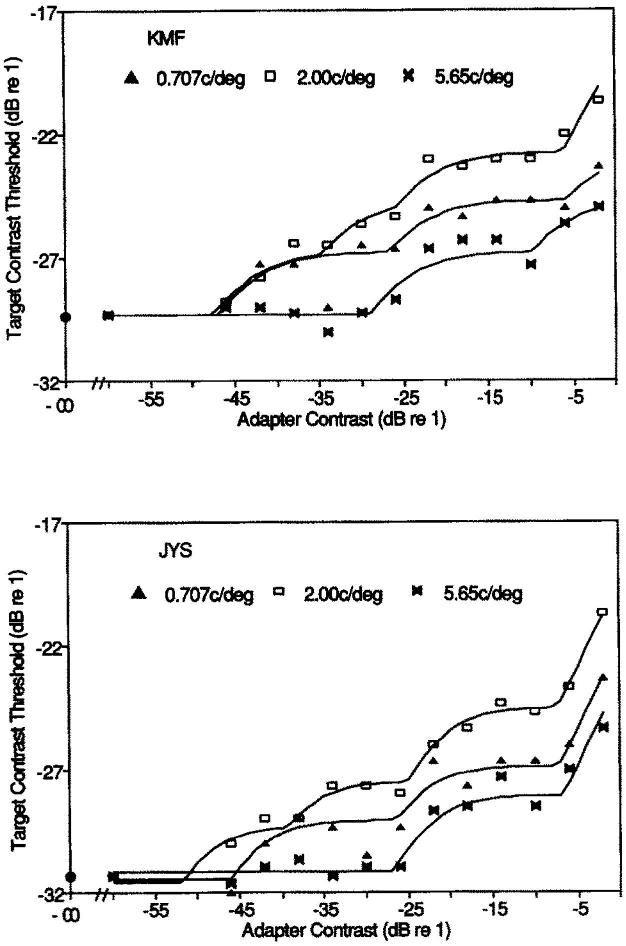

FIGURE 10. Experiment 8. Target contrast threshold in dB as a function of adapter contrast for three adapter spatial frequencies. Adapter had a temporal frequency of 5 Hz, a duration of 30 sec with a 2 sec refresh, and ended in-phase with the target. Continuous curves correspond to the best version of the theory. The solid circle corresponds to the measured absolute threshold, $n = 3$. Mean standard errors were: KMF, 0.52 dB; JYS, 0.53 dB;. Top, KMF; bottom, JYS.

follows:

$$f_i = r_{ia}^{-p}, \tag{2}$$

where:

$$p = \begin{cases} 0, \text{if } r_{ia} < 1 \\ u(1 - E_0)\,[wE_1 + (1 - w)E_2], \text{otherwise} \end{cases}$$

and

$$E_0 = e^{(-D_a/d_a)}$$

$$E_1 = e^{(-D_{\text{isi}}/d_{r1})}$$

$$E_2 = e^{(-D_{\text{isi}}/d_{r2})}.$$

The symbol d_a is the time constant of desensitization, d_{r1} and d_{r2} are the time constants of two recovery processes, and w is a weighting parameter ($0 \leqslant w \leqslant 1$). It is only in this equation that the theory differs from that in Foley and Yang (1991). This equation looks more complex than it is. It says that the desensitization factor, f_i, is inversely related to the response to the adapter raised to a power. This power increases as a function of adapter duration and decreases as a weighted sum of two exponential decay functions with different time constants. The parameter u determines the minimum value of f_i, which occurs when D_a is long and $D_{isi} = 0$.

When a target is presented the response of any mechanism i is given by:

$$r_{it} = C_t s_{it} f_i \tag{3}$$

and the combined response over all n mechanisms is:

$$\mathbf{r}_t = [\sum_{i=1}^{n} |r_{it}|^q]^{1/q}. \tag{4}$$

At the target contrast threshold,

$$\mathbf{r}_t = 1. \tag{5}$$

Equations (3), (4), and (5) are solved to yield the value of C_t at the performance threshold, C_{tt}:

$$C_{tt} = [\sum_{i=1}^{n} |s_{it} f_i|^q]^{-1/q}. \tag{6}$$

In Expts 2 and 6 there was only a single value of D_{isi}. As a consequence it was not possible to estimate the parameters u, w, d_{r1}, and d_{r2} independently. Instead we

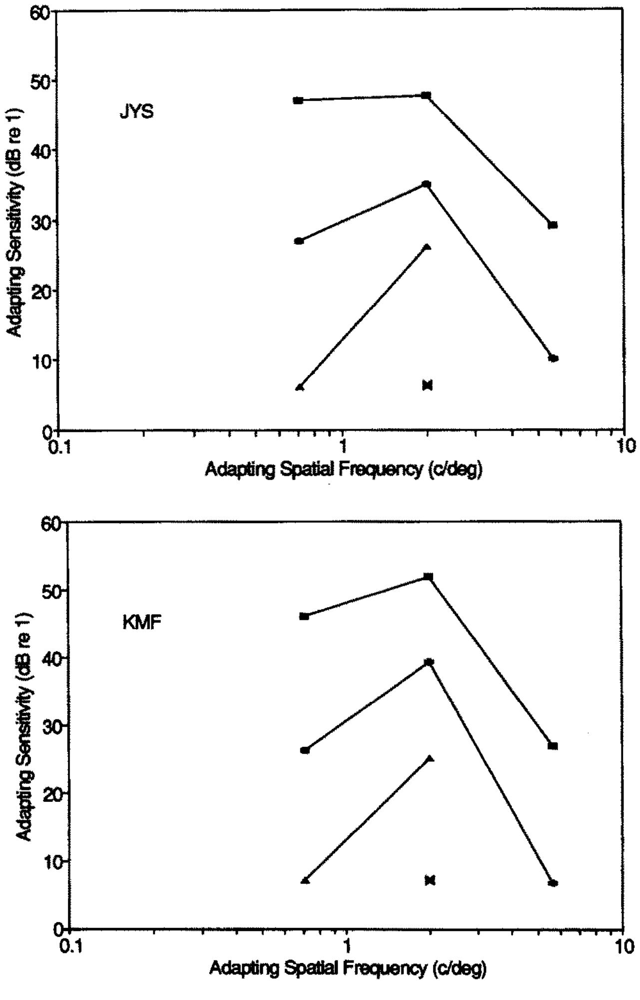

FIGURE 11. Experiment 8. Adapting sensitivity estimated by the theory from the data of Expt 8. Four mechanisms are required for the best version of the theory for each data set, although it is not possible to estimate the sensitivity of all mechanisms to all spatial frequencies. Top, JYS; bottom, KMF.

estimated the single parameter v, where:

$$p = \begin{cases} 0, \text{if } r_{ia} < 1 \\ v(1 - E_0), \text{otherwise.} \end{cases}$$

In Expts 7 and 8 it was not possible to estimate any of the three time constants. Instead, we estimated the single parameter y, where:

$$p = \begin{cases} 0, \text{if } r_{ia} < 1 \\ y, \text{otherwise.} \end{cases}$$

In Expts 3 and 4 there was only a single value of adapter/masker contrast. As a consequence it was impossible to get independent estimates of s_{ia} and u. Instead we estimated the parameter $f_{\text{imin}} = r_{ia}{}^{-p}$, where $p = u$. In Expt 5 all the variables that influence the desensitization function were varied and it was possible to estimate all the parameters of this function.

This theory was fitted to the data of Expts 2–8 and its parameters estimated. In fitting the data we used a numerical analysis routine that sought the parameter values that minimized the sum of the squared deviations between measured and predicted thresholds. The routine is described in Foley and Yang (1991).

We proceeded as follows in fitting the theory to the data. With each data set we started with a general version of the theory which had 2–4 mechanisms and allowed s_{ia}, u, w, d_a, d_{r1}, and d_{r2}, to vary with one of the experimental variables. Our general version for each data set was made general enough that it would fit the data well. We then fitted reduced versions of the theory, which eliminated one of the mechanisms and/or equated a parameter value across adapting and masking that had been independently determined in the general version. We used a test of change in goodness of fit (Khuri & Cornell, 1987, pp. 43–46) to determine if the reduced theory produced a significant worsening of fit. We took the version of the theory with the least parameters, which produced a fit not significantly worse ($P = 0.05$) than the general version of the theory, as the *best version* for each data set. The smooth curves in the figures correspond to these best versions of the theory with the parameters that produced the lowest sum of squared errors (SSE) for that version of the theory. Note that the theory yields values for all thresholds including the absolute threshold, which is shown as a horizontal line in the graphs. Tables 2–8 summarize the fit of this best version to each data set and give the estimated parameter values. Empty cells in the tables mean that the corresponding parameter was not used in the best version of the theory. This best version has a somewhat higher SSE than the general version of the theory. We characterize goodness of fit by giving the mean of the squared deviations (mean square error). It can be seen that the fits are generally good with the mean square error approximately equal to the variance of the mean measurement. This means that the theory accounts for essentially all of variability in the data except for random measurement variability. An exception to this is that the theory does not account for the facilitation effects that occur in a few conditions.

TABLE 9. Symbols used in the article

Experimental variables	
Adapter/masker	
F_a	Spatial frequency of adapter/masker
a	Adapter/masker index
W_a	Temporal frequency of adapter/masker
C_a	Contrast of adapter/masker
D_a	Duration of adapter/masker
Target	
F_t	Spatial frequency of target
W_t	Temporal frequency of target
C_t	Contrast of target
D_t	Duration of target
Temporal parameters	
D_{isi}	Duration of interstimulus interval
Theoretical variables	
n	Number of mechanisms
i	Mechanism number
s_{ia}	Sensitivity of mechanism i to adapter/masker a
r_{ia}	Response of mechanism i to adapter/masker a
s_{it}	Sensitivity of mechanism i to target
r_{it}	Response of mechanism i to target
f_i	Desensitization factor for mechanism i
p	Exponent of desensitization function
u	Parameter of desensitization function
w	Relative weighting of recovery processes
$f_{\text{imin}} = r_{ia}{}^{-u}$	Minimum value of desensitization factor
d_a	Time constant of desensitization
d_{r1}, d_{r2}	Time constants of recovery
$E_0 = e^{(-D_a/d_a)}$	Negative exponential of desensitization
$E_1 = e^{(-D_{\text{isi}}/d_{r1})}$	Negative exponential of recovery
$E_2 = e^{(-D_{\text{isi}}/d_{r2})}$	Negative exponential of recovery
$v = u[wE_1 + (1 - w)E_2]$	Parameter of simplified desensitization function
$y = u(1 - E_0)[wE_1 + (1 - w)E_2]$	Parameter of simplified desensitization function
$z = s_{21}/s_{11}$	Ratio of sensitivity of two mechanisms to the same frequency, but different durations
q	Exponent of nonlinear summation
$\mathbf{r}_t$	Nonlinear sum of mechanism responses

On the basis of our results and our theoretical analysis of them, we make the following statements about pattern adaptation and forward pattern masking.

(1) *In the adapt and refresh paradigm, a 2 sec refresh combined with a 2 sec recovery interval maintains constant performance in the three sets of conditions that we examined* [Fig. 2(b, c, d)]. These conditions include pretrial adapter durations of 2 and 3 min, adapter temporal frequencies of 0, 1, and 15 Hz, and adapters that terminate in or out of phase with the target. We do not claim that this regime always maintains constant performance.

(2) *Desensitization is very rapid.* Increasing adapter duration beyond 200 msec has little or no effect on the target contrast threshold in the first few msec after

adapter offset (Fig. 3). Our estimates of the time constant of desensitization are in the range of 10–50 msec. Thresholds may increase slowly over a long term, but our results show that for adapter durations between 200 msec and 2 min the increase is not more than 1 dB. This result is in disagreement with the literature, but we believe that the discrepancy can be explained by the fact that we measured thresholds very soon after adapter offset. Some of our results are not consistent with the threshold vs duration relation expressed in equation (2) That equation requires that the threshold increase monotonically with adapter/masker duration. Yet, in Expts 5, 6 and 7 (Figs 6, 7, and 9) a brief pulse raises the threshold more than a 1 Hz adapter presented for 30–120 sec and refreshed for 2 sec on each trial even when the adapter ends in phase with the target (Fig. 9). The difference is greatest at low contrasts. Thus there appear to be interactions between temporal frequency, duration, and contrast during the first second of desensitization.

(3) *Recovery is very rapid during the first 100–200 msec and then it becomes slow.* Adapter duration has very little effect during the initial stage of recovery. At longer ISIs recovery is slower for longer adapter durations (Fig. 4). The relation between target threshold in dB and ISI may be described by the weighted sum of two exponential decay functions. The shorter time constant is about 50–100 msec and may be independent of adapter duration (see Table 5, which describes an experiment in which a single value of d_{r1} was found to fit adapting and masking data). The longer time constant is much longer and increases with adapter duration. Our estimates range from 1 to 25,000 sec. These are very imprecise, because we did not measure thresholds at long ISIs; they should not be taken seriously. It is important to note that our fast process is very short, shorter than the ISIs used in most adaptation experiments, so it would not be expected to manifest itself in those experiments.

(4) *At an ISI of 1 sec, desensitization is 3–4 dB for an adapter of −2 dB re 1 presented for 2 min and refreshed for 2 sec during every 4 sec trial* (Fig. 4). For similar adapters at similar ISIs several studies in the literature have reported threshold elevations of 10–20 dB. A difference in method may explain this difference in results. More specifically, our use of a spatially limited target, counterphase modulation, spatial forced-choice with targets centered at ±0.8 deg above and below the fixation point, short duration targets, or some combination of these factors may explain the difference.

(5) *TvC functions for both adapting and masking are step-like in some conditions.* In other conditions the rising part of the function is a single line in log–log coordinates. The occurrence of step-like functions has already been shown for forward masking by Foley and Yang (1991) and in adapting by at least one of the observers of Greenlee *et al.* (1991). The form of the TvC function depends on the frequencies of the target and adapter/masker and on the ISI (Figs 6, 7, and 8). The theory attributes the steps in the function to the intrusion of spatial frequency mechanisms that are too insensitive to detect the target when adapter/masker contrast is low, but become effective when the initially most sensitive mechanism becomes desensitized. For example, in Fig. 7(a, bottom), a transition is inferred at a target contrast of about −26 dB. The mechanism that becomes the most sensitive at this point is much less sensitive than the first to maskers of 0.83 and 2 c/deg, but about equally sensitive to the first for a masker of 4.76 c/deg. One way to understand these transitions is the following: the form of the TvC function for an individual mechanism is constant. It consists of a horizontal segment at low contrasts and a linearly rising segment (on log–log coordinates) at higher contrasts. The vertical position of the horizontal segment corresponds to the threshold of the mechanism for the target. The horizontal position of the elbow corresponds to the adapter/masker contrast at which threshold elevation begins (the adapting or masking threshold). This depends on the adapter/masker frequency. For a specific target and adapter/masker each mechanism will have its TvC function in a specific position. If the TvC functions for different mechanisms cross, there will be a mechanism transition as adapter/masker contrast increases. The performance threshold at any contrast will generally correspond to the TvC function that is lowest at that contrast. However, when two mechanisms are close in threshold, both will contribute to detection, and the performance threshold will be lower than the threshold of either mechanism. It is this summation across mechanisms that causes the TvC function to curve near a mechanism transition.

(6) *Increasing ISI decreases the slope of the rising parts of TvC functions for both adapting and masking.* One consequence of this is that at relatively long ISIs the initially most sensitive mechanism remains the most sensitive throughout the contrast range and the TvC function has a single rising segment (Fig. 6). This means that, if threshold elevation is measured for different adapter/masker frequencies at the same adapter/masker contrast, the form of the threshold versus frequency (TvF) function will depend on ISI. Even if only a single mechanism is involved, the bandwidth of the TvF function will increase as ISI increases. This may explain some of the variation in bandwidth measurements in the literature.

(7) *Adapting and masking sensitivity vs spatial frequency functions are similar in form.* Figure 8 shows the values of these functions estimated from the theory for the data of Expt 6 and Fig. 11 shows them for Expt 8. For Expt 6 the best version of the theory was one in which the sensitivities were estimated independently for adapting and masking. For JMF the adapting sensitivity function is broader than the masking sensitivity function for both mechanisms; for LAT the relation is opposite for one mechanism and cannot be determined for the other. More research will be required to determine the relative bandwidths. Note that the sensitivity functions for the same mechanism are displaced vertically; three of the four mechanisms are more sensitive to masking than to adapting. The most sensitive mechanism has a peak sensitivity around 2 c/deg and is more

sensitive to masking than to adapting for both observers. In three of four cases the less sensitive mechanism also has peak sensitivity around 2 c/deg. In the fourth case (LAT masking) the sensitivity at 4.76 c/deg is too high to measure and suggests a mechanism with peak sensitivity above 2 c/deg. It is this fourth pattern that Foley and Yang (1991) found in every case in their study of forward masking. The difference in results may be due to the fact that in the present study the targets are centered at ±0.8 deg eccentricity and a different second mechanism may mediate performance. For JMF the second mechanism is more sensitive to adapting than to masking. For LAT it is more sensitive to masking than to adapting. Figure 11 shows the sensitivities inferred from Expt 8. Here four mechanisms were required for the best fit. The most sensitive is almost lowpass and the next is bandpass with a peak about 2 c/deg. For the least sensitive mechanism only 1 or 2 points on the SvF function could be estimated. The sensitive lowpass mechanism may have been hidden by facilitation in Expt 6 where the ISI was shorter. It is interesting that in Expt 8 the TvC functions do not cross and as a consequence the inferred TvC functions do not cross. Clearly there is more research to be done before a definitive statement about the spatial frequency sensitivity of these mechanisms can be made.

(8) *Temporal frequency of the adapter/masker has a relatively small effect over the range of 0–15 Hz.* In Expt 2 (Fig. 3) there is very little difference between adapter/maskers of 0 and 15 Hz. In Expt 4 on forward masking (Fig. 5) threshold vs ISI functions are very similar for temporal frequencies of 0, 7.5 and 15 Hz. The greatest effect is found at ISI = 0, where the threshold after a 0 Hz stimulus is highest. For ISI > 150 msec the difference decreases to < 1 dB. Our theoretical analysis (Table 4) suggests temporal frequency may affect the shorter recovery time constant, but not the longer one, just the opposite of the duration effect. The relative lack of temporal tuning found here is consistent with the existence of a mechanism with a low pass temporal sensitivity function. Evidence for such a mechanism has been found by Kulikowski and Tolhurst (1973) and others using a pattern detection task, by Pelli (1981) using temporal noise masking and by Mandler and Makous (1984) using temporal frequency discrimination. However, sensitivity functions found in these studies decrease substantially over the range of 0–15 Hz. Furthermore, a comparison across experiments suggests that adapters of 1 Hz (Expts 5, 6, and 7) may raise thresholds <0, 5 or 15 Hz (Expts 3 and 8). A more thorough examination of the effect of adapter/masker temporal frequency seems warranted.

Our theory requires four mechanisms to account for the data of Expts 7 and 8, two mechanisms to account for the data of Expts 5 and 6, and only one to account for the data of Expts 2–4. Since the threshold changes cover approximately the same range in all these experiments, there is a question of why all mechanisms do not manifest themselves in all experiments. In Expts 2–4 all the threshold vs duration functions are relatively steep. Transitions among functions with similar first derivatives are very difficult to detect. In Expts 5 and 6 some of the mechanisms may be desensitized by the 1 Hz adapter/masker at low contrasts, so that they are never sufficiently sensitive to detect the target. Alternatively, the data may not be sufficiently precise to reveal all the mechanisms.

Our theoretical analysis shows that the recovery function can be described as a weighted sum of two decay functions, one fast and one slow. The fast one depends on adapter/masker temporal frequency, but not on duration; the slow one depends on adapter/masker duration, but not on temporal frequency (at least over our range of 0–15 Hz). These findings suggest that at least two distinct processes underlie adapting and masking. What are these two processes? The fast recovering process seems likely to be the same process that produces simultaneous masking. It is not yet completely clear what this process is. Legge and Foley (1980) proposed a theory in which a nonlinear excitation–response function in the detecting mechanism produces both masking and facilitation. Ross and Speed (1991) have presented evidence which they interpret as showing that the excitation–response function varies with both the frequency and the contrast of the stimuli. In the context of cortical cell electrophysiology, Heeger (1991) has proposed that the compressive part of the nonlinearity is due to divisive inhibition from other cortical cells. It appears that both excitation and inhibition produced by the adapter/masker contribute to the fast recovering process. These contribute to threshold elevation in adapting and forward masking because they persist briefly after stimulus offset. The slow recovering process, which may last many minutes, is even less well understood. It has often been attributed to fatigue, which in this context seems to mean simply a loss in sensitivity to excitation. Barlow and Földiák's (1989) idea is that adaptation corresponds to a temporary increase in the sensitivity of inhibitory synapses among mechanisms that are stimulated together. In this view, a target threshold is higher after adaptation because the mechanisms that respond to it inhibit one another more than they did before adaptation. This is consistent with our finding that we get less long-term threshold elevation with our small targets than other researchers have with larger targets.

Another view, which can be formulated in a way that is equivalent to the fatigue hypothesis, is that adaptation corresponds to a decrease in contrast gain. This hypothesis predicts that adaptation will reduce the contrast discrimination threshold at high contrast. Greenlee and Heitger (1988) found this effect, but Määttänen and Koenderink (1991) did not find it. There is evidence from single-unit recording for a gain change in cortical cells of both cat (Ohzawa, Sclar & Freeman, 1985) and monkey (Sclar, Lennie & DePriest, 1989).

Our theory of adapting and forward masking is an extension of the theory of forward masking proposed by Foley and Yang (1991). It shares several assumptions in common with the theory of pattern adaptation proposed by Georgeson and Harris (1984), although its predictions, particularly the form of the TvC functions, are quite different. Breitmeyer hypothesized that forward masking is mediated by two processes: (1) integration of target and masker activity and (2) inhibition of channels activated by the target by channels activated by the masker. Both of these may contribute to the fast recovering process, but it is unlikely that they persist long enough to account for the entire duration of forward masking, which may be a second or more. Ross and Speed (1991) proposed a theory of adaptation and masking that employs an S-shaped response function, all three parameters of which change with adaptation. They suggest that this complexity is necessary to account for certain interactions between adaptation and simultaneous masking. This may be correct. Although our results for both adapting and forward masking are well accounted for by the theory presented here, we think that modifications will be necessary to account for a wider range of adapting and masking phenomena.

CONCLUSION

We have described the effects of five variables on the target contrast threshold in masking and adapting paradigms. Our results show that the desensitization, recovery, and TvC functions have forms that are different than those reported in the literature. These differences may be due to differences in method including differences in the values and ranges of our experimental variables. We have shown that a relatively simple theory gives a good description of our data from both adapting and forward masking. The differences between adapting and masking are reflected in differences in some of the theoretical parameter values. This suggests that adapting and forward masking are mediated by the same processes. Persisting responses to the adapter/masker (excitatory and inhibitory) and a longer lasting change in the sensitivity of synapses may be these processes.

REFERENCES

Barlow, H. B. (1990). A theory about the functional role and synaptic mechanism of visual aftereffects. In Blakemore, C. (Ed.), *Vision: Coding and efficiency* (pp. 363–375). Cambridge: Cambridge University Press.

Barlow, H. B. & Földiák, P. (1989). Adaptation and decorrelation in the cortex. In Durbin, R., Miall, C. & Mitchison, G. M. (Eds), *The computing neuron* (pp. 54–72). New York: Addison-Wesley.

Blakemore, C. & Campbell, F. W. (1969). On the existence of neurons in the human visual system selectively sensitive to orientation and size of retinal images. *Journal of Physiology, 203,* 237–260.

Blakemore, C. & Nachmias, J. (1971). The orientation specificity of two visual aftereffects. *Journal of Physiology, 213,* 157–174.

Blakemore, C., Muncey, J. P. J. & Ridley, R. M. (1973). Stimulus specificity in the human visual system. *Vision Research, 13,* 1915–1931.

Bodinger, D. M. (1978). The decay of grating adaptation. *Vision Research, 18,* 89–91.

Braddick, O. J., Campbell, F. W. & Atkinson, J. (1978). Channels in vision: Basic aspects. In Held, R., Leibowitz, H. & Teuber, H. L. (Eds), *Handbook of sensory physiology* (Vol. 8). Heidelberg: Springer.

Breitmeyer, B. G. (1984). *Visual masking: An integrative approach.* New York: Oxford University Press.

DeValois, K. K. (1977). Spatial frequency adaptation can enhance contrast sensitivity. *Vision Research, 17,* 1057–1065.

Foley, J. M. & Legge, G. M. (1981). Contrast detection and near-threshold discrimination in human vision. *Vision Research, 21,* 1041–1053.

Foley, J. M. & Yang, Y. (1991). Forward pattern masking: Effects of spatial frequency and contrast. *Journal of the Optical Society of America A, 8,* 2026–2037.

Georgeson, M. A. (1988). Spatial phase dependence and the role of motion detection in monocular and dichoptic forward masking. *Vision Research, 28,* 1193–1205.

Georgeson, M. A. & Georgeson, J. M. (1987). Facilitation and masking of briefly presented gratings: Time course and contrast dependence. *Vision Research, 27,* 369–379.

Georgeson, M. A. & Harris, M. G. (1984). Spatial selectivity of contrast adaptation: Models and data. *Vision Research, 24,* 729–741.

Gorea, A. (1987). Masking efficiency as a function of stimulus onset asynchrony for spatial frequency detection and identification. *Spatial Vision, 2,* 51–60.

Graham, N. (1972). Spatial frequency channels in the human visual system: Effects of luminance and pattern drift rate. *Vision Research, 12,* 53–68.

Graham, N. (1989). *Visual pattern analyzers.* New York: Oxford University Press.

Greenlee, M. W. & Heitger, F. (1988). The functional role of contrast adaptation. *Vision Research, 28,* 791–797.

Greenlee, M. W., Georgeson, M. A., Magnussen, S. & Harris, J. P. (1991). The time course of adaptation to spatial contrast. *Vision Research, 31,* 223–236.

Heeger, D. J. (1991). Nonlinear model of neural responses in cat visual cortex. In Landy, M. S. & Movshon, J. A. (Eds), *Computational models of visual processing.* Cambridge, Mass.: MIT Press.

Heggelund, P. & Hohmann, A. (1976). Long-term retention of the "Gilinsky-Effect". *Vision Research, 16,* 1015–1017.

Hood, D. C. & Finkelstein, M. A. (1986). Sensitivity to light. In Boff, K., Kaufman, L. & Thomas, J. P. (Eds) *Handbook of perception and human performance (Vol. 1).* New York: Wiley.

Jones, R. M. & Tulunay-Keesey, U. (1980). Phase selectivity of spatial frequency channels. *Journal of the Optical Society of America, 70,* 66–70.

Kelly, D. H. & Burbeck, C. A (1980). Motion and vision. III. Stabilized pattern adaptation. *Journal of the Optical Society of America, 70,* 1283–1289.

Khuri, A. I. & Cornell, J. A. (1987). *Response surfaces: Designs and analysis.* New York: Dekker.

Kulikowski, J. J. & Tolhurst, D. J. (1973). Psychophysical evidence for sustained and transient mechanisms in human vision. *Journal of Physiology, 232,* 149–163.

Legge, G. E. & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America, 70,* 1458–1471.

Määttänen, L. M. & Koenderink, J. J. (1991). Contrast adaptation and contrast gain control. *Experimental Brain Research, 87,* 205–212.

Magnussen, S. & Greenlee, M. W. (1985). Marathon adaptation to spatial contrast: Saturation in sight. *Vision Research, 25,* 1409–1411.

Mandler, M. B. & Makous, W. (1984). A three channel model of temporal frequency perception. *Vision Research, 24,* 1881–1887.

Nachmias, J. & Sansbury, R. V. (1974). Grating contrast: Discrimination may be better than detection. *Vision Research, 14,* 1039–1042.

Ohzawa, I., Sclar, G. & Freeman, R. D. (1985). Contrast gain control in the cat's visual system. *Journal of Neurophysiology, 54,* 651–667.

Pantle, A. & Sekuler, R. (1968). Size detecting mechanisms in human vision. *Science, 162,* 1146–1148.

Pelli, D. G. (1981). Effects of visual noise. Ph.D. thesis, Cambridge University, England.

Rose, D. & Evans, R. (1983). Evidence against saturation of contrast adaptation in the human visual system. *Perception and Psychophysics, 34,* 158–160.

Rose, D. & Lowe, I. (1982). Dynamics of adaptation to contrast. *Perception, 11,* 505–528.

Ross, J. & Speed, H. D. (1991). Contrast adaptation and contrast masking in human vision. *Proceedings of the Royal Society of London B*, *246*, 61–70.

Sclar, G., Lennie, P. & DePriest, D. D. (1989). Contrast adaptation in striate cortex of macaque. *Vision Research*, *29*, 747–755.

Stecher, S., Sigel, C. & Lange, R. V. (1973). Spatial frequency channels in human vision and the threshold for adaptation. *Vision Research*, *13*, 1691–1700.

Stiles, W. S. (1978). *Mechanisms of colour vision*. London: Academic Press.

Swift, D. J. & Smith, R. A. (1982). An action spectrum for spatial frequency adaptation. *Vision Research*, *22*, 235–246.

Tolhurst, D. J. (1972). Adaptation to square-wave gratings: Inhibition between spatial frequency channels in the human visual system. *Journal of Physiology*, *236*, 231–248.

Tolhurst, D. J. & Barfield, L. P. (1978). Interactions between spatial frequency channels. *Vision Research*, *18*, 951–958.

Watson, A. B. & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception and Psychophysics*, *33*, 113–120.

Watson, A. B., Nielson, K. R. K., Poirson, A., Fitzhugh, A., Bilson, A., Nguyen, K. & Ahumada, A. J. Jr (1986). Use of a raster framebuffer in vision research. *Behavior Research Methods and Instrumentation Computers*, *18*, 587–594.

Wilson, H. R. (1980). A transducer function for threshold and supra-threshold human vision. *Biological Cybernetics*, *38*, 171–178.

Wilson, H. R., McFarlane, D. K. & Phillips, G. C. (1983). Spatial frequency tuning of orientation sensitive units estimated by oblique masking. *Vision Research*, *23*, 872–882.

Acknowledgements—We thank Jerome Tietz for creating the stimulus generation and experimental control programs and Kathleen Foley, Sergio Fukusima, Paul Lebby, Julie Shieh, and Linda Tripp for serving as observers. This research was supported by U.S. Public Health Services Grant EY 07201 from the National Eye Institute.