SPATIAL CONTRAST ADAPTATION CHARACTERISTICS OF NEURONES RECORDED IN THE CAT'S VISUAL CORTEX

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SUMMARY

1. Spatial contrast adaptation, produced by prolonged exposure to high contrast grating patterns, has become an important psychophysical method for isolating spatial and orientation selective channels in the human visual system. It has been reasonably argued that this adaptation may be fundamentally dependent upon the activity of neurones in the striate cortex. To test the validity of this hypothesis, and several others, we measured the general adaptation characteristics of 144 striate neurones using a stimulus protocol comparable to the typical psychophysical methods.

2. In general, during prolonged high contrast stimulation, the responses of most cells exponentially decayed from a transient peak response to a sustained plateau response; following adaptation, the responses to lower contrasts were depressed relative to the unadapted state but then gradually recovered from the transient depression to a sustained plateau. Such adaptation was a property common to both simple and complex cells (the distributions of the quantitative indices of adaptation were overlapping); there were however small but reliable differences.

3. We compared the neurophysiological contrast adaptation with two psychophysical estimates of human contrast adaptation (threshold contrast elevation and apparent contrast reduction) and found that the time courses and the magnitudes were quite similar.

4. The effect of contrast adaptation on the spatial frequency tuning was assessed by measuring the contrast response function at several different test spatial frequencies before and after adaptation at the optimum centre frequency. We found that the effect of adaptation decreased as the difference between test and adaptation frequency increased.

5. Grating contrast adaptation has been alternatively described as ‘constructive gain control’ on the one hand and as ‘deleterious fatigue’ on the other. We tested the effect of contrast adaptation on the contrast response function and found (a) that adaptation shifts the curves vertically downward parallel to the response axis (thus reflecting a decrease in the maximum rate of firing and a deleterious compression of the response range) and (b) that adaptation shifts the curves horizontally to the right parallel to the contrast axis (thus reflecting a true sensitivity shift of the remaining response range for constructive maintenance of high differential sensitivity around the prevailing background level).
To specifically test whether contrast adaptation could have advantageous consequences in terms of the maintenance of high differential contrast sensitivity, we measured the responses during prolonged sequential contrast alternation and found that adaptation did enhance the differential response modulation at higher contrasts.

INTRODUCTION

Prolonged viewing of a high contrast spatial stimulus produces a variety of adaptation-related perceptual after-effects (Blakemore & Campbell, 1969; Blakemore & Sutton, 1969; Blakemore, Nachmias & Sutton, 1970; Blakemore, Muncey & Ridley, 1971, 1973; Sekuler, 1975; Sekuler, Pantle & Levinson, 1978). Such effects have generally been interpreted as the result of selective adaptation (or fatigue) of neurones responding to the spatial stimulus. This pattern selective adaptation has become an important psychophysical tool for studying the properties of channels in the human visual system and is in many respects the psychophysical cornerstone of the multiple-channel model proposed by Campbell & Robson (1968; for general reviews of this and related issues see: Sekuler, 1974; Robson, 1975, 1980; Braddick, Campbell & Atkinson, 1978; De Valois & De Valois, 1980).

Because the contrast adaptation effect shows interocular transfer and is specific to the spatial frequency and orientation of the adapting grating (Blakemore & Campbell, 1969; Blakemore & Nachmias, 1971; Movshon & Blakemore, 1973), it has been reasonably argued that neurones at the level of the striate cortex (as first described by Hubel & Wiesel, 1962, 1968) may play a fundamental role in these behavioural phenomena. Striate neurones are in fact relatively selective for spatial frequency and orientation and most can be stimulated by both eyes (for a general review of this neurophysiological literature see: De Valois, Albrecht & Thorell, 1982; De Valois, Yund & Hepler, 1982). Further, several neurophysiological studies have shown that some cortical cells do show appreciable adaptation qualitatively similar to the psychophysical adaptation (Maffei, Fiorentini & Bisti, 1973; Vautin & Berkley, 1975; Albrecht, 1978; Movshon & Lennie, 1979).

Adaptation to prolonged steady-state stimulation is a general characteristic of sensory systems which, among other practical benefits, allows a small (limited capacity) dynamic response range to span a comparatively larger stimulus intensity range, by shifting along the intensity axis according to the over-all ambient prevailing level (thus maintaining high differential sensitivity). Light and dark adaptation in the visual system exemplify this basic principle (e.g. Craik, 1938; for general reviews see: Barlow, 1972; Werblin, 1974b). It seems reasonable to ask whether contrast adaptation may serve a similar function; that is, does the adaptation reflect 'constructive gain control' for maintenance of high differential sensitivity (Ohzawa, Sclar & Freeman, 1982), or is the adaptation more appropriately characterized as a 'deleterious fatigue' with no advantageous consequences? (Barlow, MacLeod & Van Meeteren, 1976).

In the present series of experiments, we wanted to investigate three basic aspects of cortical cell contrast adaptation. Our first goal was to provide quantitative statistics, from a large population of cells, regarding the over-all (a) susceptibility
to adaptation, (b) rate of induction, and (c) rate of recovery, using a stimulus protocol comparable to a typical psychophysical experiment. Among other things, this data should allow us to compare the neurophysiological adaptation process with the psychophysical adaptation process.

Our second goal was to assess the effect of adaptation on the contrast response function and the spatial frequency tuning. Contrast adaptation might reflect a true sensitivity shift or might also reflect an over-all compression of the response range. These components can be mathematically formalized and the predictions tested by measuring the contrast response function (across a full range of contrasts) following adaptation. Quantitatively indexing the shifts in the contrast response function should help us assess the relative validity of the constructive gain control hypothesis as opposed to the deleterious fatigue hypothesis.

Our third goal was to test some specific functional predictions of a gain control (or range shifting) hypothesis: we wanted to assess the effect of adaptation on differential contrast sensitivity. To do this, we measured the ability of cortical cells to respond differentially to changes in contrast during the course of adaptation. Such a task is similar to a psychophysical contrast discrimination task and might thus help us compare the neurophysiological and psychophysical consequences of contrast adaptation.

METHODS

The apparatus and general single-cell electrophysiological recording procedures, along with the computer-based oscilloscope visual display, have been recently described elsewhere (Albrecht & De Valois, 1981; Albrecht & Hamilton, 1982). Using these methods, we recorded the responses of 144 striate neurones (from a total of fifteen domestic cats) as a function of luminance-modulated visual stimuli.

Experimental procedure

Once the response of a single cell was clearly isolated, its receptive field was located and centred on the display scope. Its preferred orientation, direction of movement, spatial frequency, temporal frequency and length were determined by listening to the spike trains while varying these parameters. Bar stimuli were then used to classify the cell as simple or complex according to the criteria of Hubel & Wiesel (1962). On the basis of these preliminary measurements, the responses of the cell to various spatial frequencies, temporal frequencies and contrasts were quantitatively measured in an interleaved fashion (ten contiguous cycles repeated four times at every spatial frequency, temporal frequency, and contrast sampled). The average peristimulus time histograms were collected in 5-ms time bins; from these peristimulus time histograms an on-line Fourier harmonic analysis was computed. For complex cells, the average response rate (minus the spontaneous activity), the 'continuous' (d.c.) component, was used as the response measure; for simple cells, amplitude of modulation (minus any spontaneous modulation), the first harmonic component, was used as the response measure. Following these experiments, we then proceeded to the adaptation experiments.

In the first series of experiments (Part I), we wanted to measure the general adaptation characteristics of striate cells. The stimulus protocol consisted of three 30-s intervals: pre-adapt, adapt, post-adapt. During these three intervals we drifted the optimum spatial frequency grating pattern across the receptive field and varied only the contrast; the drift rate was generally set at 4 or 6 Hz, with the exception of a few cells which required 2 Hz. In the first 30-s interval, the pre-adapt interval, the contrast of the grating was set to evoke a 'near threshold' response (approximately 10% of the maximum response). After this measurement of the pre-adapt sensitivity, we then presented no-pattern mean luminance for 120 s to insure recovery from any adaptation which may have occurred during the presentation of the low contrast grating. In the next 30-s interval, the
adapt interval, the contrast of the grating was set to evoke the maximum saturated response (the high-saturation contrast value and the low-threshold contrast value were obtained from the preliminary quantitative measurements of the unadapted contrast response function). In the final 30-s interval, the post-adapt interval (immediately following the high contrast interval), the grating contrast was reduced to the pre-adapt (near threshold) value to assess the effect of the high contrast adaptation. The error variance associated with these measurements was reduced by repeating the entire protocol a minimum of four times and a maximum of eight times (the exact number was determined by viewing an on-line display of the cumulative averaged responses) with a 3-min waiting period between each repetition. The responses were then averaged together into 1-s time bins, and within each 1-s bin we computed the mean of the repeated samples.

In the second series of experiments (Part II), we wanted to measure the effect of contrast adaptation on the contrast response function and the spatial frequency tuning. Responses to various test spatial frequencies and test contrasts were thus measured following 30 s of adaptation to the optimum grating presented at various adapting contrasts. Post-adapt responses were averaged over the first 4 s immediately following the adapt period. This protocol was repeated four to eight times for each test stimulus, each repetition separated by a 3-min rest interval. The unadapted spatial and contrast responses (for comparison purposes) were measured using the same protocol except that the 30-s 'adapt' interval consisted of no-pattern mean luminance (rather than an adapting contrast).

In the third series of experiments (Part III), we wanted to assess the ability of striate cells to respond differentially to contrast differences at different adaptation levels. The spatial pattern consisted of the optimum grating; the contrast of the grating was alternated from a low value to a high value every 2 s for a total of 40 s. The responses were averaged over synchronous 2-s time bins. This protocol is analogous to one described by Werblin (1974a,b) which assessed the effect of luminance adaptation on the differential response of retinal neurones.

RESULTS

Part I: general adaptation characteristics

The first goal of this study was to characterize both qualitatively and quantitatively the general effects of contrast adaptation on the response properties of neurones in the striate cortex. To facilitate a comparative analysis, we tested each cell with methods comparable to a typical psychophysical adaptation experiment. The stimulus consisted of the optimum spatial grating pattern drifted across the receptive field at a low contrast for 30 s (pre-adapt), high contrast for 30 s (adapt), and then the original low contrast again for 30 s (post-adapt). The basic pattern of results can be seen in Fig. 1, where the averaged responses of six representative cells are shown.

In general, during the high contrast adapt interval, the response rate of most cells gradually decays from a transient peak value to a sustained plateau value; during the low contrast post-adapt interval, the response rate of most cells is transiently reduced (relative to the pre-adapt response rate) and then gradually recovers to a sustained plateau level (only slightly less than the plateau of the pre-adapt interval).
in response which occurs during the adapt interval: the cells at the top are less susceptible to adaptation and thus show a more sustained response as compared to those at the bottom which are quite susceptible to adaptation and thus show a more transient response. The cells are ordered from left to right in terms of the magnitude of the adaptation effect shown during the post-adapt period (the arrow indicates the response rate at the end of the pre-adapt interval); the cells on the right show a larger effect of the high contrast adaptation on the low contrast response. The smooth curves through the data points are the best fitting (least-squares) decay and recovery exponential functions (see Table 1 for definitions); the optimized parameters are specified for each curve. As a rule, the exponential function did provide a reasonable fit for the majority of cells, however, the characteristics of some cells restricted the generality of the formalized parameters for describing the whole population. Some of the problems are evident in Fig. 2 ('delayed response cells') and in the post-adapt of Fig. 1D (zero response rate), the adapt of Fig. 1 A, and the pre-adapt of Fig. 1 E (linear decay and recovery curves).
This type of behaviour can be described using the exponential functions shown in Table 1; the responses of the cells shown in Fig. 1 have been fitted using these functions. Originally we had hoped to be able to use the parameters of these exponentials to characterize the total population of cells; however, since the adaptation responses of many cells could not be fitted by these functions, we derived the simpler statistics, described below (Figs. 1 and 2 illustrate some of the advantages and disadvantages of using the exponentials).

### Table 1. Mathematical formulations

<table>
<thead>
<tr>
<th>Exponential decay</th>
<th>response ( t ) = ( pk \cdot e^{-t/d} + pt )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exponential recovery</td>
<td>response ( t ) = ( pt \cdot (1 - e^{-t/r}) + tr )</td>
</tr>
</tbody>
</table>

- \( pk \): peak response
- \( pt \): plateau response
- \( tr \): trough response
- \( d \): decay constant
- \( r \): recovery constant
- \( t \): time

<table>
<thead>
<tr>
<th>H ratio</th>
<th>response ( c ) = ( R_{max} \cdot \frac{C^n}{(C^n + C_{50}^n)} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( R_{max} ): maximum response</td>
<td></td>
</tr>
<tr>
<td>( C_{50} ): semi-saturation constant</td>
<td></td>
</tr>
<tr>
<td>( n ): power exponent</td>
<td></td>
</tr>
<tr>
<td>( C ): contrast</td>
<td></td>
</tr>
</tbody>
</table>

Mathematical formulations used in this study. The exponential decay and recovery functions were used to characterize the contrast adaptation decay and recovery responses. The \( H \) ratio was used to characterize the contrast response functions.

Not all cells conform to the pattern of results illustrated in Fig. 1. Specifically, while most cells produce their maximum rate of response during the first second or two of stimulation, a sizable population of cells (some 28%) actually take some period of time to reach their maximum response rate. The two cells shown in Fig. 2 are representative of this group of cells. If we examine the responses during the high contrast adaptation interval for the cell shown in Fig. 2A (our most extreme example), it can be seen that this cell took over 15 s to reach its peak rate of response; the cell shown in Fig. 2B, a more typical example, took over 7 s to reach the peak rate. The average delay (or rise time) to the peak response rate was 7.5 s (s.e. of the mean = 0.7).

It is important to emphasize that there was a great deal of heterogeneity from cell to cell in terms of the adaptation characteristics. One particularly salient variation can be seen in the over-all susceptibility to adaptation, that is, the amount of response decrement which occurs during the adaptation interval; the cells in Fig. 1 have been ordered from top to bottom in terms of the magnitude of this decrement. The cells in the top part of the Figure show very little decrement in their response rate during the course of the high contrast adaptation interval; the cell shown in Fig. 1A, for example, maintains some 80% of its maximum rate of response after 30 s of high contrast stimulation. The cells in the bottom part of the Figure, however, show a rather dramatic decrease in their response during the high contrast adaptation interval; the cell shown in Fig. 1F, for example, has decreased its rate of responding by 90% at the end of the 30-s high contrast interval. As this Figure illustrates, there was considerable variation in terms of the susceptibility of cortical cells to contrast adaptation.
Fig. 2. Two examples of some 28% of the population of cells (forty cells) which took some period of time to reach the maximum rate of firing during the adaptation interval. The cell shown in A took over 15 s to reach its peak rate of firing (the most extreme example); the cell in B took over 7 s to reach the peak rate of firing. The smooth curves through the data points show that the best fitting exponential functions (with optimized parameters as specified; see Table 1 for definitions) in A the recovery exponential was used for all three intervals. The average rise time to the peak response was 7.5 s (S.E. of the mean = 0.7). Of the forty cells, twenty-five were simple cells and fifteen were complex cells; the average delay times compared across these two types of cells were quite similar (simple: mean = 7.0, S.E. of the mean = 0.9; complex: mean = 8.2, S.E. of the mean = 1.0).

To quantify this variation, we indexed the percentage of the transient maximum rate of response which was maintained at the end of the 30-s adapt interval (an index similar to the adapt index introduced by Adrian & Zotterman, 1926). The distribution of the adapt index is shown in Fig. 3 for the entire population of cells (broken down across simple and complex cells). As can be seen, for some cells contrast adaptation over the 30-s interval was virtually complete, reducing the response rate to less than 10% of the initial maximum, whereas for other cells the effect of contrast adaptation
Fig. 3. Distributions of the adapt index for all cells, as well as broken down for the populations of simple and complex cells (the means, standard errors, and medians of these distributions are shown in Table 2). The adapt index for each cell is the sustained plateau rate of firing at the end of the 30-s high contrast adaptation interval expressed as a percentage of the initial transient peak rate of firing (which occurred at the beginning of the adapt interval). The index thus provides a quantitative indication of the over-all susceptibility, or adaptability of the total population of cells. As can be seen, the population shows considerable heterogeneity: some cells show a large decrement in response such that the final sustained plateau rate of firing is less than 10% of the initial peak, while other cells maintain some 90% of the initial peak firing at the end of the 30 s of high contrast stimulation. The distributions for simple and complex cells are overlapping and quite similar; nevertheless, the mean values are reliably different (see Table 2); in general, complex cells tend to maintain a smaller percentage of their initial transient peak response.

was quite small. The means and standard errors for this index are shown in Table 2. While the distributions for simple and complex cells were overlapping and on the whole rather similar, there was nevertheless a reliable difference between the two: simple cells maintained a larger percentage of their initial transient maximum; complex cells showed a larger decrement in response (the difference in the means shown in Table 2 is considerably larger than the standard errors).
There was also a great deal of heterogeneity, from cell to cell, in terms of the rate of response decay during adaptation and the rate of response recovery following adaptation. As can be seen in Fig. 1, the decay time constant for some cells was less than 5 s whereas for other cells the decay constant was greater than 30 s. To quantify the rate of decline, we indexed the amount of time required to reduce the response rate by a factor of one-third. The distribution of this statistic for all cells is shown in Fig. 4 (broken down in terms of simple and complex cells). As can be seen, some cells achieve this criterion decrement in less than 5 s while others do not decrease by one-third even at the end of the 30 s. The means and standard errors for this index are shown in Table 2 (values of the decay index which exceeded the observation interval of 30 s were set equal to 30 s for this and subsequent analyses). The difference between simple and complex cells was small but once again reliable: complex cells decayed more rapidly, simple cells decayed more slowly.

Finally, to quantify the rate of recovery from contrast adaptation, we asked how long it took the response rate to resume one-third of the final maintained plateau during the post-adapt interval. The distribution of this index (broken down for simple and complex cells) is shown in Fig. 5. As can be seen, most of the cells achieve this criterion response increase within 5–10 s after high contrast adaptation. The means and standard errors for this index are shown in Table 2. Once again, the difference

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### Table 2. Adaptation indices

<table>
<thead>
<tr>
<th></th>
<th>All cells</th>
<th>Simple cells</th>
<th>Complex cells</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>n</strong></td>
<td>(144)</td>
<td>(64)</td>
<td>(80)</td>
</tr>
<tr>
<td><strong>Adapt index</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>48.9</td>
<td>53.3</td>
<td>48.8</td>
</tr>
<tr>
<td>s.e. of the mean</td>
<td>2.1</td>
<td>3.2</td>
<td>2.6</td>
</tr>
<tr>
<td>Median</td>
<td>(48.2)</td>
<td>(57.5)</td>
<td>(43.0)</td>
</tr>
<tr>
<td><strong>Decay index</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>14.2</td>
<td>17.0</td>
<td>11.9</td>
</tr>
<tr>
<td>s.e. of the mean</td>
<td>0.9</td>
<td>1.4</td>
<td>1.1</td>
</tr>
<tr>
<td>Median</td>
<td>(9.1)</td>
<td>(12.5)</td>
<td>(7.1)</td>
</tr>
<tr>
<td><strong>Recovery index</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>4.9</td>
<td>6.0</td>
<td>3.9</td>
</tr>
<tr>
<td>s.e. of the mean</td>
<td>0.4</td>
<td>0.6</td>
<td>0.4</td>
</tr>
<tr>
<td>Median</td>
<td>(3.9)</td>
<td>(4.9)</td>
<td>(2.8)</td>
</tr>
<tr>
<td><strong>Post/pre</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>90.0</td>
<td>80.9</td>
<td>97.3</td>
</tr>
<tr>
<td>s.e. of the mean</td>
<td>3.9</td>
<td>6.0</td>
<td>4.5</td>
</tr>
<tr>
<td>Median</td>
<td>(88.4)</td>
<td>(75.0)</td>
<td>(96.1)</td>
</tr>
</tbody>
</table>

Quantitative indices used to describe the adaptation characteristics of the entire population of cells. The adapt index is the sustained plateau response rate at the end of the adapt interval (expressed as a percentage of the initial transient peak response rate). The decay index is the number of seconds required during the adapt interval for the response rate to lose 33% of the initial peak. The recovery index is the number of seconds required during the post-adapt interval for the response rate to recover 33% of the final plateau rate. Post/pre is the ratio of the response rate at the end of the post-adapt interval expressed as a percentage of the response rate at the end of the pre-adapt interval.
between simple and complex cells was small but reliable: complex cells recovered more rapidly. (One might have expected there to be a correlation between the time course of decay and recovery, however analysis of the scatterplot of the decay and recovery indices showed that the two parameters were not well correlated.)

Relationship to spatial, temporal and contrast response functions. In addition to measuring the adaptation characteristics of all 144 cells, we also measured the spatial frequency tuning, the temporal frequency tuning and the contrast response functions.
We were interested in looking for possible relationships between these properties and the adaptation properties. For the spatial frequency tuning, we indexed the spatial peak and the overall bandwidth (measured in terms of octave width at half-amplitude; refer to Albrecht, 1978; or De Valois et al. 1982). For the temporal frequency tuning, we indexed the peak of the response function. For the contrast response function, we indexed the semi-saturation contrast (that is, the contrast required to evoke 50% of the cell's maximum response; refer to Albrecht & Hamilton, 1982). We indexed...
the adaptation characteristics, as described above (adapt, decay, and recovery). With all of these indices (the spatial, temporal and contrast properties on the one hand, and the adaptation properties on the other), we then analysed the data for possible correlations, but found none.

![Diagram of sensitivity, compression, and sensitivity and compression shifts](image)

**Fig. 6.** Theoretical mathematical formulations of how contrast adaptation could potentially affect the contrast response function of striate neurons (Hood, 1978, presents a similar analysis illustrating how light adaptation could potentially affect luminance-intensity response functions). The function used to generate these curves (the H ratio, see Table I) provides a good characterization of striate cell contrast response functions (as well as retinal intensity response functions). In A (sensitivity shift), the effect of contrast adaptation is to shift the entire dynamic response range horizontally to the right; such a lateral shift increases the value of the semi-saturation ($C_{so}$) parameter only (cf. Werblin, 1971, 1974b). In B (compression shift), the effect of contrast adaptation is to shift the curves vertically downward; such a horizontal compression shift decreases the value of the maximum rate of response ($R_{max}$) parameter only (cf. Normann & Werblin, 1974; Werblin, 1974b). In C (sensitivity and compression shift), there is both a sensitivity shift to the right and a compression shift downward: $C_{so}$ increases with the adapting contrast and $R_{max}$ decreases (cf. Kleinschmidt & Dowling, 1975; Hood, 1978).

**Part II: the effects of adaptation on the contrast response function and the spatial frequency tuning**

**Contrast response.** In this series of experiments, we wanted to investigate how adaptation affected the contrast response function of striate cells. From the results presented above, it is clear that for most cells, contrast adaptation decreases the response to a given test contrast; it is not clear, however, whether this response decrease reflects a true sensitivity shift of the entire dynamic response range (a horizontal sensitivity shift to the right) or whether the decrease reflects a compression of the dynamic response range (a decrease in the maximum response rate and thus a vertical shift downward). The three sets of theoretical contrast response functions shown in Fig. 6 graphically illustrate that a decrease in response, following contrast adaptation, can result from three different modifications of the contrast response function.

We have shown elsewhere (Albrecht & Hamilton, 1982) that the response as a function of contrast for most striate cells increases in a linear fashion over some 50–60% of the maximum response range and then begins a compression to an ultimate
saturation response; such behaviour is well characterized by the H ratio equation shown in Table 1. The H ratio function was first used by Naka & Rushton (1966) to fit voltage intensity data from retinal S potentials and has since been used to describe intensity response functions and adaptation characteristics of retinal neurones in a wide variety of vertebrate species (Baylor & Fuortes, 1970; Boynton & Whitten, 1970; Dowling & Ripps, 1972; Fain & Dowling, 1973; Werblin, 1974a; Kleinschmidt & Dowling, 1975; Hemila, 1977); the same function has also been used in human psychophysical studies to describe the effect of adaptation on luminance sensitivity (Alpern, Rushton & Torri, 1970; Hood, 1978; Hood, Ilves, Maurer, Wandell & Buckingham, 1978; Geisler, 1981).

The three parameters of the H ratio provide very useful and meaningful quantitative descriptions of contrast response functions: $R_{\text{max}}$ is the maximum saturated response rate, $C_{\text{50}}$ is the contrast required to reach 50% of the response rate (the semi-saturation contrast), and $n$ is the power function exponent which determines the rate of change. The three sets of curves shown in Fig. 6 were generated using the H ratio; the curves illustrate that the parameters of this function enable us to quantitatively test several different theoretical predictions (cf. the retinal physiology and human psychophysical studies cited in the above paragraph).

If only the sensitivity of a cell is altered following adaptation, then the entire dynamic response range should shift to the right parallel to the contrast axis (as shown in Fig. 6.A); under these circumstances the semi-saturation contrast parameter ($C_{\text{50}}$) increases with adapting contrast. This type of shift is found for the intensity response curves of vertebrate cones (Normann & Werblin, 1974; and other retinal neurones. Werblin, 1971, 1974b) measured at different adaptation levels. If however, adaptation produces a compression of the dynamic response range, then the dynamic range shifts downward parallel to the response axis (Fig. 6.B); under these circumstances the maximum response rate ($R_{\text{max}}$) decreases with contrast. This type of shift is found for the intensity response curves of rods in the mudpuppy retina (Normann & Werblin, 1974; Werblin, 1974b) when measured under different levels of adaptation. Fig. 6.C illustrates the results of shifting both $C_{\text{50}}$ and $R_{\text{max}}$ by equivalent amounts. This type of shift describes the adaptation characteristics of gecko photoreceptors (Kleinschmidt & Dowling, 1975) and human increment sensitivity (Hood, 1978).

To distinguish which of these modifications of the dynamic response range best describes the effect of adaptation on striate cell responses, it is necessary to use a wide range of test contrasts which cover both the lower rates of responding as well as the higher rates; the effects of all three types of shift are very similar over low rates of response (i.e. responses near threshold). We have therefore measured the contrast response function over a wide range of contrasts following adaptation to three different adapting contrasts. the results of this experiment are shown for two representative cells in Fig. 7.

Qualitatively, it can be seen (in Fig. 7.A and D) that contrast adaptation does in fact decrease the response to any given test contrast and that this decrease is due to both a sensitivity shift to the right along the contrast axis as well as a compression shift downward along the response axis. Quantitatively, by examining the descriptive parameters of the best fitting H ratios (see Table 3), it is apparent that $R_{\text{max}}$
Fig. 7. The effect of contrast adaptation on the contrast response function is illustrated. The responses as a function of contrast are shown for two representative striate neurones, measured following 30 s of adaptation to three different adapting contrasts. Qualitatively, it can be seen that as the adapting contrast is increased, the curves shift both laterally to the right and vertically downward; there is both a sensitivity shift and a response compression. The optimized parameters of the best fitting $H$ ratio were found for each set of data points (see Table 3); these were used to generate the smooth curves. The effect of adapting contrast is plotted for $R_{\text{max}}$ (the maximum rate of response) in $B$ and $E$ and for $C_{50}$ (the semi-saturation contrast) in $C$ and $F$. As can be seen, as the adapting contrast increases, the maximum rate of response decreases and the contrast required to evoke half the maximum rate increases.

decreases with adapting contrast and that $C_{50}$ increases with adapting contrast. To provide some indication of the relative contribution of these two effects (response compression and sensitivity shift) we plotted the decrease in $R_{\text{max}}$ ($7B$ and $E$), and the increase in $C_{50}$ ($7C$ and $F$), as a function of adapting contrast (on log-log) coordinates.

We were able to complete this entire experiment (measurement of the contrast response function following adaptation to three separate adapting contrasts) on a
sample of eleven cells. We found that the average slope for $R_{\text{max}}$ (plotted as a function of adapting contrast on log-log coordinates as in Fig. 7B and E) was $-0.49$ (s.d. = 0.25); the average slope for $C_{50}$ (plotted as in Fig. 7C and F) was 0.62 (s.d. = 0.12). From this we can conclude that both the sensitivity shift and the compression shift are important factors in cortical cell contrast adaptation.

**Table 3. Adaptation of contrast response**

<table>
<thead>
<tr>
<th>Adapt contrast</th>
<th>$n$</th>
<th>$C_{50}$</th>
<th>$R_{\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fig. 8A</td>
<td>4.4</td>
<td>3.8</td>
<td>3.8</td>
</tr>
<tr>
<td>Fig. 8D</td>
<td>4.4</td>
<td>5.1</td>
<td>4.2</td>
</tr>
<tr>
<td></td>
<td>6.6</td>
<td>6.8</td>
<td>2.6</td>
</tr>
<tr>
<td></td>
<td>4.0</td>
<td>4.0</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td>4.3</td>
<td>3.7</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td>11.5</td>
<td>4.2</td>
<td>12.4</td>
</tr>
</tbody>
</table>

The three parameters of the best fitting $H$ ratios (see Table 1) are shown for the contrast response functions of two representative cells measured following three different levels of contrast adaptation; as the adapting contrast increased, the maximum rate of response decreased, the semi-saturation contrast increased, and the slope was relatively unaffected.

**Spatial frequency.** In this series of experiments we wanted to assess the effect of adaptation on the spatial frequency tuning of striate cells. We therefore measured the contrast response function, using several different test spatial frequencies, before and after contrast adaptation. The results of such an experiment are shown in Fig. 8 for a representative cell.

The unadapted contrast response functions measured using different test spatial frequencies are shown in Fig. 8A. The same series of measurements following 30 s of adaptation are shown in Fig. 8B; the adapt interval consisted of the peak (the centre) frequency presented at 10% contrast (a contrast which evoked a near saturation response). Qualitatively, it can be seen that for this cell all test spatial frequencies were affected by adaptation at the peak frequency: the contrast response functions were all shifted to the right along the contrast axis and downward along the response axis. However, the adaptation was most effective on the centre (adapt) frequency and less effective at the other more distant frequencies. The resultant spatial frequency tuning curves derived at a constant 6.6% test contrast before and after 30 s of adaptation are plotted in Fig. 8C.

The effect of centre frequency adaptation on the dynamic response range of other test spatial frequencies can be quantitatively compared by examining the changes in the descriptive parameters of the best fitting $H$ ratios. These values are shown in Table 4 before and after adaptation, along with a comparative ratio (after adapt/before adapt) to index the relative magnitude of the adaptation effect on the various test spatial frequencies. The effect of adaptation on these quantitative parameters is illustrated in Fig. 8D where the comparative ratio is plotted for $C_{50}$, $R_{\text{max}}$ and the response at 6.6% contrast: the adaptation effect is largest at the adaptation frequency and then diminishes at more distant frequencies.

The protocol for the experiments illustrated in Fig. 8 required several hours and
Fig. 8. The effect of contrast adaptation on spatial frequency tuning is illustrated for a representative striate neurone. The contrast response function, measured at several different spatial frequencies is plotted before (A) and after (B) 30 s of adaptation to the centre frequency at 10% contrast (a contrast which produces a near maximum response in the unadapted state). The best fitting H ratio was found for each set of data points and the values of the parameters (shown in Table 4) were used to generate the smooth curves. Qualitatively, it can be seen that centre frequency adaptation has shifted all of the curves to the right and downward, however the adapting effect diminishes as the distance between the test and adapt frequency increases. The spatial frequency response functions, measured at 66% contrast before and after the adaptation, are plotted in C; again, these illustrate that while the whole tuning curve is shifted downward, the adapting effect is strongest when the test and adapt frequencies are similar. To express the relative effect of centre frequency adaptation on the various frequencies measured, we took the values of three different measurements, $R_{max}$, $C_{50}$ and the response at 66% contrast, and computed a ratio (the value after adaptation relative to the value before adaptation); these ratios are plotted in D.
was thus only completed on a sample of seven cells. The quantitative analysis on this
sample of cells was in agreement with the results described above: the effect of centre
frequency adaptation was found on all test frequencies but adaptation decreased to
some extent as the difference between the test and adapt frequencies increased. To
provide a quantitative indication from a larger sample of cells, we performed the
following, less time-consuming, experiment.

Table 4. Adaptation and spatial frequency

<table>
<thead>
<tr>
<th>Frequency (cycles/deg)</th>
<th>n</th>
<th>C50</th>
<th>R_{max}</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.75</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Before adapt</td>
<td>2.2</td>
<td>4.3</td>
<td>0.80</td>
</tr>
<tr>
<td>After adapt</td>
<td>3.2</td>
<td>7.6</td>
<td>0.40</td>
</tr>
<tr>
<td>(After/before)</td>
<td>1.5</td>
<td>1.8</td>
<td>0.40</td>
</tr>
<tr>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Before adapt</td>
<td>2.5</td>
<td>4.7</td>
<td>0.50</td>
</tr>
<tr>
<td>After adapt</td>
<td>3.5</td>
<td>7.3</td>
<td>0.30</td>
</tr>
<tr>
<td>(After/before)</td>
<td>1.5</td>
<td>1.5</td>
<td>0.67</td>
</tr>
<tr>
<td>1.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Before adapt</td>
<td>3.3</td>
<td>4.4</td>
<td>0.50</td>
</tr>
<tr>
<td>After adapt</td>
<td>4.2</td>
<td>7.2</td>
<td>0.21</td>
</tr>
<tr>
<td>(After/before)</td>
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<td>1.6</td>
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<tr>
<td>Before adapt</td>
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<td>0.12</td>
</tr>
<tr>
<td>After adapt</td>
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</tr>
<tr>
<td>(After/before)</td>
<td>2.0</td>
<td>1.3</td>
<td>0.17</td>
</tr>
</tbody>
</table>

The parameters of the best fitting H ratios (see Table 1) are shown for the contrast response
functions of a representative cell measured using four different spatial frequencies. The three
parameters describe the contrast response function at each spatial frequency before and after
contrast adaptation from the peak spatial frequency (0.75 cycles/deg): the ratio (after/before)
expresses the relative effect of adaptation on each pattern. As can be seen, the effect of adaptation
on \( C_{50} \) and \( R_{max} \) diminishes as the distance between the test and adapt frequency increases. It is
worth noting that, for this cell, adaptation not only affected \( C_{50} \) and \( R_{max} \) but also increased the
slopes; for most cells (compare Fig. 7 and Table 3) the slope was relatively unaffected.

Using a protocol similar to that of the first series of experiments (shown in
Fig. 1), we presented a low contrast grating for 30 s which evoked approximately
10% of the cell's maximum response before (pre-adapt) and after (post-adapt) 30 s
of high contrast adaptation. The adaptation frequency was always the centre fre-
cuency presented at a contrast which produced a saturation response, however, the
test frequency used in the pre-adapt and post-adapt intervals was one of the follow-
ing frequencies (chosen from the unadapted spatial frequency tuning curve): (a) the
peak frequency, (b) the frequency half-way down the low frequency side and (c) the
frequency half-way down the high frequency side.

To index the effect of centre frequency adaptation on the test frequencies, we
compared the average response rate which occurred during the last 4 s of the pre-adapt
period with the average response rate which occurred during the first 4 s of the
post-adapt period; we took these two values and expressed them as a ratio (post/pre).
The mean values of this ratio (averaged across a sample of twenty-three cells for the
three test frequencies are shown in Table 5. As can be seen, centre frequency adaptation decreased the post-adapt responses (relative to the pre-adapt responses) for all of the three test frequencies; however, the magnitude of the adaptation effect diminished when the test frequency was higher or lower than the centre frequency.

Part III: the effects of adaptation on the differential contrast response

In the preceding experiments, we have shown that following prolonged steady-state stimulation, most cortical cells adapt and thus decrease their over-all response to an adapting contrast. Further, this effect is due to both a sensitivity shift of the dynamic response range (a shift to the right) as well as an over-all compression of the response range (a shift downward). In this final series of experiments, we wanted to test one hypothesis concerning the possible functional significance of this contrast adaptation. Specifically, we wanted to test whether the differential response to contrast could be enhanced following adaptation.

To provide some indication of the effect of contrast adaptation on the ability of a cortical cell to 'discriminate contrasts', we performed an experiment which has been used to demonstrate the effects of sensitivity shifts in the retina (Werblin, 1974a; Figs. 9 and 10). We modulated the contrast of an optimum grating pattern for a prolonged period of time and recorded the response. The grating was drifted across the receptive field and the contrast alternated every 2 s from high to low to high, etc., over a period of 40 s. This procedure was repeated using pairs of contrasts from different portions of the contrast domain.

One of the more interesting test conditions (in terms of the effect of adaptation on differential sensitivity) occurs when both contrasts are high enough to evoke equivalent undiscriminable responses (e.g. when both contrasts evoke the maximum response range (a shift to the right) as well as an over-all compression of the response range (a shift downward). In this final series of experiments, we wanted to test one hypothesis concerning the possible functional significance of this contrast adaptation. Specifically, we wanted to test whether the differential response to contrast could be enhanced following adaptation.

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Fig. 9. The effect of contrast adaptation on the differential sensitivity of a striate cell representative of those cells which show a strong adaptation effect. In A, the unadapted contrast response function is plotted for the cell. In B, the response during 30 s of high contrast adaptation is plotted; from this, the cell's exponential decay constant was estimated. For C–E, the stimulus consisted of the optimum grating drifted across the receptive field; the contrast of the grating was alternated from high to low every 2 s. Data points, connected by the dashed lines, show the average response rate over each 2-s interval. In A, when the contrast modulation was centred on the linear portion of the unadapted contrast response function, the effect of adaptation was minimal and the magnitude of the differential response modulation was large throughout the 40 s (○, 4%; ●, 2%). In D, adaptation during the course of the experiment reduced the average rate of firing while increasing the magnitude of the differential response modulation (○, 11%; ●, 5.5%). In E, the initial responses to 16 (●) and 32% (○) contrast were large and indistinguishable, however during the course of the experiment, the average firing rate decreased while the differential modulation increased. The smooth decaying exponential curves (see Table 1) were fitted to the maximum and the minimum values of the envelope of the response modulation (for each contrast, the peak response parameter was taken from the measurements shown in A and the decay constant from the measurements shown in B, thus leaving only the plateau parameter free to vary).

saturated response) in the unadapted state. One might expect (if adaptation shifts the curves as described above) that during the course of the 40-s presentation of the alternating contrasts, the over-all rate of firing would decrease (reflecting a vertical compression of the contrast response function) while the percentage modulation around the average rate would increase (reflecting a horizontal sensitivity shift of the contrast response function); that is, before adaptation, the pair of high contrast values should produce equivalent saturated responses with little or no response modulation, whereas after adaptation, the pair of high contrast values should produce a modulation of the remaining response rate.

The results of performing this experiment on a representative cell are shown in
Fig. 9. Following preliminary measurements of the unadapted contrast response function (Fig. 9A) and the general time course of the adaptation to a high contrast grating (Fig. 9B), we then modulated the contrast from 4 to 2%, (2 s up and 2 s down) for 40 s; the dashed lines of Fig. 9C trace the modulating responses during the course of this alternating stimulation. Over the first 2 s, during the 4% interval, the cell produced an average of 39 spikes/s; over the next 2 s, the 2% interval, the cell produced an average of 5 spikes/s, etc. This response differential changed very little during the course of the contrast alternation; very little adaptation was evident and the results are what one would expect from the unadapted contrast response function (the 2–4% contrast range falls along the steepest portion of the unadapted contrast response function).

In the next condition, we modulated between a pair of higher contrasts (5.5 and 11%); the results are shown in Fig. 9D. While the over-all magnitude of the response for this pair of contrasts is larger (in the unadapted state), the response differential is comparatively smaller. During the course of the alternating contrast and resultant adaptation, however, the over-all response rate decreased while the modulation of the response rate increased. This general trend is even more apparent in the final condition where the contrast alternated between 16 and 32%; the results are shown in Fig. 9E. In the unadapted state, both 16 and 32% produced equivalent large amplitude (saturated) responses, however during the course of the alternating contrast protocol, the average response rate decreased while the differential response modulation increased.

This cell was quite susceptible to contrast adaptation (adapt index = 29%), and as can be seen, the over-all effect in terms of the differential contrast response is quite beneficial. For comparative purposes, Fig. 10 shows the same series of experiments performed on a cell which was not as susceptible to contrast adaptation (adapt index = 76%). As expected, the effect of adaptation on the differential contrast response was less pronounced.

A quantitative indication of how contrast adaptation affected the differential response for these two cells is shown in Fig. 11. The smooth curves, representing the time course of the responses over the three pairs of adapting contrasts, have been taken from Figs. 9 and 10 and then superimposed in Fig. 11A and B respectively. From these curves we then computed an index of modulation (max.−min./max.+min.) and compared the value of this index at the beginning and at the end of the alternating contrast experiment.

The modulation index was plotted in Fig. 11C and D for each cell as a function of the logarithmic centre of each pair of contrasts. As can be seen, contrast adaptation can significantly enhance the ability of a cell to differentially signal contrast changes. The effect is particularly evident when the cell shown on the left (A and C) was stimulated with the 16–32% contrast pair; before adaptation (at the beginning of the alternation) there was no response modulation, whereas after adaptation (at the end of the alternation), the cell was capable of modulating some 20% of its average rate of firing. We have performed this experiment on a sample of twenty-seven cells and we find that for those cells which are reasonably susceptible to adaptation, response modulation is enhanced during the course of adaptation to the average level of contrast.
DISCUSSION

General adaptation characteristics

When presented with a high contrast grating pattern for a prolonged period of time, most cortical cells decrease their over-all rate of firing and contrast sensitivity. There is however a great deal of individual variation in terms of the (a) susceptibility to adaptation, (b) rate of decay and (c) rate of recovery. The quantitative measurements from this sample of 144 cells indicate that contrast adaptation is a property common to both simple and complex cells; further, the distributions of the quantitative measures were all very similar in terms of the range of values covered. Nevertheless, the average values of all three indices were reliably different when compared across simple and complex cells. In general, complex cells tended to be slightly more susceptible to adaptation and the decay and recovery occurred more rapidly.

Psychophysical and neurophysiological adaptation

One goal of the present series of neurophysiological experiments was to assess the similarities and differences of cortical cell adaptation and psychophysical adaptation. While the relations between stimulus strength, neural activity, behavioural discrimination and sensation magnitude are certainly not obvious or experimentally
demonstrated, it is nevertheless worth examining the behaviour of neurones under conditions similar to those used in psychophysical experiments and comparing the results of the analogous experiments (cf. Werner & Mountcastle, 1965; De Valois, 1965, 1973; Talbot, Darian-Smith, Kornhuber & Mountcastle, 1968; Barlow & Levick, 1969; Mountcastle, LaMotte & Giancarlo, 1972).

We know from psychophysical studies that prolonged viewing of a grating contrast produces both a decrease in apparent contrast as well as a decrease in contrast sensitivity. Under comparable conditions (prolonged contrast stimulation), cortical cells show both a decrease in their over-all rate of firing as well as a decrease in their contrast sensitivity. It therefore seems appropriate to compare the temporal dynamics and the magnitudes of these parallel phenomena.

Fig. 12 A provides a comparison of the induction process. One pair of curves
(Blakemore & Campbell, 1969) shows the percentage change in human contrast sensitivity (1/threshold contrast), as a function of adapting time, using two different adapting contrasts. Another pair of curves (Blakemore et al. 1973) shows the effect of adapting time on human judgements of apparent contrast for two different test contrasts. The third pair of curves shows the effect of adapting time on the average normalized responses for the total population of simple and complex cells. As can be seen, while not identical, these various estimates of contrast adaptation are remarkably similar both in terms of the over-all rate of change as well as the magnitude of the change.

Fig. 12B provides a comparison of the recovery process. Two of these curves are psychophysical estimates: one plots the recovery of contrast sensitivity following 60 s of high contrast adaptation (Blakemore & Campbell, 1969), while the other plots the recovery of apparent contrast following 30 s of adaptation (Blakemore et al. 1973). The other two curves are neurophysiological estimates (derived from the average response of all cells during the adaptation protocol, both simple and complex cells):
one plots the percentage recovery during the post-adapt period relative to the initial peak value of the pre-adapt period, while the other plots the percentage recovery during the post-adapt period relative to the plateau value of the pre-adapt period. As can be seen, the psychophysical and neurophysiological estimates of the adaptation recovery are quite similar.

Functional considerations: responses to spatial contrast

Adaptation to steady-state stimulation is a general property of sensory systems which can serve to extend the effective stimulus range while also maintaining high differential sensitivity around the prevailing level. It seems reasonable to propose that contrast adaptation in the visual cortex may serve a comparable function (Ohzawa et al. 1982); that is, that adaptation may shift the response range along the contrast axis for maintenance of high differential contrast sensitivity.

Many cortical cells, like other sensory mechanisms, have a limited response range which cannot accommodate the full stimulus intensity range. The slopes of the cortical cell contrast response functions are quite steep for many cells (Albrecht & Hamilton, 1982) and thus the effective differential response range spans only a limited portion (often less than 0·5 log units) of the full range of environmental contrasts (which exceeds 2·0 log units). There are several properties of cortical cells which undoubtedly help signal the full range of contrasts.

One potential solution to this range problem comes from the general adaptation process. For comparison purposes, if we look at the effect of luminance adaptation in the photoreceptors of mudpuppy, we find that the over-all effect in the rods is a vertical compression of the response range whereas the effect in the cones is a horizontal sensitivity shift of the entire dynamic response range (Normann & Werblin, 1974; Werblin, 1974b). In the cat’s cortex, we find that contrast adaptation produces both a deleterious compression and a constructive sensitivity shift. It seems reasonable to suggest that cortical cell contrast adaptation thus reflects both fatigue (a decrease in the over-all maximum rate of firing) as well as a gain control shift of the remaining available response range to the ambient-prevailing level. To the extent that the contrast curves do shift horizontally, high differential contrast sensitivity will be maintained over an extended range.

A second potential solution to the range problem comes from the fact that there is a great deal of variation in the location of the dynamic response range from cell to cell (Albrecht & Hamilton, 1982) and thus the over-all contrast sensitivity (De Valois et al. 1982); this range variation (‘range fractionation’) is independent of peak spatial frequency. Finally, while the slopes of the contrast response functions of some cells are very steep, it is important to point out that the slopes of other cells are such that the response ranges could effectively cover a wide range of absolute contrast levels. These three properties (adaptation, range fractionation, gradual slopes) could all combine in concert to help span the full range of contrasts found in the natural environment while also maintaining high differential sensitivity, high contrast sensitivity, and information concerning the absolute level of contrast.

Contrast adaptation and differential sensitivity

Given that some cortical cells do show contrast adaptation and that such adaptation can potentially extend the effective range of differential sensitivity, it is
somewhat surprising that Barlow et al. (1975), were unable to demonstrate any enhanced behavioural contrast discrimination following contrast adaptation. In one of their psychophysical experiments (quite comparable to the neurophysiological experiment shown in Fig. 9–11) they tracked the differential contrast threshold during the course of high contrast adaptation and found no compensatory advantage. From the neurophysiological experiments reported by Ohzawa et al. (1982), and those reported here, one might have expected that the increment in contrast required to detect contrast flicker, around a high contrast grating, would have become smaller as adaptation proceeded, since some of the cortical cell contrast response functions (in cat, at least) would gradually adapt and thus the response pattern to the differential stimulation would shift from a static-saturated pattern to a dynamic-modulated pattern. Speculations regarding this apparent contradiction (beyond the obvious species differences) are perhaps best left for future investigations. One might only suggest that adaptation is but one of several important factors: when the population of cortical cells is considered as a whole, all of the different methods (discussed above) for spanning the spatial contrast dimension (adaptation, range fractionation, and gradual slopes) could potentially contribute to behavioural contrast discrimination.

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REFERENCES


