Dynamic coding of temporal luminance variation

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The range of variation in environmental stimuli is much larger than the visual system can represent. It is therefore sensible for the system to adjust its responses to the momentary input statistics of the environment, such as when our pupils contract to limit the light entering the eye. Previous evidence indicates that the visual system increasingly centers responses on the mean of the visual input and scales responses to its variation during adaptation. To what degree does adaptation to a stimulus varying in luminance over time result in such adjustment of responses? The first two experiments were designed to test whether sensitivity to changes in the amplitude and the mean of a 9.6° central patch varying sinusoidally in luminance at 0.6 Hz would increase or decrease with adaptation. This was also tested for a dynamic peripheral stimulus (random patches rotating on the screen) to test to what extent the effects uncovered in the first two experiments reflect retinotopic mechanisms. Sensitivity to changes in mean and amplitude of the temporal luminance variation increased sharply the longer the adaptation to the variation, both for the large patch and the peripheral patches. Adaptation to luminance variation leads to increased sensitivity to temporal luminance variation for both central and peripheral presentation, the latter result ruling retinotopic mechanisms out as sole explanations for the adaptation effects.   © 2012 Optical Society of America

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1. INTRODUCTION

The human visual system faces an essentially insurmountable problem in accurately representing each nuance of the visual world at any given time [1–3]. The system must prioritize. Such prioritization is seen, for example, during selective attending to particular features or objects [4–7], but there are other possible ways of efficient information coding that the system can utilize.

One such mechanism is efficient coding of input statistics such as during adaptation to ambient luminance levels. At low levels of luminance, an increase in luminance is easier to detect than an increase of the same absolute magnitude under higher luminance levels (the well-known scaling of the just noticeable difference, sometimes called Weber's law [8]). Such coding is sensible because the system adjusts its responses to the mean and range of the external stimulation.

This raises the question of whether other types of adaptation may result in efficient coding. Evidence from some well-known paradigms does indeed show how the visual system changes its response properties following prolonged viewing of a particular stimulus. The motion and tilt aftereffects are good examples of this [9]. Accordingly, strong benefits of adaptation to motion upon speed discrimination have been observed [10–12], driven by adaptation to temporal modulation of luminance rather than motion *per se* since the direction of motion was not critical [13]. Such benefits from adaptation have also been found for discrimination of small changes in orientation [14,15] and even for the perception of faces [16]. These findings indicate that the visual system changes its responses depending on the statistical properties of the environment [17,18]. Various aftereffects in vision appear therefore to be no mere curiosities. They reflect changes in processing that serve the purpose of accurately representing the environment.

Helson [19,20] was among the first to suggest that adaptation played a vital functional role in vision. Helson argued that, for a given discrimination task, there is a threshold that then varies depending upon a flexible anchor determined by the input to the visual system over a certain temporal interval. This is consistent with the finding that discrimination thresholds for luminance varied strongly as a function of the luminance level observers were adapted to [21]. An influential framework for such adaptation principles, mainly applied in the literature on visual psychophysics, was proposed by Clifford *et al.* [22]. According to their model, increased viewing of a particular stimulus pattern will have two simultaneous effects: adjustment to the mean of the stimulation (called centering) and to its variation (scaling). This framework has mostly fared well in accounting for various effects of adaptation upon visual function [23].

A. Adaptation to Variation in Luminance

The aim with the experiments described here was to measure the effects of adaptation to temporal variation in luminance upon discrimination of changes in the amplitude (experiment 1A) and mean (experiment 1B) of the variation. If adaptation serves a functional role, sensitivity to variation in luminance should increase with longer viewing. Several findings on adaptation to luminance variation show aftereffects following viewing of such patterns [24] (see Section 8), but any functional role remains underexplored [18].

In experiment 1, observers adapted to sinusoidal variation in time around a mean luminance level of a large circular patch at screen center against a dark background. Following, 4, 8, 12, or 16 s the amplitude of variation changed slightly (experiment 1A; see Fig. 1A), while a slight mean luminance change followed the adaptation period in experiment 1B (see Fig. 1B). 4 s following the change, the observers were
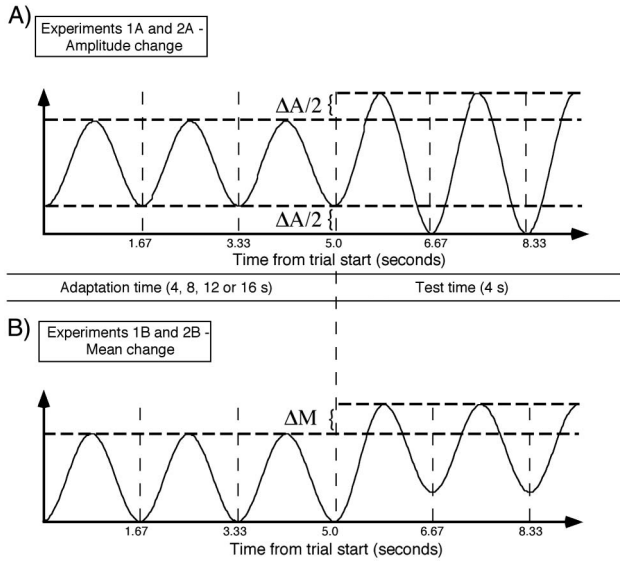
Fig. 1.   Nature of the two possible changes to the 0.6 Hz sinusoidal temporal luminance variation. Here the change in amplitude or mean is, for convenience, denoted as occurring following three full cycles (5 s) of the sinusoidal variation, while the actual change times varied (see methods for each experiment). The amplitude (A) and mean (M) increase in both cases, while they could both increase or decrease in the experiments. A. In experiments 1A and 2A, the amplitude of the luminance variation either increased or decreased (by ΔA) following the adaptation time (its mean was constant throughout). B. In experiment 1B and 2B, the mean (M) of the variation changed (by ΔM) following the adaptation period (the amplitude was unchanged). Note that the temporal frequency of the variation was kept constant, however, so that it could not serve as a cue. As the figure shows, the transition from the old to the new amplitudes and means was smooth, so no abrupt luminance changes could serve as cues to the changes [see Eqs. (1) and (3) and methods for further information].

prompted to respond whether the amplitude or mean had increased or decreased. In experiments 2A and 2B, the observers adapted to eight smaller peripheral patches, arranged on an imaginary circle during fixation on a central cross. The luminance of these patches changed sinusoidally similarly to experiments 1A and 1B (albeit one at a time), while which patch contained a given luminance level of the sinusoidal variation varied randomly (the other patches retained their luminance level until it was their turn to change). During all this, the patches rotated, clockwise or counterclockwise around the center of the screen at a rate of 1.4 deg/s.

The main experimental question was whether thresholds for discrimination of change in amplitude or mean of the sinusoidal variation would be modulated by adaptation length. A clear prediction in light of previous findings on adaptation is that they will decrease.

2. EXPERIMENT 1A—CHANGE IN AMPLITUDE OF LUMINANCE VARIATION

In experiment 1 observers viewed a large (9.6 deg) circular patch that varied sinusoidally in luminance in time against a dark background at a rate of 0.6 Hz (full cycle). The observers' task was to indicate whether they thought that the amplitude of the variation around the mean luminance had increased or decreased following the adaptation period. This was, in other words, a 2 (increase/decrease in amplitude) by 4 (adaptation times) by 8 (changes in amplitude) experimental design.

A. Methods

1. Observers
Two practiced psychophysical observers (one was the author, while the other was naïve) participated in all experiments, in addition to seven observers (four female aged 21–28 years) who participated in short versions of experiments 1A and 1B.

2. Apparatus
The stimuli were generated with color look-up table animation on a G4 Macintosh computer and appeared on a 14 in. Apple CRT display with a refresh rate of 67 Hz. The minimum luminance value of the monitor was 1.8 cd/m^2, while the maximum luminance was 125.6 cd/m^2. The custom-made stimulus presentation software was programmed in C using functions from the Vision Shell library [25]. The viewing distance was 67 cm, and the observers' head was stabilized with a chinrest during the experiment. A Konica photometer was used to measure the luminance levels. The experiments were performed in a dimly-lit room with no screen reflectance.

3. Stimuli and Procedure
The two observers who took part in the long version participated in 5120 trials each, yielding 80 trials for each cell in the full factorial design. In addition, seven observers participated in a shorter version of the experiment, in 200 trials each (a random without replacement procedure determined the number of trials of each type).

A trial started with the presentation of the circular patch (9.6 deg) at random phase of the sinusoidal cycle. Its luminance changed at rate of 0.6 Hz (from peak to trough of the sinusoidal variation). The patch was viewed against a dark (1.8 cd/m^2) background. At an unpredictable time following presentation of the patch (4, 8, 12, or 16 s), the amplitude of variation either increased or decreased and then continued to vary at that amplitude for an additional 4 s before a short beep (250 ms, 65 Hz) was heard, at which point the observers were required to respond by key press whether the amplitude had increased or decreased. There were four different mean levels around which luminance varied (20, 35, 50, and 75 cd/m^2). The peak-to-trough amplitude of the sinusoidal variation at the start was 10 cd/m^{-2}. There were four different levels of amplitude change following the adaptation period: $\pm 2, 4, 6,$ and 8 cd/m^2.

For the change in amplitude (in both experiments 1A and 2A), the luminance variation at any given time (t) was initially defined by

$$\mathrm{Lum}(t) = M + \left[\sin\left(\frac{t}{f(t)}\right) * \pi\right] * A_{\mathrm{pre}}. \tag{1}$$

M is the mean luminance of the variation, $f(t)$ is the temporal frequency of the variation, and A_{pre} denotes the initial amplitude. From the first trough of the variation after it reached the time assigned for change in amplitude, a constant was recursively added to A_{pre} with each luminance increase, to reach the peak luminance following the change (see the luminance profile in Fig. 1A). Then, to reach the trough following the change smoothly within the next half-cycle, a constant was recursively subtracted from M until the trough was reached, after which A_{pre} changed to A_{post}. This procedure ensured smooth luminance transition from one amplitude to another.

The procedure was reversed in the cases where the next extreme value following the time for change was a peak rather than a trough. The outcome of the function normally does not result in an integer, so the closest integer value determined the gray level on that presentation. Note importantly that, even though the amplitude of the sinusoidal luminance variation changed, the temporal frequency of the variation remained constant, as Eq. (1) makes clear. This ensured that the temporal frequency of the peak-to-trough variation could not cue the nature of the change. While every effort was made to ensure that the amplitude of the variation was equal for the different mean levels, for hardware reasons this was not always possible.

4. Data Analysis

Psychometric functions were fit to the proportion of amplitude-increase responses $[P(iA)]$ for each of the different amplitude changes as a function of adaptation time:

$$P(iA) = \frac{1}{1 + e^{-(b_0 + b_1 * \Delta A)}}. \qquad (2)$$

$P(iA)$ denotes the proportion of trials where the amplitude of the variation was judged as having increased, b_0 and b_1 are regression coefficients, and ΔA denotes the change in amplitude of the variation.

The psychometric function measures the discriminability of amplitude changes as a function of adaptation time, when the difference between the points, where 25% and 75% of the changes are judged as increases, is taken, and then divided by two. This yields, in other words, an estimate of the discrimination thresholds following each adaptation time. A three-way repeated-measures analysis of variance (ANOVA) was used to estimate the effects of adaptation time and amplitude changes for the seven observers who participated in the short version of the experiment.

B. Results

The left panels of Figs. 2A–2D present the results from experiment 1A, where the amplitude of the sinusoidal luminance variation changed following the adaptation time. Figure 2A shows the average thresholds estimated from the psychometric functions for the seven observers in the short version of the experiment. Figure 2B shows separately the thresholds estimated for the two observers in the long version of the experiments. Figure 2C shows the percent correct results for the observers who participated in the short version of the experiment (200 trials each), while Fig. 2D shows similar results for the two observers in the long version. In Figs. 2C and 2D, different symbols denote different adaptation times, while the abscissa shows the change in amplitude. A three-way ANOVA (there was no significant differential effect of the four variation levels upon performance, so they were pooled for the analysis) on the results for the seven observers from the long version with the factor adaptation time (four levels) amplitude change (four levels) by type of change (two levels, upward or downward) showed a significant effect of adaptation time $[F_{(3,18)} = 6.97, \ P = 0.003]$ and amplitude change $[F_{(3,18)} = 9.87, P < 0.001]$, but there was no effect of whether the change was an increase or decrease in amplitude $[F(1,6) = 0.96, \ P = 0.37]$. None of the interactions were significant (all $p > 0.2$).

All in all, both sets of results from experiment 1A show that adaptation improves detection thresholds for the amplitude change approximately linearly over the intervals tested. This shows that sensitivity to amplitude changes in the sinusoidal luminance variation increases as a function of adaptation time. This result is analogous to what has been seen before for adaptation to tilt and motion and can be considered further support for adaptive coding of the statistical properties of the environment. This coding is dynamic, becoming more efficient the longer the adaptation time. To rephrase slightly, the larger the sample of the stimulus in question, the more accurate its representation becomes.

3. EXPERIMENT 1B—ADAPTATION TO CHANGES IN MEAN OF LUMINANCE VARIATION

A neural mechanism that adjusts its responses to a particular level of stimulation would be of little use if it only worked for a single rather abstract stimulus attribute. Experiment 1A showed that the longer the adaptation to a luminance-varying pattern, the more easily changes in the amplitude of the variation are noticed. But other properties of such a temporally varying stimulus can change. The aim with experiment 2A was to test whether analogous results would be obtained for changes in mean luminance for a similar luminance-varying stimulus as in experiment 1A.

A. Methods

The same observers participated in similar long (5120 trials) and short (200 trials) versions as in experiment 1A. Methods were similar to experiment 1A, except that, instead of a change in the amplitude of the variation following the adaptation period, the mean of the variation either increased or decreased by 2, 4, 6, or 8 cd/m^2.

For the change in mean, a similar sinusoidal function to the one in experiment 1A determined the luminance level at any given time (t), which at the start had the following form:

$$\text{Lum}(t) = M_{\text{pre}} + \left[\sin\left(\frac{t}{f(t)} \right) * \pi \right] * A. \qquad (3)$$

Following the first extreme (peak or trough) following $t =$ time to change, the amplitude (A) was recursively increased with each luminance change to allow the luminance to reach the peak or trough value for M_{post} within the same temporal frequency in a smooth manner, after which the amplitude was again equal to A (see Fig. 1B). Following this, the luminance was determined by Eq. (3), except that M_{post} changed to M_{post}.

As in experiment 1A, the results were fit with a psychometric function:

$$P(iM) = \frac{1}{1 + e^{-(b_0 + b_1 * \Delta M)}}, \qquad (4)$$

where $P(iM)$ denotes the proportion of trials where the mean of the variation was judged as having increased, b_0 and b_1 are regression coefficients, and ΔM denotes the change in mean following adaptation. Thresholds were estimated by halving the distance between the 25% and 75% correct points on the function. In all other respects, methods were similar to those described for experiment 1A.
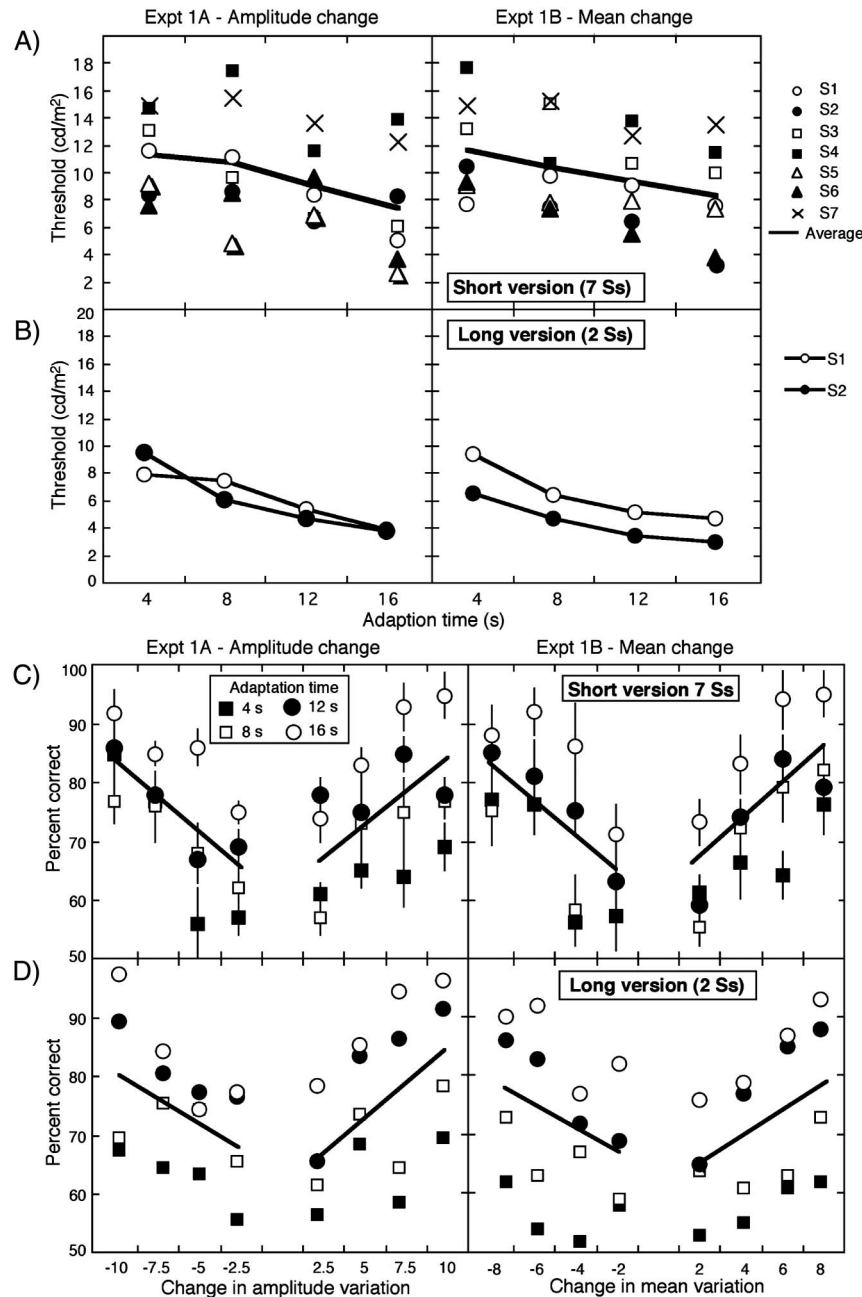
Fig. 2.   Results from (left) experiment 1A and (right) experiment 1B. A. Thresholds estimated from the psychometric functions for the seven participants in the short version of the experiments. The solid line traces the mean of the seven thresholds. B. Thresholds estimated from the fitted psychometric functions for the two observers tested on 5120 trials each for the different adaptation times. C. Percentage correct for the seven observers tested in the short versions of the experiments for the different adaptation times and different size of changes in amplitude (experiment 1A) and mean (experiment 1B). D. Similar average results as in C for the two observers in the long versions of the experiments.

B. Results

The right panels of Figs. 2A–2D present the results from experiment 1B. Figure 2A shows the average thresholds estimated from the psychometric functions for the seven observers in the short version of the experiment. Figure 2B shows separately the thresholds estimated for the two observers in the long version of the experiments. Figure 2C shows the percent correct results for the observers who participated in the short version of the experiment (200 trials each), while Fig. 2D shows similar results for the two observers in the long version. In Figs. 2C and 2D, different symbols denote different adaptation times, while the change in the mean is shown on the abscissa. For the observers tested on the short version, a similar three-way repeated-measures ANOVA as in experiment 1A (there was no effect of luminance level so the results were pooled) revealed a main effect of adaptation time $[F(3, 18) = 5.18, P = 0.009]$ and of the size of mean change $[F(3, 18) = 10.95, P < 0.001]$, but not for change direction $[F(1, 6) = 1.16, p = 0.32]$. As in experiment 1A, none of the interactions were significant. The results both for the observers in the long and short versions show that, with increased adaptation time, discrimination performance improves strongly, this time for changes in the mean of the luminance-varying pattern.

4. DISCUSSION OF EXPERIMENTS 1A AND 1B AND INTRODUCTION TO EXPERIMENT 2

Experiments 1A and 1B show that sensitivity to small changes in luminance variation over time increases following adaption to a central luminance-varying patch. Two informative cases were tested involving changes in the amplitude and the mean of the sinusoidally varying large patch. This pattern of results is consistent with the proposal that adaptation effects are manifestations of a process where the visual system adjusts its responding to the input over a given time period.

There is evidence from neurophysiology that retinal cells change their response properties following adaptation (see Section 8). The aim with experiments 2A and 2B was to find out to what degree the adaptation effects uncovered in experiments 1A and 1B reflect local retinal adaptation. To address this, similar sinusoidal variation as in 1A and 1B was used, while this time the variation was spread out over different locations in the visual field so that any single retinal region was exposed to only a very small sample of the total variation. To further reduce any local retinotopic adaptation, the patches rotated around the fixation point at a velocity of 1.4 deg/s, either clockwise or counterclockwise between trials.

5. EXPERIMENT 2A—SINUSOIDAL LUMINANCE VARIATION AT RANDOM LOCATIONS: AMPLITUDE

Eight 4.1 deg patches (see Fig. 3) appeared on a circle around fixation (screen center to center of patch eccentricity = 8.6 arc deg). They changed in luminance *one at a time* at the same rate as in experiments 1A and 1B (0.6 Hz full cycle from peak to trough of the sinusoidal luminance variation). Central fixation was required throughout. At any given refresh, a randomly selected patch was chosen to present the corresponding luminance of the sinusoid making up the luminance distribution pattern [see Subsection 2.A and Eq. (1)]. The luminance value for each patch was, in other words, sampled from a similar sinusoidal distribution as in experiment 1A [see Eq. (1) and Fig. 1A], but the amplitude of the variation was larger (see below). The peripheral discs rotated around the fixation cross (at constant eccentricity, clockwise or counterclockwise, randomly determined) at a velocity of 1.4 deg/s to further reduce the likelihood of any retinotopic cues to the variation. This motion of the stimulus also helps to eliminate any danger of Troxler fading or other peripheral adaptation effects, which have been known to result in fading [26,27].

Only two different ranges of variation were tested in experiments 2A and 2B, both larger than the ranges in experiment 1, since pilot experiments indicated that this task was harder than the one in experiments 1A and 1B, so the range and magnitude of change in amplitude and the luminance variation needed to be approximately two times larger. The two means around which the sinusoids varied were 40 and 70 cd/m² and varied by ±18 cd/m². In experiment 2A, the possible luminance changes were 5, 10, 15, or 20 cd/m², while in experiment 2B they were 3, 8, 13, and 18 cd/m². In other respects the methods were similar to what was presented for previous experiments. Because the results for the observers tested on the brief versions of experiments 1A and 1B were, for all purposes of interest, identical to those for the observers
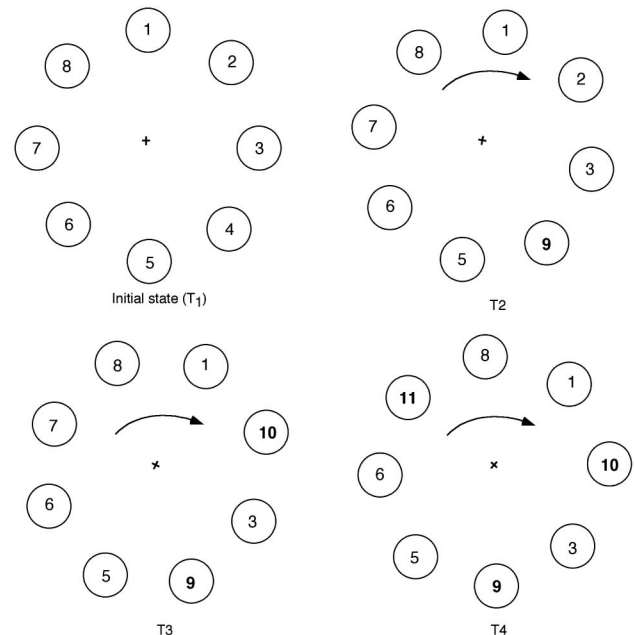

Fig. 3.   Schematic of the luminance-varying stimulus used in experiments 2A and 2B at four different times (T_1 to T_4). The different numbers denote a given luminance value of the sinusoidal luminance variation at a given time. At T2, one of the patches (randomly chosen) takes on the next value (9 in the figure) of the sinusoidally varying pattern, at T3 another randomly chosen patch takes on the next value (10), at T4 another one took the next value (11), and so on. The patch that changed at any given moment was chosen randomly, with the only algorithmic constraint that the same patch was never chosen again before three changes had occurred. The arrows serve to indicate that the display items rotated throughout (clockwise or counterclockwise, randomly determined) at a velocity of 1.4 deg/s.

tested in the long version, only two practiced observers (same as in experiment 1) were tested in this experiment, on a similar number of trials as in the long versions of experiments 1A and 1B. In other respects, the methods were similar to those described for previous experiments.

A. Results
The results for discrimination of the amplitude change as a function of adaptation time are shown in Fig. 4A. The figure shows the thresholds estimated from the psychometric functions [fitted to the proportion of responses that the amplitude had increased following the adaptation period; see description
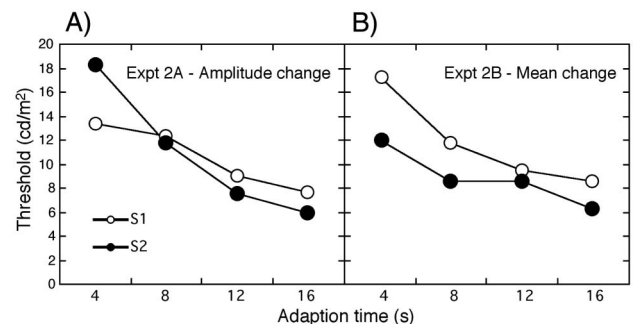

Fig. 4.   Results from experiments 2A and 2B. A. Estimated thresholds (using similar psychometric functions as presented for experiments 1 and 2) for discrimination of amplitude change (experiment 2A); B. thresholds for discrimination of changes in mean (experiment 2B) as a function of adaptation time.

in experiment 1, Subsection 2.A.4 and Eq. (2)] for the four different adaptation times for the two observers. The figure shows that the thresholds were overall much higher than for the uniform fields, while most importantly they still showed a notable decrease as a function of adaptation, indicating that the longer the exposure to the variation, the better the discriminability of the amplitude of the variation.

6. EXPERIMENT 2B—SINUSOIDAL LUMINANCE VARIATION AT RANDOM LOCATIONS: CHANGES IN AMPLITUDE

The only difference between experiments 2A and 2B was that, instead of an amplitude change following the adaptation period, the mean of the sinusoidal variation could either increase or decrease by 3, 8, 13, or 18 cd/m^2 (see Fig. 1A). Otherwise the luminance variation was similarly distributed across different locations as in experiment 2A. The same two experienced observers as in the long version of experiment 1 and 2A participated.

A. Results
Figure 4B presents the results for the change in mean luminance variation as a function of adaptation time in experiment 2B. The figure plots the thresholds estimated from the psychometric functions [fitted to the proportion of responses that the mean of the variation had increased; see Eq. (4)] for the four different adaptation times. As in experiment 2A, the thresholds were much higher than for the uniform field tested in experiment 1, but both observers still showed a notable threshold decrease with longer adaptation. The results therefore agree with previous experiments showing how increased adaptation time results in better discrimination of the properties of the adapting stimulus.

7. DISCUSSION OF EXPERIMENTS 2A AND 2B

The results of experiments 2A and 2B show that the adaptation effects observed in experiments 1A and 1B cannot be solely traced to activity modulations of retinotopic mechanisms. Any given region on the retina was not exposed to enough information in experiments 2A and 2B to perform the task accurately. A higher-level nonretinotopic mechanism must play a role since the information was unpredictable and nonsystematic at any given retinal location. On the other hand, the fact that the thresholds were much higher for this sort of stimulus indicate that the adaptation effects are stronger for the larger patches—perhaps not unexpectedly, which undeniably opens up the possibility that some, though not all, of the adaptation may reflect retinotopic mechanisms. But the dynamic nature of coding of luminance variation is clearly not solely dependent upon lower-level retinotopic mechanisms.

8. GENERAL DISCUSSION

Functionally beneficial changes in discrimination thresholds of mean and amplitude changes of sinusoidal luminance variation were observed with prolonged viewing of a large, centrally presented, luminance-varying patch (experiments 1A and 1B). Adaptation to a certain range of variation led to increased sensitivity to changes in mean and amplitude of the sinusoidal luminance variation. This echoes previous findings on motion adaptation and adaptation to orientation (see

Section 1). Experiments 2A and 2B showed that this could not completely be accounted for by adaptation of retinotopic mechanisms since the collective variation occurred at varied and unpredictable locations in the visual field.

The findings show that coding of luminance variation is dynamic. The visual system can benefit from prolonged input of a certain type using it to adjust its responses for a more accurate representation of the characteristics of the stimuli in the environment. This means that the variation in environmental stimuli may be more important for an accurate representation of the environment than the absolute levels of stimulation at any given time. The visual system therefore does not appear to strive to represent absolute levels of stimulation. For useful representations of the environment the *changes* may be more important as many have indeed argued [17,20,23,28–32].

Other ways in which the visual system uses previous history to predict the future is learning in attention deployments [33,34]. One example of this is how observers orient preferentially to task-relevant parts of briefly presented cues [35–37], priming of attentional choice [38], and of visual search [39]. The well-known phenomenon of neural repetition suppression following repeated presentation of the same stimulus [40–44] is another example of such effects of stimulus history.

A. Relation to Other Findings on Adaptation to Luminance Variation
Numerous studies have shown how the visual system adapts to variation in luminance. An intriguing example is sawtooth adaptation [24,45], where repeated presentation of a ramp increasing or decreasing in luminance leads to the opposite percept when the varying pattern is replaced by a nonchanging stimulus.

Another finding worth mentioning is how adaptation to peripheral flicker leads to threshold increases [26,27] and eventual perceptual disappearance of an adapting pattern. At first glance this may seem inconsistent with the findings here since the changing pattern fades from conscious perception. Note, however, that this effect is confined to task-irrelevant locations in the visual periphery, not central presentation as in the current experiments. Phenomena such as Troxler fading are more pronounced in the periphery, and in the case where peripheral stimulation was used (experiments 2A and 2B here), the patterns rapidly changed location and were also of relatively high contrast against the background. As Anstis [27] notes, peripheral flicker will usually prompt a saccade, but such stimuli are seldom present long enough in the periphery to need prolonged representation or analysis, so central fixation may lead to fading, while the constantly changing stimulus in the experiment reported here does not. Shady *et al.* [46] have then shown that adaptation to rapid flicker, too fast to be perceptible, can nevertheless cause adaptation effects upon visual sensitivity. Note that sawtooth adaptation raised the detection thresholds for incremental light pulses and steps [47]. This is, however, not necessarily inconsistent with the results reported here, since the current benefits from adaptation occur on the varying pattern *itself*, precisely what one would expect from the workings of a mechanism adapting to environmental statistics. The fact that brightness discrimination thresholds following adaptation are lowest around the adaptation level [21] is consistent with this. Threshold increases in color discrimination thresholds from adaptation

to stimuli varying sinusoidally in chromaticity have been found [48], which may on the surface appear at odds with the results here, but note that there are important methodological differences between that study and the current one, most notably that, in the former, the test did not involve discrimination of slight changes to the adapting stimuli themselves. In fact, many effects of adaptation with subsequent decreases in performance, such as dents in the contrast sensitivity function following adaptation to stimuli of a particular spatial frequency [49] share this separation of adapter and test. But more research is needed for better insights into this. More recent studies of color adaptation [18] show how the appearance of colors in natural images can be altered by adaptation to the color distributions and contrast range of the scenes, which falls in line with the arguments made here.

B. Brief Notes on Retinal Physiology

The well-known phenomenon of contrast gain control [50–53] contributes to brightness constancy under different illumination levels. Shapley and Enroth-Cugell [50] concluded in an extensive review that retinal responses are nonlinear. They depend strongly on contrast levels in the environment. It is likely that similar mechanisms manifest themselves here, adjusting the gain of the system to the apparent variation. A recent study [54] of adaptation of retinal neurons in macaques and salamanders to temporal contrast (in other words the intensity modulation of a randomly flickering uniform patch) showed that retinal cells contribute to this adaptation. Results from another study [55] showed that retinal ganglion cells of salamanders and rabbits adapt not only to image contrast but also to within-scene spatial correlation, all in all showing great adaptability in their responding. The authors presented stimuli whose mean intensity remained constant throughout, but whose second-order statistics changed abruptly at long intervals. Overall, these findings must be considered broadly consistent with our results here.

C. Some Caveats

Some precautions should be noted. The role of memory representations [56] in mediating the increased sensitivity is not directly addressed here. It is, of course, possible that better memory of the adapting stimulus with increased exposure to it could affect the results observed here. How such a memory representation would lead to aftereffects in the opposite direction to the adapting stimulus (see the tilt aftereffect, sawtooth adaptation, and the motion aftereffect) is mysterious, though. It is, nevertheless, hard to rule out such effects here, nor in other studies showing increased sensitivity from adaptation [10–15]. Any role that memory representations play in mediating effects of adaptation and perceptual aftereffects may nevertheless be an interesting unexplored question.

D. Conclusions

There are many phenomenological and physiological examples of how the visual system of human observers operates with reference to what has been previously perceived. Adaptation to variation in brightness as studied here is clearly one example of such dynamic coding. Adaptation can obviously have advantages. Especially during detection or discrimination of relatively minute changes to stimulation. The visual systems responses at any given time depend on the momentary input, but this does not tell the whole story, since preceding input is taken into account and in some cases accounts for large portions of what is actually perceived.

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