Evidence against saturation of contrast adaptation in the human visual system

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In many experiments on visual pattern perception, it has been assumed that the effects of adaptation to contrast saturate within a few minutes. However, we show here that such saturation does not necessarily occur. Instead, both the buildup and recovery of the threshold elevation aftereffect fit closely a power function.

Following the work of Blakemore and Campbell (1969), it has been widely accepted that adaptation of the human visual system to high-contrast stimuli saturates after about 1 min. In numerous studies, residual visual capacity after adaptation has been tested during brief intervals that were separated by intervals of reexposure to the adapting stimulus; the latter were assumed to resaturate or "top up" the mechanism of adaptation. Wide inferences have been made from experiments like these as to the properties of channels carrying information about the orientation, spatial frequency, and stereoscopic depth of visual stimuli, and parallels have been drawn with the properties of cells in the visual cortex (Anstis, 1975; Blakemore & Campbell, 1969; Braddick, Campbell, & Atkinson, 1978; De Valois & De Valois, 1980; Georgeson, 1979; Movshon & Lennie, 1979).

However, we noticed that the effects of adaptation did not always stabilize in experiments of this type. Two examples are shown in Figure 1. The stimulus was a vertical sinusoidal grating generated electronically on an oscilloscope screen. Figure 1 shows how threshold was elevated after 50 sec (upper) or 3.5 min (lower) of continuous adaptation (striped horizontal bars). The threshold was tested within 5 sec of the end of adaptation, and then a further 5 sec of adaptation was given. Alternate periods of 5-sec testing and 5-sec readaptation continued for about 10 min. The threshold during this period was sometimes stable but often drifted. In these two experiments and in each of four similar experiments using flickering or stationary patterns, there was at first a drop in threshold (probably due to overshoot in the initial settings) and then a significant upward drift in threshold, which continued throughout the test-readapt period (which was 24 min in one experiment). When the readaptation periods were discontinued (arrows in Figure 1), recovery was initially fast, but after about 30 sec it continued much more slowly.

We therefore undertook a reinvestigation of the time course of the buildup of threshold elevation during adaptation and the recovery of threshold after adaptation.

METHOD

The following procedure was adopted in order to minimize potential artifacts due to sudden changes in contrast or adaptation to just suprathreshold stimuli (Rose & Lowe, 1982). In each experiment, adaptation was for a single period only, and threshold was tested briefly at intervals during recovery, with the subject

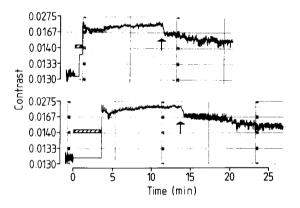


Figure 1. Contrast thresholds before (at left) a period of continuous adaptation (striped horizontal bars), then during 5-sec test periods interspersed with 5-sec periods of readaptation, and finally after adaptation ceased (at arrows). The stimulus had a mean luminance of 60 cd m⁻² and a spatial frequency of 0.83 cycles/ deg, and was phase-reversed sinusoidally at 15 Hz (Rose, 1978, 1980). Subject D.R. viewed the 5 deg wide \times 4 deg high display binocularly from a distance of 1.4 m. He adjusted stimulus contrast with a potentiometer until the flicker on the screen was at the threshold of visibility. The instantaneous contrast setting was monitored continuously on a pen recorder (Blakemore & Campbell, 1969). The subject oscillated the contrast slightly above and below his threshold, except during periods of adaptation, which therefore show as straight lines on the pen recorder tracings. The arrows mark the ends of the last exposure of the adapting grating (Michelson contrast 0.4) in each experiment. (Each experiment was performed on a different day.) In these experiments, the final recovery phase was monotonic, although this was not always the case (Rose & Lowe, 1982).

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watching a blank screen (of the same mean luminance as the grating) in between these tests. Adaptation periods ranged between 1 and 20 min, and recovery was followed until baseline was reached. During the test periods, contrast was adjusted with a 1-dB stepping attenuator, and at least five threshold settings were made in rapid succession for each test (which took less than 60 sec); these settings were later averaged. Because the threshold is changing very rapidly immediately after the end of adaptation (Figure 1), the first test did not begin until 60 sec after the end of adaptation. Subsequent tests began 5 min after the end of adaptation and at 5-min intervals thereafter. All the data were averaged across three repetitions of each experiment, and experiments were performed in pseudorandom order with at least 1 h between each experiment. The stimulus was a stationary grating of 8.3 cycles/deg and mean luminance 40 cd m⁻². Adapting contrast was 0.6, and the subjects moved their eyes over the grating during adaptation to prevent afterimage formation. Complete results were obtained with three subjects: the two authors and N.M., who was naive as to the purposes of the experiments. Subjects R.E. and N.M. set thresholds by the ascending method of limits; D.R. used the method of adjustment. All had corrected-to-normal vision. Standard errors of settings were less than 0.06 log unit.

RESULTS

The threshold elevation found on the first test after adaptation rose progressively as adaptation time lengthened (Figure 2, left). The effect did not level off after 60 sec. In fact, no evidence for saturation was found. For each subject a higher correlation between threshold elevation and adaptation time was found when the data were plotted on doublelogarithmic axes (mean value of product-moment correlation coefficient r = 0.989) than when the plot was on semilogarithmic or linear axes (Friedman p = 0.017). The buildup of threshold elevation thus approximates closely to a power function of time. The exponent, or slope, of the function averaged 0.465 (SD 0.042) for the three observers.

Recovery to baseline took longer as adaptation time was increased—about 90 min after 20 min adaptation (Figure 2, right). The time course of recovery was closer to a straight line on double-logarithmic

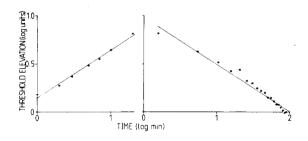


Figure 2. Buildup and decline of effect of single periods of adaptation; Subject R.E., double-logarithmic axes. Left panel: Thresholds 1-2 min after adaptation for the period shown on the abscissa. Right panel: Recovery of threshold over 90 min after 20 min of adaptation; points are plotted at the midpoint in time of collection, for example, 1.5 min for the first point. Thresholds are expressed relative to the threshold before adaptation. Data shown are the averages across three repetitions of each experiment. The lines plotted are least-squares fits.

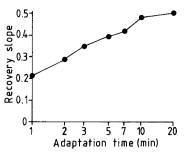


Figure 3. Values of slope of recovery phase, averaged across Subjects R.E., D.R., and N.M. The number of points per plot varied from 3 (after 1-min adaptation) to 19 (20-min adaptation). All the slopes are negative, but the minus signs have been omitted here.

coordinates than on semilogarithmic or linear axes (mean value of r on double-logarithmic axes, over all experiments, was -0.969). The slope of the power function changed monotonically with adaptation time from -0.214 after 1 min adaptation to -0.509after 20 min adaptation (Figure 3).

In control experiments, the threshold was found to remain constant to within 1 dB if the above test procedures were followed without any prior adaptation period.

Finally we wished to establish the generality of the results we had obtained from the three experienced observers. Accordingly, we studied eight naive subjects who had never taken part in psychophysical experiments before. Two adaptation times were used-3 and 10 min—and full recovery to baseline was followed in the 10-min condition. The subjects were counterbalanced for order of conditions, and other experimental details were as for the three main observers. There was no significant difference in the rates of buildup or recovery between the two groups. plotted on any combination of linear and logarithmic axes (t tests). For example, on double-logarithmic coordinates, the rate of buildup for the eight naive observers was 0.348 (SD 0.225) and the rate of recovery after 10 min adaptation was -0.408 (SD 0.134; mean r = -0.968), which is similar to the corresponding value of -0.488 for the experienced observers (Figure 3).

DISCUSSION

The buildup and recovery of the effects of adaptation obviously have time courses much greater than those reported originally (Blakemore & Campbell, 1969). A few other studies have noted that this was the case (Blakemore, Muncey, & Ridley, 1973; Blakemore, Nachmias, & Sutton, 1970; Bodinger, 1978; Heggelund & Hohmann, 1976; Mecacci & Spinelli, 1976), but none of them attempted mathematical descriptions of both buildup and recovery. Our analysis has shown that power functions fit all the data well. A similar conclusion has also been reached from a study with different experimental procedures and adaptation times ranging from 5 sec to 6 min (Rose & Lowe, 1982; in these experiments, the threshold was tracked continuously from within a few seconds after the end of adaptation, as in the experiment of Text-figure 2 of Blakemore & Campbell, 1969).

The long time course of contrast adaptation is in line with recent suggestions that simple and contingent aftereffects do not differ as radically as was previously supposed in that their time courses can be similar (Favreau, 1979; Rose & Lowe, 1982). However, quantitative modeling of the mechanisms that determine the time courses of these two types of aftereffect is not easy, because high-contrast stimuli adapt many "channels," to various relative extents. The sensitivity of any channel at a given time after a change of input intensity is a complex function of the gains and time constants of all the affected channels and of the gain functions, latencies, and summation mechanism of the interactions that occur between channels. Each of these factors remains to be quantified in isolation.

We do not wish to claim that all experiments that have assumed that saturation occurs should now be reevaluated. Under some circumstances, the testreadapt paradigm might lead to stable levels of visual capacity: the effect of readaptation could, in principle, balance exactly the amount of recovery that occurs during testing. Indeed, a few workers have reported qualitatively that stable levels of performance can be achieved under this paradigm (Anderson, Mitchell, & Timney, 1980; Blakemore & Campbell, 1969; Blakemore, Muncey, & Ridley, 1973; Blakemore, Nachmias, & Sutton, 1970). We suggest, in the light of our results, that the degree of variability observed in future experiments of this type should be made quantitatively explicit.

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