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Analysis of the Effect of Pattern Adaptation on Pattern Pedestal Effects: A Two-process Model

JOHN M. FOLEY,*† CHIEN-CHUNG CHEN*

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Pattern contrast thresholds for vertical Gabor patterns were measured on pattern pedestals that were vertical or horizontal. Contrast of the pedestal was varied to measure the function relating target contrast threshold to pedestal contrast (TvC function). TvC functions were measured without an adaptor and after adaptation to vertical, horizontal and plaid patterns. For a pedestal with the same orientation as the target, the vertical and plaid adapters increased thresholds at low pedestal contrasts, but not high. For the pedestal orthogonal to the target, the same two adaptors increased thresholds over the whole range of pedestal contrasts. These asymmetric effects are described by a model of adaptation and masking derived from a model of masking (Foley, 1994a) by allowing two parameters to vary with the adapt state; one of them is an additive parameter in the denominator of the response function, which can be interpreted as adaptor-produced divisive inhibition that persists after adaptor offset; the other is the sensitivity to pedestal-produced divisive inhibition, which is changed by adaptation for the pedestal orthogonal to the target. Other models do not account for both effects. © 1997 Elsevier Science Ltd

Spatial Pattern Detection Adaptation Masking Model

INTRODUCTION

After a pattern has been presented, several aftereffects occur. One of them is a loss of sensitivity to similar patterns that has been shown to be distinct from light adaptation (Kelly & Burbeck, 1980). This sensitivity loss has been attributed to a process called pattern adaptation and has been studied extensively since it was first reported by Gilinsky (1968), Pantle and Sekuler (1968) and Blakemore and Campbell (1969). Most studies of pattern adaptation have measured the elevation of the absolute threshold after the offset of the adaptor. Although the threshold elevation effect is robust and its magnitude is often more than a factor of two, studies have given inconsistent results concerning some basic properties of the effect, such as the form of the function relating threshold elevation to adaptor contrast (TvC$_a$ function). Graham (1989) and Foley and Boynton (1993) reviewed this literature.

Although measurement of the elevation of the absolute threshold after adaptor offset has been the principal paradigm in the study of pattern adaptation, several other paradigms have been used. One of these, the measurement of contrast discrimination after adaptation, seems particularly promising because it has the potential to show how the response functions of the detecting mechanisms are affected by pattern adaptation. Early studies showed little or no effect of pattern adaptation on contrast discrimination (Barlow *et al.*, 1976; Legge, 1981). However, using a high adaptor contrast (0.8) and a wide range of base contrasts, Greenlee and Heitger (1988) found that the effect of pattern adaptation was to increase contrast discrimination thresholds at low base contrasts and decrease them at high base contrasts. Later studies have generally found increased contrast discrimination thresholds at low base contrasts and essentially no effect at high base contrasts (Määttänen & Koenderink, 1991; Ross & Speed, 1991; Ross *et al.*, 1993). Wilson and Humanski (1993) found that adaptation produces a threshold increase at all but the highest base contrasts. Contrast discrimination is a special case of the detection of a pattern that is superimposed on another pattern (a pedestal or masker). The experiments to be reported here describe the effect of adaptation in the more general case.

The threshold elevation effect has been often attributed to "fatigue" in the detecting pattern mechanisms produced by the mechanism response to the adaptor. To be made testable, "response-produced fatigue" must be given a specific interpretation within the context of a model. In practice, fatigue has often been assumed to correspond to a multiplicative decrease in the excitatory sensitivity of the detecting mechanism so that a higher contrast stimulus is needed to produce any specific

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*Department of Psychology, University of California, Santa Barbara, CA 93106-9660, U.S.A.

†To whom all correspondence should be addressed [*Fax* +1-805-893-4303; *Email* foley@psych.ucsb.edu].

response (Graham, 1989). In some models, but not all, this is equivalent to a reduction in the effective contrast of the stimulus patterns (reduction in contrast gain) prior to a nonlinear transform. Another interpretation of fatigue, which is also consistent with the common language meaning, is a multiplicative decrease in the response of the mechanism. In mechanisms that have a maximum response, this kind of fatigue will reduce the maximum and not simply require a higher contrast to produce it. The first class of fatigue models in which adaptation is interpreted as decreased sensitivity to excitation is the most highly developed (Graham, 1989). Models based on this idea have been shown to account for widely different sets of threshold vs adaptor contrast functions by assuming different numbers and types of mechanisms (Swift & Smith, 1982; Georgeson & Harris, 1984; Foley & Boynton, 1993). However, other results including threshold increases produced by adapting patterns thought not to excite the target mechanism (Dealy & Tolhurst, 1974), threshold decreases for some patterns that are different from the adapting pattern (DeValois, 1977) and decreases in threshold elevation that occur when specific second components are added to an adaptor (Tolhurst, 1972; Nachmias *et al.*, 1973) are not accounted for by fatigue models. Here again there has been inconsistency in the results and some failed attempts to produce these effects. Hypotheses based on inhibition among mechanisms or inhibition plus fatigue have been proposed to account for these effects. These models have not been as fully developed and tested as the desensitization models.

The effect of pattern adaptation on contrast discrimination together with other developments have led to new models of pattern adaptation. Until quite recently models of pattern vision generally, including models of pattern adaptation, have been built on a model of pattern mechanisms that consists of a linear receptive field followed by a fixed function that transforms the net excitation summed over the receptive field to the mechanism response. This function is sometimes linear, but more often it is S-shaped (Legge & Foley, 1980). Results of pattern masking studies (Ross & Speed, 1991; Ross *et al.*, 1993; Foley, 1994a) are inconsistent with this model, as are results from single unit recording in animals (Albrecht & Hamilton, 1982; DeValois & Tootell, 1983; Bonds, 1989, 1991).

The nature of the failures of static nonlinear models led to new models of cortical cells (Albrecht & Geisler, 1991; Heeger, 1991) and new models of psychophysical mechanisms (Ross & Speed, 1991; Wilson & Humanski, 1993; Foley, 1994a). Although these models are similar, they differ in important respects and they describe different phenomena. Albrecht and Geisler's model and Heeger's model are models of cat cortical cells. Heeger's model is the basis of a psychophysical model (Teo & Heeger, 1994). Wilson and Humanski's model is a model of human pattern vision that accounts for their results on contrast discrimination after adaptation. Foley's model is a model of human pattern vision that accounts for a wide range of masking phenomena. Ross and Speed's model attempts to account for both adaptation and masking effects. The principal difference between these models and the older models is that in these models each mechanism receives a broadly tuned divisive inhibitory input, in addition to an input from a linear receptive field.

As general models of pattern vision become more complex, it is necessary to reformulate hypotheses about the processes that underlie pattern adaptation in the context of these more general models. The number of possible processes that might underlie pattern adaptation has increased with the complexity of the models. A fundamental question about a pattern vision model is whether it can describe detection performance in the presence of pedestals while under different states of adaptation. If it can, then explanations of adaptation may be expressed in terms of changes in model parameters with adaptation. Here, we report experiments which show that pattern adaptation affects performance in a detection-on-pedestal task and these effects depend on both the pedestal and the adaptor. We show that Foley's (1994) model 3 fits the results of all conditions with only two parameters that vary with the adapt state. The two model parameters that vary with the adapt state are parameters of the pattern vision mechanisms. All the other parameters remain the same across the adapt states. Thus, we are able to derive an adaptation/masking model from a masking model by allowing two parameters to change with the adapt state. When the system is adapted to a homogeneous field, the predictions of the adapting/masking model are the same as those of the original masking model.

MODEL

Our model of adaptation/masking in the detection-on-pedestal task is a minor modification of a masking model proposed by Foley (1994a, model 3). It is illustrated in Fig. 1. Each mechanism receives two types of inputs. The first shown coming in from the bottom is an input produced by the excitation of a linear receptive field. The second shown coming in from the left is called a divisive inhibitory input, since it has an approximately divisive effect on the response. Masking experiments have shown that sensitivity to divisive inhibition is much more broadly tuned along the various pattern dimensions than is sensitivity to excitation.

The mechanism response is computed as shown in Fig. 1. The stimulus is expressed as the sum of component patterns, such as a target and a pedestal, each of which has a contrast. A pattern mechanism has an excitatory sensitivity to each component, and the excitation produced by a component in the mechanism is the product of component contrast times mechanism excitatory sensitivity to that component. Net excitation is the sum of component excitations. Net excitation is half-wave rectified and then raised to a power p, which is generally greater than 2. The excitatory term is divided by a sum of inhibitory terms, one for each component of the stimulus, plus Z. Each inhibitory term is the product

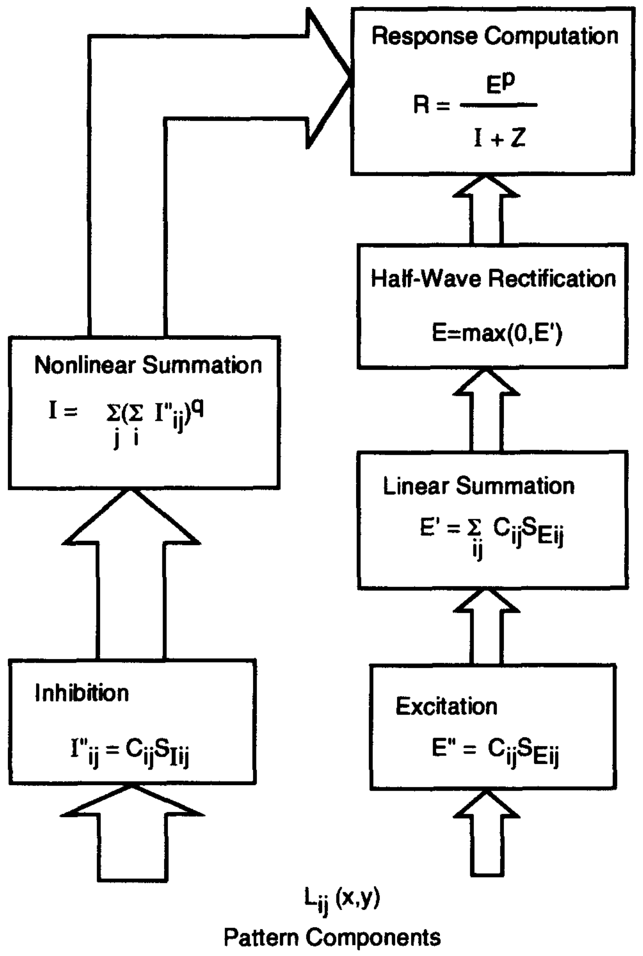

FIGURE 1. Model of human pattern vision mechanisms. This model is referred to as model 3 in (Foley, 1994a). This model provided the best fit, of the three models considered, to the pedestal detection results in that study. Inhibitory terms corresponding to the same orientation, *j*, are summed prior to being raised to the power *q*; inhibitory terms corresponding to different orientations are raised to the power *q* before summing.

of a pattern component contrast and a divisive inhibitory sensitivity, S_{Iij}. Inhibitory terms corresponding to the same orientation, *j*, are summed prior to being raised to the power *q*; inhibitory terms corresponding to different orientations are raised to the power *q* before summing. In this study there are two types of pattern components, pedestals (*p*) and targets (*t*), and we use the symbols S_{Et}, S_{Ep}, S_{It}, and S_{Ip} to represent their excitatory and inhibitory sensitivities. Inhibitory terms corresponding to different orientations are raised to the power *q* before summing. *Z* is independent of the current stimulus, but may depend on the state of adaptation. Each inhibitory term is raised to a power, *q*, after first combining terms that correspond to components of the same spatial frequency and orientation. The exponent *q* has been found to be less than *p*. Two stimuli are discriminated when the mechanism responses that they produce differ by a constant. This model has been shown to account for masking of patterns that vary in orientation (Foley, 1994a), spatial phase and SOA (Foley, 1994b), temporal frequency (Boynton & Foley, 1994), and color direction (Chen *et al.*, 1996).

Here we are concerned with the effect of pattern adaptation on detection-on-pedestals. Since pattern adaptation changes performance in this task and the original model makes no reference to adaptation, it is clear that the model has to be modified in some way to account for this change. The simplest possible modification to this model is to allow one or more of its parameters to change with the adapt state. This is the model of adaptation/masking that we test here.

Our test consists of two experiments on the effect of adaptation on detection in the presence of a pattern pedestal. In both of them the target was a vertical Gabor pattern. In one the pedestal was a vertical Gabor pattern which was identical to the target except for contrast (contrast discrimination). In the other the pedestal was a horizontal Gabor pattern. We varied the contrast of the pedestal and measured the target contrast threshold as a function of pedestal contrast (TvC function). TvC functions for both pedestals were measured before and after adaptation to three patterns. The three adaptor patterns were a vertical Gabor pattern of the same form as the target, a horizontal Gabor, and the sum of these two patterns (plaid Gabor).

The rationale for selecting these conditions is as follows: all past research on the effect of adaptation on detection-on-pedestals has used a target and a pedestal that are the same in orientation and spatial frequency. We know that pedestal TvC functions vary greatly with the relative orientations of target and pedestal (Foley, 1994a). It seemed possible that adaptation will act differently on functions for different relative orientations. We chose the most extreme relative orientations, parallel and orthogonal to the target. Likewise, it seemed likely that the orientation of the adaptor relative to both the target and the pedestal would be an important variable. Again we chose the two extreme cases, parallel and orthogonal. The plaid adaptor was used to determine whether adaptor components interact in their effect on detection-on-pedestal performance. More specifically, this condition tests Barlow and Földiák's (1989) hypothesis that when two mechanisms are activated by an adaptor, the mutually inhibitory links between them are strengthened. This hypothesis, when combined with our model, implies that the plaid adaptor will increase masking by an orthogonal pedestal more than an adaptor containing either pedestal alone.

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 MB video memory, a contrast mixer and attenuator circuit, and two video monitors (Sony, model CPD-1304). Truevision Stage graphics software was used for image generation and control. The pedestal was generated on one monitor and the target on the other, and they were combined by a beam splitter. Images of the fixation field, the pedestal 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 *et al.* (1986) were adapted to our system and to the detection-on-pedestal-after-adapting paradigm. Target and pedestal waveforms were stored in separate segments of graphics memory. Their contrasts were controlled independently by look-up tables and could be further attenuated by an analog circuit to produce low contrasts without loss of waveform definition. The look-up tables had the dual role of controlling contrast and correcting for the nonlinear relation between voltage and screen intensity.

Stimuli

The fixation field was uniform except for a small dark fixation point at the center. A two-alternative spatial forced choice paradigm was used. The stimuli appeared above and below the fixation point. All stimulus components were gaussian windowed sinewave gratings (Gabor patterns) in cosine phase with the fixation point. The center spatial frequency was 2 c/deg and the 1/e half-width (space constant) was 0.5 deg. The stimuli used in the experiment were a single vertical Gabor target pattern, two pedestals (horizontal and vertical), which were simultaneous with the target, and three adaptors (horizontal, vertical and plaid) which came and went off prior to the pedestal and target. The pedestals were a vertical Gabor pattern of the same form as the target (vertical pedestal) and the same pattern rotated 90 deg (horizontal pedestal). Two of the adaptors had the same form as the two pedestals and the third was the sum of the first two (plaid adaptor). Thus, all pattern components were circular patches of sinewave grating which faded in both vertical and horizontal directions. The patterns were kept relatively small so that they would stimulate a region of the retina that is relatively homogeneous with respect to spatial properties. Both target and pedestal had rectangular temporal waveforms and durations of 300 msec. Their onsets and offsets were simultaneous. Contrast for all patterns was defined as (peak luminance−background luminance)/background luminance. This is equivalent to the Michelson contrast of the underlying cosinewave. Adaptor contrast was 0.5 for the horizontal and vertical adaptors and 1.0 for the plaid adaptor. The adaptor was modulated in counterphase at 1 Hz with a square-wave temporal waveform. The background luminance and the space-average luminance of the patterns was 26 cd/m^2. Viewing distance was 162 cm and the visual angle subtended by the stimulus field was 7 deg horizontal by 5 deg vertical.

Procedure

The observer fixated on the fixation point during the adaptor presentation (if any) and throughout each trial sequence. A two-alternative spatial forced-choice method was used to determine target contrast thresholds. On each trial the target was presented centered either 0.8 deg above or 0.8 deg below the fixation point. The position was determined randomly with the probability of each position being 0.5. The time interval during which the target was on was indicated 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 (Watson & Pelli, 1983) was used to adjust the contrast so as to seek the contrast corresponding to a probability correct of 0.90. This procedure provides an estimate of this contrast which we will refer to 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. An outlier test was performed (Rousseeuw, 1991) and measurements that exceeded the outlier criterion were excluded from analysis. Three of the 704 measurements were excluded, less than 0.5%.

In the adapting conditions, the adaptor was presented for 1.5 min prior to the start of the trial sequence. The adaptor was reversed in phase by 180 deg (counterphase flicker) with a squarewave temporal waveform with a frequency of 1 Hz. The adaptor was always offset at the end of an out-of-phase half-cycle. The trials began immediately after the offset of the adaptor. Each trial consisted of a 2 sec re-presentation of the adaptor (refresh), followed by an interstimulus interval of 133 msec, a target/pedestal presentation interval of 300 msec and an intertrial interval of 1566 msec. This temporal regime has been previously shown to maintain constant performance over a long trial sequence (Foley & Boynton, 1993).

There were two observers. One was one of the authors and the other was naïve with respect to the purpose of the experiment. Both were young adults with visual acuity of 20/20, with correction for CCC, and no visual problems. Four measurements were made of the threshold in each condition.

RESULTS

The results are shown in Figs. 2 and 3. Each graph shows the mean target contrast threshold as a function of the pedestal contrast. Contrast is specified in decibels re 1, where # dB re $1 = 20 \log C$, where C is contrast. Different symbols are used for the four adaptation conditions. The upper panels show TvC functions for the vertical pedestal and the lower panels, for the horizontal pedestal. Mean standard errors in dB were: vertical pedestal, CCC, 0.95, AHS, 0.89; horizontal pedestal, CCC, 0.98, AHS, 0.75. There was no trend in standard error with pedestal contrast.

When the pedestal is in the same (vertical) orientation as the target (upper panels) and there is no adaptor, the TvC function decreases and then increases as pedestal contrast increases. This "dipper shaped" form was first reported by Nachmias and Sansbury (1974) and has been replicated many times since. The decrease in threshold is called "facilitation" and the increase is called "masking".

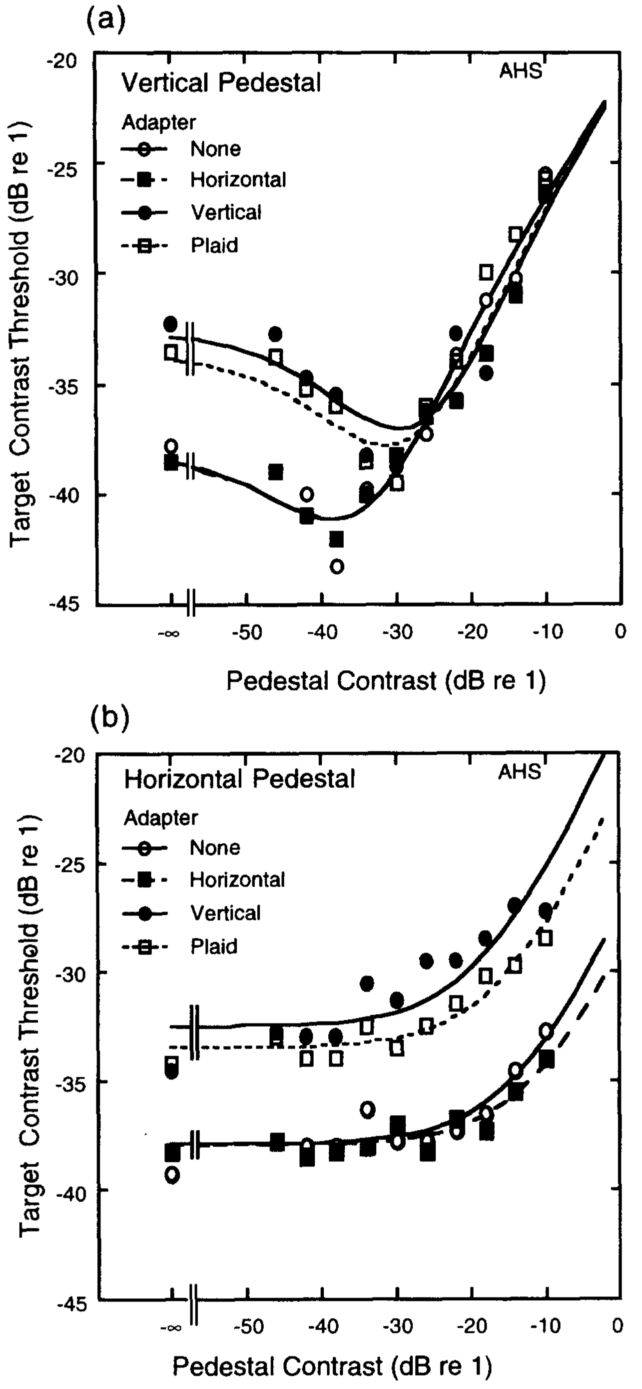

FIGURE 2. TvC functions for observer AHS for the four adaptation conditions. (a) Same orientation pedestal; (b) orthogonal orientation pedestal, $n = 4$. Mean standard error in dB = 0.82. Curves correspond to the best fit of the model described in the text.

The threshold increase is approximately 1 dB for every 2 dB increase in pedestal contrast. The horizontal adaptor has essentially no effect in this condition. Both the vertical and the plaid adaptors increase both the absolute threshold and the discrimination thresholds at low pedestal contrasts, and they produce essentially no effect at high pedestal contrast. There is essentially no difference between the effects of the vertical and the plaid adaptors in this condition. There is an indication that the TvC functions for these adaptors cross-over those for the other conditions before merging with them. Ross and Speed (1991) and Ross *et al.* (1993) have reported similar results for the case in which adaptor and pedestal have the same orientation.

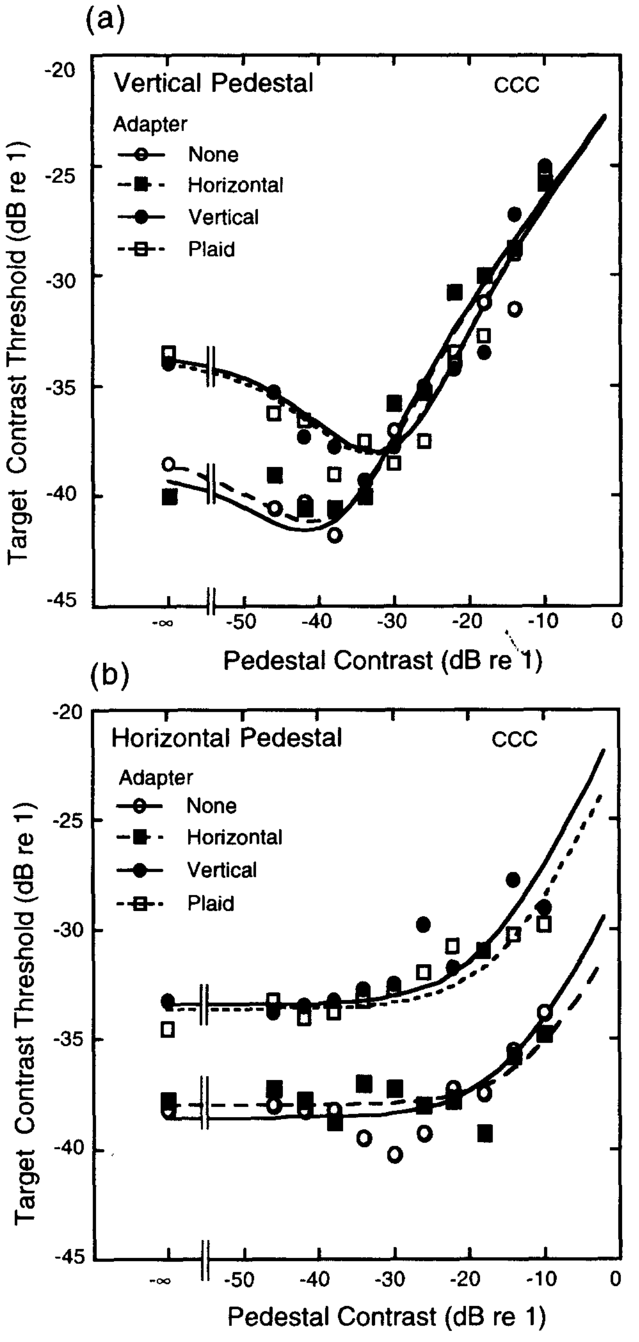

FIGURE 3. TvC functions for observer CCC. Mean standard error in dB = 0.97. Otherwise same as Fig. 2.

The results for the case where the pedestal is horizontal (orthogonal to the target) are shown in the lower panels. Here there is no facilitation. CCC shows a small decrease in threshold, but a t-test showed that the lowest threshold is not significantly lower than the absolute threshold ($t_6 = 1.94$, $P = 0.19 > 0.05$). The target contrast threshold increases with pedestal contrast. The TvC function for the horizontal adaptor is slightly lower than that for no adaptor at high pedestal contrasts. Both the vertical and

TABLE 1. Model analysis

Variable	AHS	CCC
Number of data points	88	88
Mean standard deviation (dB)	1.93	1.64
Mean standard error (dB)	0.97	0.82
Model fit		
Number of free parameters	11	11
Sum of squared errors (dB^2)	92.97	95.03
Mean error (dB/data point)	1.06	1.08
Parameter values		
p	1.90	2.16
q	1.43	1.63
Sensitivities to target and vertical pedestal		
S_{Et} and S_{Ep}	40.00	40.00 (fixed)
S_{It} and S_{Ip}	33.70	36.09
Z		
no adaptor	1.09	0.80
horizontal	1.08	0.95
plaid	3.15	3.32
vertical	3.97	3.49
S_{Ip} (horizontal pedestal)		
no adaptor	15.26	14.06
horizontal	12.65	11.03
plaid	23.30	22.29
vertical	27.36	24.77

the plaid adaptors increase the absolute threshold and the discrimination thresholds at all pedestal contrasts. Unlike the vertical pedestal condition, the effect of the adaptor is approximately constant at all pedestal contrasts; the functions do not converge at high pedestal contrasts. This asymmetry in the effect of adaptation on masking by patterns of the same and orthogonal orientations relative to the target is clearly shown by both observers. Three-way mixed-model ANOVAs in which the observer is treated as a random variable were done separately for the two pedestals. They showed that for the vertical pedestal there was a significant interaction between pedestal contrast and adaptor type ($F(30,265) = 4.77$, $P = 0.0001$), but for the horizontal pedestal this interaction was not significant ($F(30,264) = 1.50$, $P > 0.05$). This suggests that different processes underlie the adaptation effect in the two cases.

Comparison with model

The smooth curves in Figs. 2 and 3 correspond to the best fit of a version of the model (Fig. 1) in which two parameters vary with adaptation: Z and S_{Ip} for the horizontal pedestal (orthogonal to the target). The model was fitted simultaneously to the eight functions obtained in the two experiments for each observer using a numerical routine which seeks the parameter values that satisfy the least squared error criterion (Foley & Yang, 1991). It was fitted separately to the data of the two observers. The parameters of these best fits are given in Table 1.

In arriving at this version of the model we fitted 11 versions of the model to the data. These versions differed in which parameters were locked together across the four adaptors and the two pedestals. Although some versions provide slightly better fits than the one described here, they require more free parameters to do so, and the gain in goodness of fit does not justify the additional parameters. The version of the model shown in the figure and described in Table 1 has 11 free parameters. Only Z and S_{Ip} vary with the adaptor, and S_{Ip} varies with the adaptor only for the pedestal orthogonal to the target. Thus, to account for the effect of adaptation on detection on a pedestal in the same orientation as the target only a change in a single parameter, Z, is required, but to account for the effect on detection on a pedestal orthogonal to the target, changes in Z and S_{ip} are required. As shown in Table 1, Z is unaffected by the horizontal adaptor and is increased by an approximately equal amount by the vertical and plaid adaptors. S_{Ip} is decreased slightly by the horizontal adaptor, increased by the vertical adaptor and increased slightly less by the plaid adaptor. The parameters p and q are somewhat smaller here than in other studies, reflecting the fact that facilitation is somewhat smaller. Note that the subscript p indicates pedestal, the lower case p is a model parameter (the exponent of the excitatory term).

The conclusion of our analysis is that pattern adaptation can be described by changes in the values of two parameters of the detecting mechanism, Z and S_{ip} for the pedestal orthogonal to the target. An adaptor in the same orientation as the target increases both parameters; and an adaptor in the orthogonal orientation to the target produces a small decrease in S_{Ip}. An increase is Z is equivalent to adding a constant to the denominator of the response function. This constant can be interpreted as a divisive inhibitory input that is produced by the adaptor and persists after adaptor offset, gradually decreasing to zero. It appears as a constant here because our measurements are made at a constant time after adaptor offset (ISI). In this interpretation, adaptation produces a persisting divisive inhibitory input to the adapted mechanism. An alternative interpretation that is equally consistent with the results is that there is a change internal to the mechanism that results in a higher value of Z. A potential problem with the idea that adaptation is a consequence of the persistence of the divisive inhibition signal that produces masking is that any orientation can mask any other, but adaptation is generally found to be more narrowly tuned. However, Foley (1996) has shown that orientation tuning depends on the temporal frequency spectrum of target and pedestal, being broader for high temporal frequency patterns. The different bandwidths for masking and adapting may be a consequence of different temporal frequency spectra.

The increase in sensitivity to a pedestal orthogonal to the target only manifests itself when such a pedestal is presented. It is puzzling that there is no increase in sensitivity to a parallel pedestal, but a version of the model that incorporates an equal change in divisive inhibitory sensitivity to both pedestals clearly fails to describe our data. Our analysis does not exclude versions of the model in which sensitivity to both pedestals increases (see the Appendix). However, the increase in sensitivity to the pedestal orthogonal to the target must be greater than the increase in sensitivity to the pedestal parallel to the target to fit our data.

When the adaptor contains a horizontal component there is a second, smaller, opposite effect on divisive inhibitory sensitivity to the horizontal pedestal (see Table 1). Divisive inhibitory sensitivity to the horizontal pedestal is *decreased* by about 20%. It is not obvious how to interpret this effect, but it is plausible that a horizontal adaptor would reduce the sensitivity of the horizontally tuned pathways and thereby reduce the horizontal pedestal divisive inhibitory signal before it reaches the vertical detecting mechanism. The small size of this effect suggests that most of this signal does not pass through the principal site of pattern adaptation in the horizontally tuned pathway, although a part of the inhibitory signal may pass through this site. Most of the divisive inhibitory signal may be fed forward and laterally from lower level sites. Our analysis is entirely in terms of sensitivity changes at the detecting mechanism, and it does not specify the origin of these sensitivity changes.

The version of the model that we have presented is the simplest version that is compatible with our measurements in that the effect of adaptation can be described by changes in just two parameters. Several other versions of the model that differ in the parameters that vary with the adapt state are also possible, and some of these make the same predictions as the one that we present. In particular, there are mathematically equivalent versions in which Z does not change with adapt state, but all the sensitivities change by different factors (see the Appendix). Our experiments and analysis do not allow us to distinguish among these versions of the model. They do, however, allow us to exclude several classes of models: (1) models in which mechanisms have a single sensitivity; (2) models in which there is both an excitatory sensitivity and a divisive inhibitory sensitivity, but only the excitatory sensitivity changes with adaptation; (3) models in which both the excitatory and divisive inhibitory sensitivities change by the same factor; and (4) models in which the entire response function is multiplied by a constant. They also exclude versions of our model in which a single parameter changes with adapt state. All of these models produce substantially worse fits to the data and most of them fail to capture qualitative features of the data.

DISCUSSION

The effect of pattern adaptation on contrast discrimination has been examined in several studies. Our results are quite similar to those of Ross and Speed (1991) and agree with Määttänen and Koenderink (1991) and Legge (1981) in showing essentially no effect at high contrast. Like Ross and Speed we found that after adaptation TvC functions for a pedestal with the same orientation as the target cross over those for no adaptor slightly before converging with them, an effect which is captured by the model. Greenlee and Heitger (1988) had reported not only a cross-over but also substantially lower thresholds in the adapted condition at high contrasts. Our results differ from those of Wilson and Humanski (1993), who found that adaptation produced an increase in contrast thresholds over most of the range with a cross-over occurring at high contrasts in some cases. Although there are differences in method, including differences in both the adapting and test stimuli, it is not evident how these differences explain the difference in results.

It is of interest to compare our results with the implications of other models of pattern adaptation. The contrast discrimination result is inconsistent with both versions of the fatigue hypothesis because the fatigue hypothesis implies an overall change in the form of the response function that would affect contrast discrimination at all contrasts. Our results are consistent with the idea that inhibition underlies pattern adaptation. The early inhibition models were based on subtractive inhibition and are not explicit enough to make predictions for our experiments. The model of Wilson and Humanski (1993) is based on the idea that pattern adaptation increases the sensitivity to a feedback signal from the active pattern mechanisms that controls the contrast gain at the detecting mechanism input. This corresponds approximately to an increase in S_I in the present model. Thus, the Wilson and Humanski model proposes one of the two processes that we have proposed to underlie pattern adaptation. Their model predicts that adaptation reduces the slope of the TvC function, a result that Wilson and Humanski obtained in their experiment, but we and others did not. Both the model presented here and the Wilson and Humanski model predict that adaptation produces an increase in sensitivity to divisive inhibition. In the Wilson and Humanki model divisive inhibition is via a feedback pathway. We have not specified whether the divisive inhibitory signal in our model is feedback, feed-forward, or both, and our data are not sufficient to determine this. Wilson and Humanski argue that, because threshold elevation produced by pattern adaptation does not occur for short test stimuli, but does occur for long test stimuli, that the effect must be mediated by a feedback signal. Foley and Boynton (1993) and Hammett and Snowden (1995), however, showed that threshold elevation does occur for short stimuli. Hammett and Snowden further showed that the increase is greater for a high temporal frequency adaptor, suggesting that short stimuli are detected by mechanisms tuned to high temporal frequency. Threshold elevation does increase with test duration which suggests a feedback process, but the fact that it also occurs with short stimuli suggests that this is not the only process of pattern adaptation. Our model proposes two processes. The effect of a change in Z does not depend on target duration. The effect of a change in S_{Ip} may depend on target duration, but masking studies indicate that this change occurs very soon after the presentation of the stimulus.

The model of Ross and Speed (1991) is based on a response function of a form similar to the Naka–Rushton equation. It has four parameters, three of which are assumed to vary with adaptation state. The principal one is the semi-saturation constant, which increases with adaptation. This parameter plays a role similar to Z in our model. Ross and Speed have shown that their model accounts for the effect of adaptation on contrast discrimination. However, their model does not have any dependence of pedestal sensitivity on adapt state, and, as a consequence, it does not account for the effect of adaptation on detection on an orthogonal pedestal.

Barlow and Földiák (1989) proposed two ideas (1) perceptual adaptation (as distinguished from light adaptation) strengthens the inhibitory links among mechanisms; and (2) the links that are strengthened are links among mechanisms that are activated at the same time by the adaptor. They show that this process would have the effect of decorrelating the mechanism responses to the adapting stimuli and allowing them to carry more information. Atick *et al.* (1993) have used these same ideas in a model of color adaptation. Although neither of these models addresses pedestal effects and neither incorporates the kind of nonlinearity needed to account for them, we can consider whether our results are consistent with the ideas about adaptation in these models. Our plaid adaptor condition was a direct test of the first idea. If simultaneous activation of mechanisms strengthens inhibitory links among them and masking increases with the strength of these links, the plaid adaptor should have increased masking of the vertical target by the horizontal pedestal more than the vertical adaptor. In fact, we found the opposite. Our analysis suggests that Barlow and Földiák are correct in proposing that adaptation strengthens inhibition among mechanisms, but it is not specifically the joint activation of the two mechanisms that leads to this strengthening. It appears that an adaptor that activates a mechanism may strengthen the inhibitory links between other mechanisms and the activated mechanism, whether or not the other mechanisms are activated.

Our model is a functional psychophysical model that does not attempt to describe the underlying biology. Nevertheless, it is of interest to compare the effect of pattern adaptation on the model mechanisms with the effect of adaptation on cells in the visual pathway. The lowest level at which pattern adaptation is manifested in cells is in the visual cortex. A common paradigm is to measure the contrast response functions of cortical cells while the animal is in various states of pattern adaptation. These data are then fitted with a function of the form: $R = R_{\max} (C^n/(C^n + C_{50}{}^n)$, where C is pattern contrast and $R_{\max}$, C_{50}, and n are parameters. The effects of pattern adaptation are somewhat different in cat (Albrecht *et al.*, 1984) and monkey (Sclar *et al.*, 1989). One difference is that the changes in the contrast–response function with adaptation are much smaller in the monkey. In both species C_{50} increases with adaptation and accounts for a large part of the adaptation effect. This corresponds quite closely to the effect of the increase in parameter Z on our model mechanism response. In the cat, $R_{\max}$ decreases with adaptation and in the monkey n increases with adaptation. We also found a change in our model parameter $S_{\rm ip}$. This does not correspond to any of the parameters in the biological function. It is most similar to a change in $R_{\max}$ in that it affects the response at all contrasts. However, the change in $R_{\max}$ seems to occur for all pattern frequencies in the cat and the change in $S_{\rm ip}$ does not occur for the parallel pedestal in the human. In the cat Movshon and Lennie (1979) and Saul and Cynader (1989) have shown that after pattern adaptation the contrast sensitivity function of the cell is decreased by a larger factor at the adapting spatial frequency than at other frequencies. The increase in the parameter $S_{\rm ip}$ that we found changes the orientation tuning of the model mechanisms. However, this change is one of narrowing the contrast sensitivity function, rather than producing a local minimum at the orientation of the adaptor. It should be noted that there is no psychophysical evidence for a local minimum at the adaptor frequency in the contrast sensitivity of individual mechanisms, although Wilson and Humanski (1993) explain properties of the tilt aftereffect in terms of such changes. In summary, in both our model mechanisms and cortical cells the principal effect of pattern adaptation is to increase an additive parameter in the denominator of the response function. There are also other effects of adaptation in all three species, but our results suggest that these changes may be different in human pattern mechanisms than in monkey and cat cortical cells.

Our results and analysis show that the effect of pattern adaptation on TvC functions for detection on pedestals that are parallel to and orthogonal to the target can be accounted for by a model in which two parameters change with pattern adaptation. One of these can be interpreted as the persistence of the divisive inhibition that produces masking after the adapting pattern has been turned off. The other can be interpreted as the strengthening of divisive inhibitory links between pathways tuned to other patterns and the mechanisms that are excited by the adaptor.

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APPENDIX

Statement of model showing the equivalency of a change in Z and changes in all the sensitivity parameters

The model used here is a one-mechanism version of model 3 in Foley (1994a). The one mechanism is the mechanism that detects the vertical target. Here we will assume that all sensitivities are positive, as was found to be the case in fitting our data. This allows us to ignore the halfwave rectification process. The response to a pedestal alone is given by:

$$R_{\mathrm{p}} = (C_{\mathrm{p}}S_{\mathrm{Ep}})^p/((C_{\mathrm{p}}S_{\mathrm{Ip}})^q + Z),$$

where C_{p} is the contrast of the pedestal, S_{Ep} and S_{Ip} are the excitatory and divisive inhibitory sensitivities to the pedestal, and p, q, and Z are parameters of the mechanism. The response to the target plus the vertical (parallel) pedestal is given by:

$$R_{\mathrm{pt}} = (C_{\mathrm{p}}S_{\mathrm{Ep}} + C_{\mathrm{t}}S_{\mathrm{Et}})^p/((C_{\mathrm{p}}S_{\mathrm{Ip}} + C_{\mathrm{t}}S_{\mathrm{It}})^q + Z),$$

where S_{Et} and S_{It} are the excitatory and divisive inhibitory sensitivities to the target.

The response to the target plus the horizontal (orthogonal) pedestal is given by:

$$R_{\mathrm{pt}} = (C_{\mathrm{p}}S_{\mathrm{Ep}} + C_{\mathrm{t}}S_{\mathrm{Et}})^p/((C_{\mathrm{p}}S_{\mathrm{Ip}})^q + (C_{\mathrm{t}}S_{\mathrm{It}})^q + Z).$$

Suppose, as in the case of the vertical pedestal, that the effect of pattern adaptation is to change the value of the parameter Z. $Z' = KZ$, where Z is the value without adaptation and Z' is the value after adaptation. After adaptation the response to the pedestal can be described by:

$$\begin{aligned} R_{\mathrm{p}} &= (C_{\mathrm{p}}S_{\mathrm{Ep}})^p/((C_{\mathrm{p}}S_{\mathrm{Ip}})^q + KZ) \\ &= (1/K)(C_{\mathrm{p}}S_{\mathrm{Ep}})^p/((1/K)(C_{\mathrm{p}}S_{\mathrm{Ip}})^q + Z) \\ &= (C_{\mathrm{p}}(1/K)^{1/p}S_{\mathrm{Ep}})^p/((C_{\mathrm{p}}(1/K)^{1/q}S_{\mathrm{Ip}})^q + Z) \\ &= (C_{\mathrm{p}}S'_{\mathrm{Ep}})^p/((C_{\mathrm{p}}S'_{\mathrm{Ip}})^q + Z), \end{aligned}$$

where $S'_{\mathrm{Ep}} = (1/K)^{1/p}S_{\mathrm{Ep}}$ and $S'_{\mathrm{Ip}} = (1/K)^{1/q}S_{\mathrm{Ip}}$.

The other two equations can be similarly transformed. Thus, any change in the last term in the denominator, such as the change that we make in Z to account for the effect of adaptation, has an effect equivalent to multiplying the excitatory and inhibitory sensitivities by different constants. A version of the model in which all the sensitivities change in this manner is mathematically equivalent to a version in which Z alone changes. In the case of the horizontal (orthogonal) pedestal, the simplest model is one in which Z and S_{Ip} change. Here also there are mathematically equivalent versions in which all the sensitivities change with adaptation. Nevertheless, we are able to exclude several classes of models including all models in which only a single parameter varies with adaptation.

Among the mathematically equivalent versions of our model, we chose to present the simplest version to describe our results; that is, the version in which the fewest parameters change with adaptation. That is a version in which Z and S_{Ip} for the horizontal pedestal change. In making fits to the data we eliminate parameter indeterminacy by specifying that the excitatory sensitivity to the target is 100 (40 dB re 1).