Contrast conservation in human vision

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Abstract

Visual experience, which is defined by brief saccadic sampling of complex scenes at high contrast, has typically been studied with static gratings at threshold contrast. To investigate how suprathreshold visual processing is related to threshold vision, we tested the temporal integration of contrast in the presence of large, sudden changes in the stimuli such occur during saccades under natural conditions. We observed completely different effects under threshold and suprathreshold viewing conditions. The threshold contrast of successively presented gratings that were either perpendicularly oriented or of inverted phase showed probability summation, implying no detectable interaction between independent visual detectors. However, at suprathreshold levels we found complete algebraic summation of contrast for stimuli longer than 53 ms. The same results were obtained during sudden changes between random noise patterns and between natural scenes. These results cannot be explained by traditional contrast gain-control mechanisms or the effect of contrast constancy. Rather, at suprathreshold levels, the visual system seems to conserve the contrast information from recently viewed images, perhaps for the efficient assessment of the contrast of the visual scene while the eye saccades from place to place.
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1. Introduction

Visual perception is a process that interprets the spatiotemporal variations of light that fall on fellow retinas, and from this input derives descriptions of the shapes, surface properties, and locations of objects. Much of our understanding of this process comes from experiments with nearly static sinusoidal gratings presented briefly at threshold contrast. The conclusions of these experiments culminated with the widely accepted *channel theory* of early vision (Blakemore & Campbell, 1969; Campbell & Robson, 1968; Graham & Nachmias, 1971), according to which one of the first stages of the human visual cortex that analyzes the retinal output consists of a bank of linear filters localized in spatial frequency and orientation, followed by a non-linear stage (Wilson & Gelb, 1984) and a contrast gain control mechanism (Bonds, 1991; Heeger, 1992; Ohzawa, Sclar, & Freeman, 1982; Wilson & Humanski, 1993).

However, natural vision deals predominately with patterns that are well above threshold contrast (Laughlin, 1983; Tadmor & Tolhurst, 2000) and undergo sudden changes such as those produced by saccadic eye movements (Buswell, 1935; Dragoi, Sharma, Miller, & Sur, 2002; Yarbus, 1967). The characteristics of the perception of contrast, orientation, spatial frequency, or color at suprathreshold contrasts are known to differ from those at threshold (Georgeson & Sullivan, 1975; Mussap, 2001; Olzak & Thomas, 1991; Olzak & Wickens, 1997; Vimal, 2000). A widely held assumption is that the structure inferred from threshold studies provides a scaffolding that will form a basis for understanding suprathreshold vision under natural conditions (Graham, 1989). Indeed, many suprathreshold results can be explained by the contrast gain control mechanism posited by the channel theory (Swanson, Georgeson, & Wilson, 1988), but others require the assumption of new, second-order mechanisms based on the outputs of the channels at the first stage (Olzak & Thomas, 1999).

Here we investigate the apparent contrast of dynamic stimuli at and above threshold. The apparent contrast of

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suprathreshold stimuli has been studied before with static gratings (Georgeson & Sullivan, 1975), or static plaids (Georgeson & Shackleton, 1994). The temporal aspects of suprathreshold contrast perceptions have also been studied with gratings (Georgeson, 1987), and modulated noise stimuli (Schofield & Georgeson, 2000). However, there have been no studies of the perception of suprathreshold stimuli that suddenly changed during presentation, similar to some of the dynamic changes that occur during natural viewing. In our study, we asked three questions. First, how do such abrupt changes in the stimuli, mimicking natural viewing, influence contrast perception? Second, how does the effect of these changes differ under threshold and suprathreshold conditions? Third, can one describe the effects of a switch on contrast perception of suprathreshold stimuli with the standard model of channel theory augmented with a contrast gain control mechanism?

We conducted two sets of experiments (one set well above contrast threshold, the other at detection threshold) on human contrast perception with three different types of stimuli that were changed during their brief presentation. To maximize the effects of stimulus changes, we first used grating stimuli with phase and orientation switches, that according to classical channel theory excite entirely different channels before and after the switch. Second, we used random noise patterns, which, unlike gratings, have a broad band spatial frequency content but lack any natural structure. Finally, we repeated the experiments with natural image stimuli, that not only have a broad band characteristic but also statistical properties to which the visual system might be particularly adapted (Bex & Makous, 2002; Elder & Goldberg, 2002; Field, 1987; Ruderman & Bialek, 1994; Sigman, Cecchi, Gilbert, & Magnasco, 2001; Simoncelli & Olshausen, 2001; van der Schaaf & van Hateren, 1996). We found that for all these stimuli the results were very different at and above threshold. At threshold contrast, the results reflected the operation of independent channels. That is, we found probability summation between the mechanisms assumed to respond independently to grating stimuli that differ in orientation or phase.

Results with the same stimuli at a suprathreshold contrast, however, showed no evidence of the operation of the underlying independent channels above the shortest durations, but showed complete algebraic summation of contrast as though only a single channel, equally sensitive to both stimuli, were excited. Explanation of these high contrast results requires a mechanism that codes and preserves information on contrast, independently of the orientations and phases of the spatial frequency components of an image: a mechanism for *contrast conservation*. We speculate that contrast conservation is well-suited for efficient representation of contrast under natural viewing conditions.

2. General methods

2.1. Apparatus

Stimuli were generated on a Macintosh G3 computer with software adapted from the VideoToolbox routines (Pelli, 1997), and displayed on a gray-scale Nanao Flexscan 6500 monitor at a frame rate of 75 Hz and a mean luminance of 50 cd/m². The luminance of the display was linearized with pseudo-12 bit resolution (Pelli & Zhang, 1991) and calibrated with a Minolta photometer. The display measured 15° horizontally (1152 pixels) and 9° vertically (870 pixels), and was 230 cm from the observer, in a dark room.

2.2. Observers

Five observers participated in all phases of the study. Two, authors JF and PJB, were familiar with the goals of the study; the other three were naïve with respect to the purpose of the study and were paid for their participation. There were no significant differences in the results between informed and naïve subjects in any of the experiments.

2.3. Stimuli

Three types of stimuli were used in the experiments: gratings, natural scenes and noise patterns. Stimuli in all experiments appeared within 2° disks centered 2° left or right of fixation, and the edges of the disks were smoothed with a raised cosine profile subtending 0.25°. All gratings were presented at 16 cpd.

Noise patterns consisted of rectangles of four pixels each (1.9′ by 1.9′), the luminances of which were randomly sampled from a uniform distribution spanning the contrast range of that trial.

Natural images were a random sample of the calibrated natural scenes of van Hateren and van der Schaaf (1998). The central 256 by 256 pixel square region was cropped from each image and the DC component removed at 16-bit resolution. The image was then scaled to span eight bits with the same mean luminance as the display (50 cd/m²) and windowed the same way as the gratings and noise patterns were. The adjustment of the DC level meant that the maximum and minimum luminances (and therefore the Michelson and RMS contrast) could differ slightly across images, but not within images (i.e., following our manipulations of rotation and mirror inversion, as described below). For contrast matching, a new natural image was selected at random on each trial. For contrast thresholds, an image was selected at random on each run because differences in detection thresholds among images prevented the use of a random image each trial.

2.4. Procedure

Two kinds of observations were made in this study: Contrast matches and two-alternative forced-choice contrast thresholds. The observer's task was identical in each case: choose the stimulus with the higher contrast. For the contrast matches, the test stimulus had a fixed 60% Michelson contrast, and an adaptive routine (Watson & Pelli, 1983) searched for the contrast of the matching stimulus that was chosen with 50% probability. The *apparent contrast* of the test stimulus is defined as the Michelson contrast of the matching stimulus. In the threshold observations, the fixed stimulus had 0% contrast, and the adaptive routine searched for the Michelson contrast of the variable stimulus that was chosen with 82% probability. This is defined as the *threshold contrast*. In pilot studies we confirmed that contrast thresholds and contrast matches were invariant of orientation and spatial phase for grating stimuli and were uniform across random noise samples. For natural images, we found that RMS and especially Michelson contrast detection thresholds greatly differed across images (Bex & Makous, 2002), but were not affected by image rotation or mirror reversal. To measure the effect of exposure duration and image changes for contrast thresholds, therefore, we used the same natural image within each run; and for switched stimuli, we switched to randomly rotated and/or mirror reversed forms of the same image. For contrast matching a new random image was selected each trial, but the same image was used in rotated or mirror reversed form for standard and match images, and thus the apparent contrast we esti-

mate is relative to that of the same image at 60% Michelson contrast.

There were four threshold and four apparent contrast experiments: two with gratings, one with noise patterns, and one with natural scenes for each of the threshold and the suprathreshold tests. Stimuli were presented in one of two ways. In *no-switch* conditions, the same stimulus was presented during the entire trial. In *switch* conditions, the stimulus was abruptly changed in the middle of the trial, to mimic some of the dynamic changes that occur under natural viewing conditions. Total duration, as used throughout this paper, refers to the duration of any stimulus, including the summed duration of the first and second components of a *switch* trial. In *half* conditions, the same stimulus was presented during the trial as in the *no-switch* condition, but the duration of the presentation was half as long. These conditions in both threshold and apparent contrast experiments are shown in Fig. 1. In those trials in which the second stimulus differed from the first, the second stimulus was either: (1) a grating that differed in phase by 180° from the grating it followed (i.e., a contrast reversal); (2) a grating that differed in orientation by 90° from the grating it followed; (3) a noise pattern that was completely independent of the random noise pattern it followed; or (4) a natural scene that differed in orientation (by 90°, 180°, or 270°, with or without mirror reflection, in random sequence) from the natural scene it followed.

The total durations of stimuli in the threshold experiments were 26.7, 53.3, or 53.3 ms with a switch in the middle. There were five total durations used in the contrast matching experiment with or without a switch in the
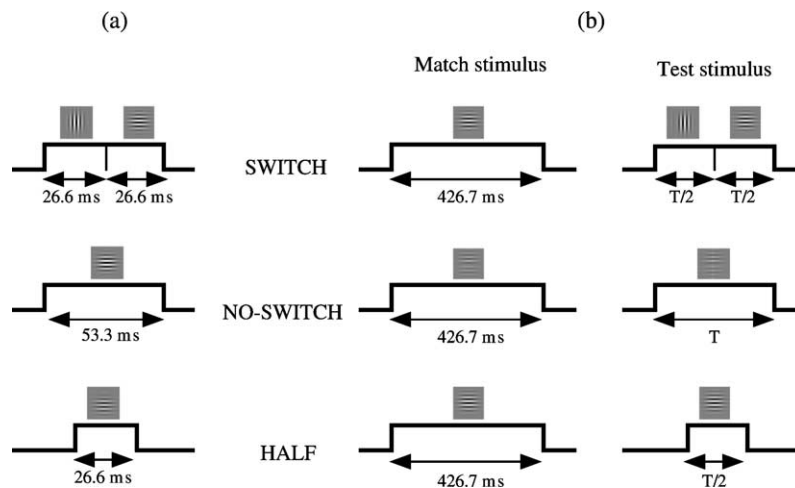

Fig. 1. The two experimental paradigms. In the threshold task (a), the stimulus appeared randomly right or left of fixation in one of three possible conditions: (1) the *switch* condition, in which a switch is made between two different stimuli in the middle of a presentation equal in total duration to that of a *no-switch* stimulus, (2) the *no-switch* condition, in which the same stimulus is presented throughout the presentation and (3) the *half-duration* condition also referred to as *independent channel* condition, identical to the *no-switch* condition except for being half as long. For these threshold experiments, the total duration for *switch* and *no-switch* stimuli as 53.3 ms, and for the *half-duration* stimuli, 26.7 ms. In the supra-threshold apparent contrast task (b), match and test stimuli were presented simultaneously on opposite sides of the fixation point, in random relative positions. The match stimulus was always 426.7 ms long, and the duration of the test stimulus (T) varied randomly among five durations: 26.7, 53.3, 106.7, 213.3 and 426.7 ms. The *switch*, *no-switch*, and *half-duration* conditions for the test stimulus were the same as those for the threshold experiments.

middle, with durations ranging from 26 to 426 ms in equal log steps. This range of durations spans the range of fixation durations in natural scenes, which has a distribution with a mean at 240 ms and 2.5% below 88 ms and above 660 ms (Henderson & Hollingworth, 1998).

Observers were instructed to maintain fixation at the central fixation point during the trial while making judgements about the stimuli. Both experiments were self-paced, in that each trial was initiated by the response to the previous one. In the threshold experiment an audible signal informed the observer about the correctness of the responses. The sequence of experiments was randomized separately for each observer. Each threshold or contrast match was based on 32 trials, and each was repeated four times. In both the matching and the threshold experiments, all statistical tests were based on *t*-tests of five differences between corresponding means of two conditions (e.g. *switch* and *no-switch* matches) for five subjects, using the standard errors of those differences (df = 4), against the null hypothesis that the difference is zero.

3. Results

3.1. Suprathreshold experiments

As the experiments fall naturally into two categories, those with gratings and those with more complex patterns, the results are described here in two corresponding sections. As the *switch* trials entail successive presentation of two stimuli, each for half the total duration, we compared the *switch* trials to *no-switch* trials of (1) the same total duration and (2) the same duration as each of the two component stimuli (i.e., *half-duration* trials), also referred to as *independent channel* condition. In all experiments, the mean of five subjects is presented with the error bars representing the standard errors across observers.

3.1.1. Experiments 1 and 2: apparent contrast of gratings with switched orientation or phase

In the *no-switch* conditions, shown by the open circles in the upper part of Fig. 2, the matching contrast of a grating was low when the duration was short, and grew with increasing duration until it approached an asymptote at the contrast of the test grating, as reported by others (Georgeson, 1987; Kitterle & Corwin, 1979). The growth of apparent contrast, C_a, is described here by an exponential saturation function,

$$C_a = C_{max}(1 - e^{-t/\tau}), \qquad (1)$$

where t is time in milliseconds, C_{max} is the asymptote, and τ is the time constant. C_{max} was set at the matching contrast, 0.6. The least-square fit of τ to the open circles in the upper part of Fig. 2 is 82 and 90 ms for the phase
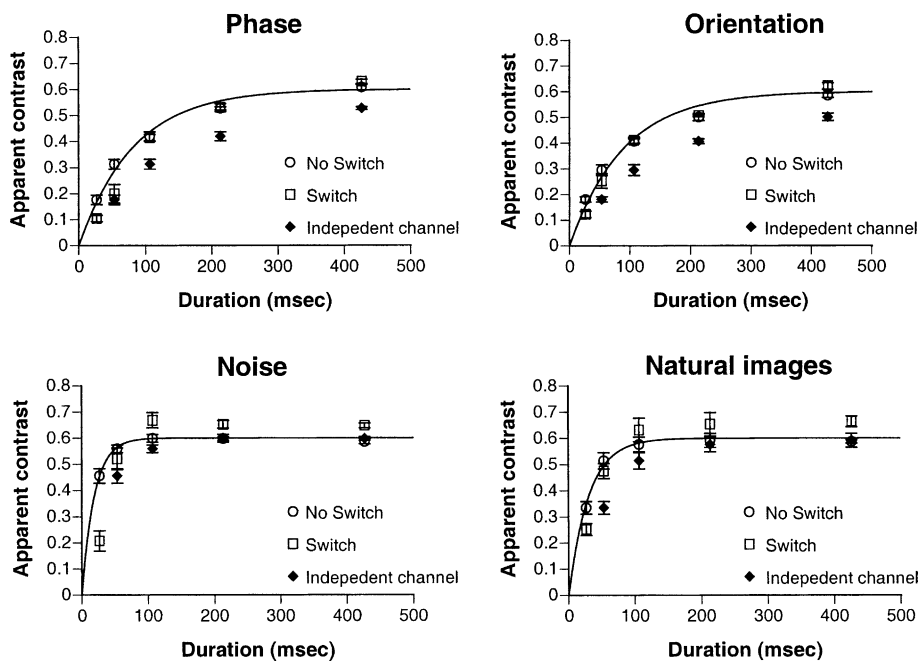

Fig. 2. Contrast matches (apparent contrast) for gratings, noise images, and natural images of varying duration, for *no-switch* (open circles), *switch* (open squares) condition, and *independent channels* (black diamonds). The black symbols, representing data for independent channels, are equivalent to the matching contrasts for the *half-duration* condition, since they show the apparent contrast that either component stimulus in the *switch* condition would have if presented alone; this is the apparent contrast predicted by an independent channel model (see Section 4). The error bars represent ± 1 standard error of the mean across observers. The solid lines are exponential contrast growth functions (Eq. 1) fit by least squares to the *no-switch* data, with the asymptote set at a contrast of 0.6 and the *y*-intercept at 0 contrast. The fitted time constants for the two curves were 82 and 90 ms for phase and orientation switches, and 21 and 31 ms for noise and natural images, respectively.

reversal and orientation switch experiments, respectively.

The results in the *switch* condition (the open squares in Fig. 2), however, were surprisingly similar to those in the *no-switch* condition (open circles). That is, the matching contrast was low when the duration was short, and grew with increasing duration until it approached an asymptote at the contrast of the test grating, and the rate of growth was nearly identical to that in the *no-switch* condition. In the case of a phase shift, any temporal integration of luminance between these opposite-phase gratings would reduce the time-integrated contrast, so that the apparent contrast of the combination must fall below that of either one of the gratings alone; full integration at each point in the stimulus would completely abolish the time-integrated stimulus. The apparent contrast of either one of the gratings is shown by the *independent channel* condition (solid diamonds) in Fig. 2. It is clear from the figure that not only did addition of a grating in opposite-phase to the first grating (open squares) fail to reduce the apparent contrast at any duration compared to the *independent channel* condition (solid diamonds), but it actually increased the apparent contrast when the duration of the stimuli was long (107 ms, $p < 0.01$; 213 ms, $p < 0.05$; 426 ms, $p < 0.01$). These increases were so great that they were not reliably less than the increase produced by addition of an identical grating (open circles) instead of a phase reversed grating (open squares). At 426 ms duration, the apparent contrast when using phase-reversed gratings was slightly but significantly greater ($p < 0.05$) than that when identical gratings were used (i.e., in the *no-switch* condition).

The effects of the 90° shift of orientation were in all respects similar to those of the shift of phase. That is, addition of a perpendicular grating increased apparent contrast reliably over that in the *independent channel* (*half-duration*) trials. This occurred earlier (53 ms) than in case of a phase shift, raising the apparent contrast the same amount as (i.e., not reliably less than, $p > 0.05$) addition of an identical grating. The increase of apparent contrast of the switched gratings at 426 ms was not reliable.

3.1.2. Experiments 3 and 4: apparent contrast of switched random noise patterns and natural scenes

The growth of apparent contrast of random patterns and natural scenes, shown by the open circles in the lower part of Fig. 2, was similar to that of gratings. As with the gratings, the matching contrast was low when the duration was short, and grew with increasing duration until it approached an asymptote at the contrast of the test stimulus. However, the time course of the growth of the apparent contrast of the complex stimuli was faster than those of gratings, with time constants of 21 and 31 ms for the random patterns and natural

scenes, respectively. This rapid growth of contrast limited the number of durations where the *no switch* and *independent channel* measurements differed significantly (and, therefore, could be used to assess whether a stimulus switch has the same effect as no switch) to one duration (53 ms) for noise and to two durations (53 and 106 ms) for natural scenes.

As with the gratings, following a random noise pattern with an uncorrelated noise pattern (*switch*) reliably increased the apparent contrast over the *independent channel* condition at all durations, including the duration (53 ms) where halving the duration (*independent channel*) reduced the apparent contrast reliably. At this duration there was no reliable difference between the *switch* and the *no switch* conditions, similar to the findings with grating switches at longer durations. Unlike with gratings, the switch between random noise patterns actually increased apparent contrast at the three longest durations ($p < 0.05$, 0.01, and 0.001) above that when a single pattern was presented for the same amount of time (*no switch*).

The pattern of results with natural scenes was similar to that with the noise patterns: a natural image followed by its randomly rotated and mirror-reflected version (*switch*) reliably increased the apparent contrast over the *independent channel* condition at all durations, including the two durations (53 and 106 ms) where halving the duration (*independent channel*) reduced the apparent contrast reliably. At those durations there was no reliable difference between the *switch* and the *no switch* conditions. Although the apparent contrast in the *switch* condition tended to be higher than that in the *no-switch* condition, the 4–5% difference was reliable at only the longest duration ($p < 0.05$).

3.2. Threshold experiments

As the results of these matching experiments differ from what one might expect on the basis of classical findings in detection experiments (see Section 4), we conducted four experiments to determine whether we could replicate those classical findings under our conditions. Although the detection threshold of gratings has been investigated under a wide variety of conditions, we are not aware of previous studies in which the grating changed during its presentation.

Fig. 3 shows the results of all four threshold experiments. Halving the duration of the grating stimulus reliably raised its threshold in all four experiments ($p < 0.01$ for grating phase and noise, $p < 0.05$ for grating orientation and natural scenes). Switching the stimuli in mid-presentation also raised its threshold reliably in three of the four experiments ($p < 0.05$ for the two grating switches, and $p < 0.01$ for the noise switch).

The difference between *switch* and *half duration* thresholds was quantitatively consistent with probability
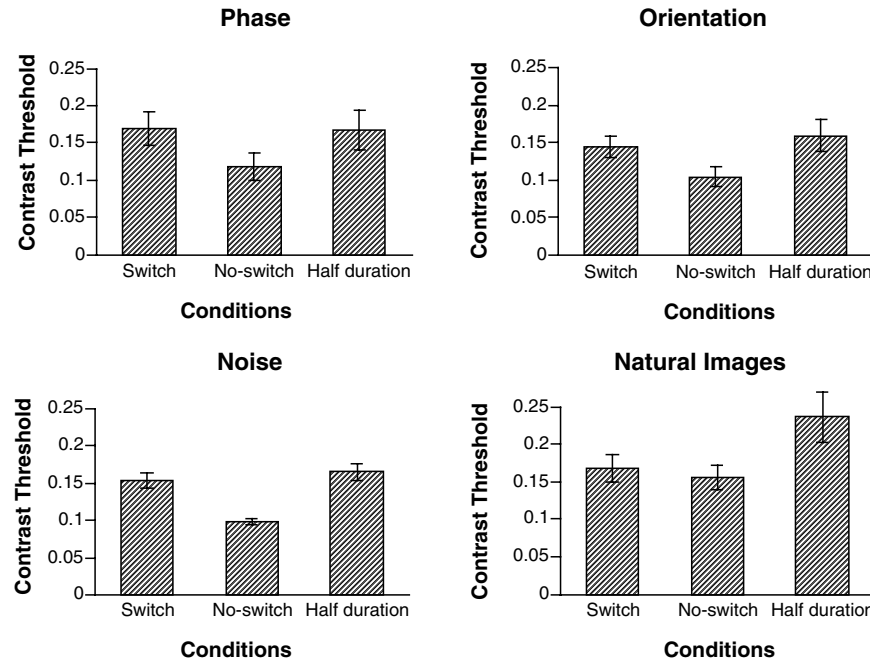
Fig. 3. Threshold contrast results for a *switch*, *no-switch*, and *half duration* conditions. Error bars represent standard errors.

summation between two independent components. Here probability summation was computed according to the conventional equation: $p_\sigma = 1 - (1 - p_\alpha)(1 - p_\beta)$, with p_σ the probability that a stimulus is detected during a *switch* presentation, and $p_\alpha = p_\beta$, the individual probabilities that specifically the first or the second stimulus is detected (Pirenne, 1943; Tyler & Chen, 2000). The probabilities were determined from the half duration thresholds as $p_\sigma = 0.9375$, since the probability correct at threshold in our experiments was defined as 0.75. From the psychometric functions fit to the QUEST data, the threshold contrast corresponding to p_σ was estimated for each subject and each of the three experiments (phase, orientation, and noise switch) in which switches caused reliable increases of threshold. The difference between each of the estimated thresholds and the thresholds observed in the *switch* condition was evaluated by a *t*-test. Only two of the 15 differences were statistically significant, but even these two were in the opposite direction from full summation. Thus these results are in line with the classical findings on thresholds.

The similarity of thresholds for stimuli that were identical between the experiments with gratings, i.e., for the *no-switch* condition (0.11 and 0.10) and for the *half duration* condition (0.17 and 0.16), is satisfactory. The higher thresholds for natural images in the *no-switch* and *half-duration* conditions are attributable to their high kurtosis and low RMS contrast compared to noise and grating images (Field, 1994).

Switching to a new natural scene in mid-presentation yielded thresholds comparable to those of switching in the other three experiments, but the increase over the

thresholds in the *no-switch* condition was not reliable ($p < 0.35$). To understand why the switch between natural scenes failed to produce a reliable increase, in a separate experiment we measured this effect while varying the stimulus duration from 26.7 to 426.7 ms in equal log steps. The results for our five observers are represented in Fig. 4 by diamonds (*no-switch*), and circles (*switch*). The thresholds approach a common asymptote at about 10% contrast, and at 53 ms, the duration used for the data in Fig. 3, both curves are too close to this asymptote to differ much from one another. However, the difference at 26.7 ms is reliable ($p < 0.05$). As the difference here depends on a single point, we sought to push the observations to shorter durations, but apparatus limitations prevented this for the four observers tested in Rochester. A 160 Hz system available at UCL permitted us to test one observer (PB) and a new naïve observer with a set of durations from 12.5 to 200 ms. These thresholds are represented in Fig. 4 by the triangles (*no-switch*) and squares (*switch*). In this case, the difference at 25 ms is comparable to that in the previous experiment, but the smaller number of observers and the variability at 25 ms prevents this difference from reaching statistical significance; however, the difference at 12.5 ms is reliable ($p < 0.05$).

These data in Fig. 4 indicate that, for natural images, both the *switch* and *no-switch* curves are too close to their asymptotes at 53 ms to allow a reliable difference between them, but there is a reliable difference at shorter durations. Therefore, we suggest that switching between natural scenes has the same effect on detection as switching between gratings and between noise patterns,
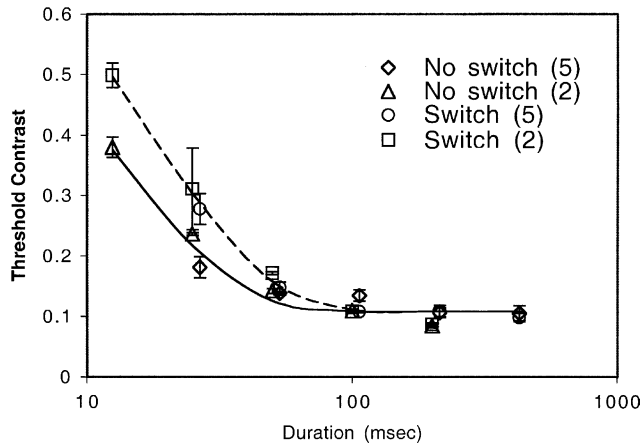
Fig. 4. Contrast threshold for natural scenes of varying duration under *switch* and *no-switch* conditions. Data at the five longer durations were collected from five observers with a 75 Hz system and at the two shorter ones from two observers with a 160 Hz system, so indicated within the caption brackets. The curves are exponential decay functions, fit to all the data, with $\sqrt{2.5}$ greater weight for the data based on five observers, and with the two curves constrained to approach a common asymptote. The time constants are 18.3 and 14.0 ms for the *no-switch* and *switch* data, respectively; and the *y*-intercepts, contrasts of 0.66 and 0.77, respectively.

and that the failure to observe a significant difference between the natural scene thresholds in Fig. 3 is because the durations were too long for these stimuli.

4. Discussion

4.1. Threshold versus suprathreshold results

In eight experiments, we found that changing the stimulus suddenly during presentation has different effects on contrast perception depending on whether the stimulus is presented at threshold or at suprathreshold contrast: at threshold, contrast was not integrated across changes, except that attributable to probability summation between independent channels; whereas at suprathreshold contrast, except at the shortest durations, the changes failed to prevent full integration and sometimes raised apparent contrast above the level of full integration.

The matching results show that beyond the 53 ms duration there was not a single case when a switch of a stimulus attribute reduced the apparent contrast of the stimulus; that is, the apparent contrasts after a *switch* were at least as great as they were on those trials in which no switch was made. This is not due to a ceiling effect or a lack of statistical power. The ceiling effect can be ruled out because the results expected if there were no integration before and after the switch (the black diamonds in Fig. 2) lie uniformly 25–33% below the *no-switch* results (open circles in Fig. 2), and so there was an

ample range for detecting even partially reduced apparent contrast. The failure to observe such a reduction of apparent contrast is not because the reductions were too small to be statistically reliable, for in a number of cases the effect of the switch was in the opposite direction, i.e., an increase of apparent contrast instead of a reduction was reliably detected.

4.2. Local temporal integration

It is well established that the visual system time-integrates the light falling on any given retinal locus over brief intervals, and this integration is manifest both at threshold, in measures of sensitivity (Gorea & Tyler, 1986; Watson, 1986), and above threshold, in measures of brightness and apparent contrast (Boynton, 1961; Georgeson, 1987; Kitterle & Corwin, 1979; White & Rinalducci, 1981), perhaps showing a transient maximum under some conditions (the *Broca–Sulzer effect*).

4.2.1. Gratings

Our observations on the effects of varying the duration of an unchanging grating are entirely consistent with previous findings on temporal integration by the visual system. The threshold-duration curves in Fig. 4 correspond satisfactorily to those reported previously (see, for example, Gorea & Tyler, 1986, Figs. 1 and 7). The growth of the contrast matches likewise are consistent with those reported in earlier studies (Bex & Makous, 1996; Georgeson, 1987; Kitterle & Corwin, 1979). The effects on thresholds caused by switching between gratings also are consistent with what one would expect on the basis of previous findings: probability summation between independent detectors.

However, the observations with switched suprathreshold gratings do conflict with the implications of earlier work on temporal integration at threshold. The time integrated contrast of a phase-switched grating is zero; any tendency to integrate these opposite-phase gratings to determine apparent contrast, as by convolution of the stimulus with the impulse response, must reduce the apparent contrast below the value it would have if no switch occurred. Similarly, integration of two orientation-switched gratings reduces the rms contrast below that of an unswitched grating by a factor of $1/\sqrt{2}$. As rms contrast is highly correlated with apparent contrast (Moulden, Kingdom, & Gatley, 1990), the apparent contrast of the switched gratings should also be reduced. Yet, no decreases of apparent contrast such as are required by temporal integration of switched gratings were observed above 53 ms duration.

As the gratings we tested were all 16 c/deg, we cannot generalize these results to all gratings. The impulse response of gratings at threshold is monophasic above 7 c/deg and biphasic at lower spatial frequencies (Watson & Nachmias, 1977); thus under specific conditions,

a switch of phase can produce a summation effect with gratings of low spatial frequencies. If the same holds true at the suprathreshold levels of our matches, temporal integration may be better for low frequency gratings under specific conditions. Since the rate at which the apparent contrast of low spatial frequency gratings grows is faster than that of high frequency gratings (Georgeson, 1987; Kitterle & Corwin, 1979), a direct test of this issue within our paradigm was not possible. However, even under conditions where the impulse response is biphasic, it cannot produce the effects of the switch observed in our experiments, for any selective effect of the impulse response on switched stimulus configurations would be highly specific to the particular timing of the switch and would not produce the same results over the range of durations where it was observed here.

4.2.2. Non-grating stimuli

Although we know of no previous literature on the contrast growth of random noise patterns and natural images, the arguments applied to gratings apply as well to these stimuli; nothing about their thresholds or the growth of contrast of unswitched images departs from expectations based on grating stimuli. Their faster growth in apparent contrast is probably a consequence of the heavy representation of low spatial frequencies in these stimuli (Field, 1987).

As with the gratings, no decreases of apparent contrast such as are required by temporal integration of switched stimuli were observed beyond the shortest durations. In fact, at longer durations, apparent contrast had a slight tendency to be higher in the *switch* conditions than in the *no switch* conditions, a phenomenon for which we have no good explanation. However, the fact that these overshoots were small and that they occurred at durations where apparent contrast has already saturated, leads us to speculate that they might be due to some process unrelated to those that govern contrast integration, such as attention.

4.3. Integration by channels

According to the almost universally accepted model, after visual signals pass through mechanisms that process local spatial interaction, beginning in the retina and continuing through the first stage of cortical processing, they then pass through parallel channels that are selectively sensitive to specific spatial frequencies and orientations over local regions of the retinal image (Graham, 1989). Both visual appearance at high contrast and thresholds are assumed to depend on the states of these channels. Moreover, the excitation of such channels, and of the cortical cells assumed to represent their physiological basis (Hubel & Wiesel, 1959, 1968), is independent of phase, at least at detection threshold

(Graham & Nachmias, 1971). This could explain the continued growth of apparent contrast in spite of the phase shifts that confound explanation on the basis of local integration. However, closer examination shows that the growth of apparent contrast in response to switched stimuli cannot be explained on the basis of temporal integration within these channels.

According to this channel model, as the duration of the first stimulus increases, excitation builds up in a set of channels selectively sensitive to that stimulus (dashed curve in Fig. 5), and if the switch is to a stimulus to which those channels are insensitive, their excitation tends to decay after the switch, while excitation begins to build up in a different set of channels (solid curve in Fig. 5) that are sensitive to the new stimulus. The dotted curve shows the time course of excitation of the first channel if the switch does not occur (it also happens to be identical to the sum of the other two curves). Under the conditions in which a switch occurs, all the channels have to be less excited than the first set of channels would have been if no switch had occurred (compare the dashed and solid curves with the dotted curve in Fig. 5). If apparent contrast depends on the most excited channel or set of channels, following the assumption of independent channels, then it cannot be as high after the switch as it is when no switch occurs.

The matches following the switches that would be expected on the basis of the most highly excited independent channel, as illustrated in Fig. 5, are shown with the data in Fig. 2 (solid diamond symbols). They are simply the *no-switch* data, shifted to the right on the *x*-axis by a factor of two, the apparent contrast the *switch* trials would have had at the end of the first stimulus. In 16 out of 16 cases, the matches are higher than predicted by independent channels; hence, this deviation is robust.
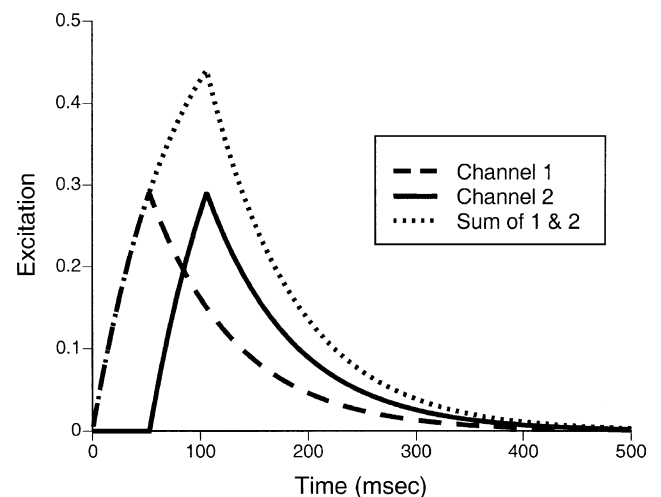

Fig. 5. Schematic representation of the excitation of oriented contrast sensitive channels by stimuli in the *switch* condition. The time delay and the time constants of the curves match the conditions of the switched orientation results at the 106.7 ms duration.

In fact, for most of these data, the apparent contrasts following the switch were indistinguishable from those in which no switch had been made (open squares versus open circles in Fig. 2), as if the switch of the pattern had no effect at all on the subjects' perception of suprathreshold contrast. These results show that whatever mechanism determines apparent contrast sums contrast signals across stimuli that have highly different Fourier spectra, unlike the conventional channels typically used to model psychophysical data. In contrast, the data in Fig. 3 show that under conditions where the contrast matching data show integration across switched stimuli, the threshold experiments fail to detect any such integration, but instead yield results consistent with probability summation between independent detectors (channels).

Hence, the evidence from these experiments supports the position that activity within selective channels forms the basis of contrast detection thresholds, but contradicts the assumption that the activity of individual channels, without additional mechanisms, forms the basis of apparent contrast at suprathreshold levels.

4.4. Can contrast constancy provide an explanation?

Previous work has shown that apparent contrast is independent of the selective attenuation of retinal contrast at different spatial frequencies that is caused by the optics of the eye, the phenomenon of *contrast constancy* (Georgeson & Sullivan, 1975; Kulikowski, 1976). Although at first sight, an explanation of our results may appear to lie in the mechanisms that produce contrast constancy, a closer look reveals that our results are qualitatively different. A widely held explanation for contrast constancy (Georgeson & Sullivan, 1975; Swanson, Wilson, & Giese, 1984), a contrast gain-control mechanism that pools excitation from stimuli differing in such properties as orientation (Heeger, 1992; Wilson & Humanski, 1993), is inconsistent with the present results. According to this contrast gain-control model, a grating stimulus of one orientation turns *down* the gain of channels sensitive to any other orientation, and so presenting the first stimulus in the *switch* condition would tend to *decrease* the overall response to the stimulus presented after the shift instead of *increasing* it, as we have observed. Other explanations of contrast constancy, such as those based on non-linear contrast responses (Brady & Field, 1995; Kulikowski, 1976) or on temporal filter properties that may be applied to stimuli of brief duration (Georgeson, 1987), fail for the same reasons that integration by channels fails: even if there is some tendency towards contrast constancy in the first channel's response, contrast growth has to start again following a switch to a newly responsive channel. So contrast constancy provides no insight into the present phenomenon.

4.5. A new concept: contrast conservation

So far, explanations of our data on the temporal growth of apparent contrast based on local light integration, integration within orientation-specific channels, and contrast constancy have been rejected. The mechanism that accounts for our results must serve as something akin to a contrast reservoir that conserves a signal representing contrast while retinal stimulation suddenly changes, as it does, for instance, during a saccade. One could say that the function of such a mechanism is *contrast conservation*. There are several mechanisms that could potentially achieve this effect:

(1) What is required is a mechanism that codes the contrast of stimuli, independent of the orientation and phase of grating stimuli or those of the components of complex stimuli—perhaps also independent of their spatial frequency, although we have not been able to test that. Schematically, such a mechanism might be parallel to the channels that are more selective along those dimensions. Neurons with such properties, responding to the level of stimulus contrast without exhibiting orientation selectivity, are well established in the neurophysiological literature (DeValois, Albrecht, & Thorell, 1982; Ringach, Shapley, & Hawken, 2002; Schiller, Finlay, & Volman, 1976), but are relatively unknown as components of psychophysical theory. Our results suggest a possible psychophysical role for such neurophysiological entities.

(2) A second possibility, not mutually exclusive with the first, is a mechanism that sums the excitation of channels selective for different properties. This possibility differs from the preceding one only in its schematic position, lying in series with the more selective channels instead of parallel. Such summation mechanisms across orientation and spatial frequency channels, although not in the context of temporal summation, have been proposed and modeled previously by a number of studies (Georgeson & Shackleton, 1994; Olzak & Thomas, 1999; Tiippana & Nasanen, 1999).

(3) Recently Dragoi and his colleagues (Dragoi, Sharma, & Sur, 2000) have reported that while presentation of an adapting grating diminishes sensitivity to that specific stimulus, responsiveness to stimuli with different orientations simultaneously increases. This work establishes the existence of a mechanism that, in principle, might explain our results through adaptation, even though there are differences between our study and theirs. That is, while the visual system is losing sensitivity to the first stimulus in a trial entailing a switch of orientation, it is simultaneously increasing its sensitivity to the orientation of the second stimulus. This increased sensitivity to

the new stimulus would tend to compensate for the loss of sensitivity associated with the switch to a new set of neurons (i.e., a new channel). However, the question is open whether the phenomenon they observed after 2 s of adaptation would occur after the 13–213 ms duration of the first stimulus in our switch experiments. Also, there is at present no evidence of an analogous phenomenon reporting a change in contrast sensitivity at a suprathreshold level.

4.6. Significance

What would be the functional significance of the contrast conservation we propose during normal visual experience? The distribution of human fixation durations (Henderson & Hollingworth, 1998, Fig. 2) shows that, under natural visual conditions, less than 0.1% of human fixations are shorter than 53.3 ms. Thus our results show that a switch within the ecologically relevant range of fixation times does not noticeably decrease apparent contrast. Preserving contrast perception from disruption by changes in other stimulus attributes results in a more stable and more nearly accurate assessment of the contrasts in a changing natural scene. For example, a phase-reversed grating constitutes a stimulus similar to a moving object, and for objects to lose apparent contrast when they move is non-veridical. Insofar as the contrasts of successive patterns falling on a given retinal location are similar, the visual system benefits from the conservation of information on past contrasts; this allows estimates of contrast to approach from the level of preceding patterns instead of starting each estimate anew from zero with each new pattern.

Such conservation of internal states that correspond to relatively stable states of the environment is well established for sensitivity regulating mechanisms, such as those that govern light and dark adaptation (Walraven, Enroth-Cugell, Hood, MacLeod, & Schnapf, 1990) and contrast gain control (Wilson & Humanski, 1993). This is accomplished in each case by low-pass filtering of the output of a particular set of neurons that one can call a mechanism. In the case of light adaptation, the mechanism is localized in the retina; in the case of contrast gain control, the mechanism consists of cortical simple cells selectively tuned to localized stimuli of specific orientation, spatial frequency, and phase. The present results show that such filtering extends to the output of a mechanism whose excitation is independent of the orientation and phase of gratings and independent, as well, of the properties that distinguish individual natural scenes and random patterns, except for contrast.

Evidence for the separation of contrast processing from the processing other spatial attributes of visual stimuli is not scarce. Judgments of orientation (Regan & Beverly, 1985), speed (McKee, Silverman, & Nakayama, 1986), and spatial and temporal frequencies (Bowne, 1990) are nearly independent of contrast, and some authors have argued that such independence requires that contrast be processed separately from these properties (Bowne, 1990; Klein, Stromeyer, & Ganz, 1974). Such separation of the encoding of contrast from that of other stimulus properties has been proposed on the basis of discrimination efficiency (Geisler & Albrecht, 1995). In particular, contrast gain control increases the information in neurons that is necessary to discriminate orientations or spatial frequencies, at the cost of lost information on contrast itself. Good discrimination between contrasts requires a separate pool of neurons that are uniquely sensitive to the level of contrast, but the cost to such neurons is an inability to discriminate well among different patterns. Our suprathreshold findings, that veridical contrast judgments are independent of switches during temporal summation, supports such a dissociation; and our results with threshold stimuli, which may be too weak or their effects too brief to activate the mechanisms responsible for summation of contrasts, show that threshold experiments are not subject to this dissociation.

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