



Spatial properties of flicker adaptation

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ABSTRACT

Prolonged viewing of a flickering region reduces sensitivity to a subsequently flickered test patch of identical extent, but the spatial properties of this adaptation are unknown. What happens to the sensitivity to a smaller flickered test patch completely contained in, but inset from, the adapted region? We show that sensitivity to the inset test patch is only slightly affected by adaptation of the larger region. This suggests that neurons that respond to the edges of the smaller test patch are not adapted by the larger flickering region. We then show that an annulus adapter designed specifically to adapt only those edges only slightly reduces sensitivity, demonstrating that neurons that do not adapt to the flickered edges are also involved in detecting flicker. This gives further evidence that flicker detection depends on at least two mechanisms – one sensitive to flickering edges and one sensitive to local flicker, and shows that these mechanisms can operate in isolation.

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1. Introduction

Prolonged viewing of a flickering region reduces sensitivity to that flicker (Pantle, 1971). This adaptation is only somewhat selective for temporal frequency (Nilsson, Richmond, & Nelson, 1975), and indeed, sensitivity to 30 Hz flicker can be reduced by adapting to (unperceivable) 60 Hz flicker (Shady, MacLeod, & Fisher, 2004). Significantly superthreshold flickering peripheral regions will fade from view when viewed under strict fixation, eventually disappearing entirely (Schieting & Spillmann, 1987). This has been shown to partially transfer between eyes, suggesting that flicker adaptation has at least some cortical component (Moulden, Renshaw, & Mather, 1984; Schieting & Spillmann, 1987).¹

These studies used the same spatial properties across adapting and testing stimuli, thus little is known about how flicker adaptation depends on spatial arrangement and scale. There is, however, some reason to expect selectivity in adaptation from other literatures. Green (1981) demonstrated reduced sensitivity to moving gratings after adapting to uniform flicker, but only for gratings of 4 cycles/degree and lower. There is also evidence that flicker detection varies with spatial frequency. Kelly (1969) conducted the first systematic study comparing sensitivity for whole field flicker (65° targets) and local contrast flicker with sharply defined edges (2°

targets), and found threshold differences he attributed to lateral inhibition operating on a single mechanism. In a later meta-analysis including Kelly's data and others, Tyler (1975) argued instead that two mechanisms were required, one responding to spatial contrast (edges), and the other to variation in light levels over time, without any local contrast. Tyler based this on a number of factors, most notably differences in psychophysical contrast threshold curves for small-field and whole-field modulation, and posited that these two mechanisms might correspond to sustained and transient mechanisms in the retina, respectively. Whether these detectors do map onto sustained and transient mechanisms in the retina or later is far from clear, however. Many studies agree that sustained mechanisms detect high spatial frequencies and transient mechanisms detect lower spatial frequencies (e.g. Legge, 1978; MacLeod, 1978), which is compatible with the mapping, but only suggestive. Furthermore, it is debatable whether there are distinct sustained and transient mechanisms, or a single mechanism behaving under two distinct regimes (Watson, 1986; Wu & Burns, 1996), which is incompatible with Tyler's claim that two distinct mechanisms are required. It is too soon to make a strong argument either way, since Tyler's proposed mechanisms are not well studied.

Here we investigate Tyler's proposal that there are separate detectors for flickering edges and for uniform regions, using a novel approach that provides converging supporting evidence, and also allows further characterization of these mechanisms. We measure the spatial properties of flicker adaptation, focusing in particular on whether a large uniform flickering region reduces sensitivity when tested with smaller regions inset within the larger one.

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¹ Adaptation is found for many other types of visual stimuli, and the purpose of adaptation is still debated. Webster (2011) provides an excellent review for those interested in these broader issues.

2. Experiment 1: adapting to uniform flicker

There are at least two different kinds of visual mechanisms that could detect luminance flicker, differing in their spatial properties. First, a spatial contrast mechanism could detect the increase or decrease in local contrast that occurs with flicker. It would respond when its receptive field intersects with the border of the flickering region, but not when stimulated by uniform flicker. The second type of mechanism is sensitive to the absolute change in luminance within its receptive field. It responds when it intersects a flickering edge, but responds even more strongly when its receptive field is entirely within the flickering region. As thus described, these two mechanisms map onto the sustained and transient retinal mechanisms identified by Tyler, but to remain agnostic as to the actual relationship we will refer to these two kinds of detectors as edge and uniform flicker detectors, respectively.

In this experiment we measure the strength of flicker adaptation for two conditions: when the test disk is exactly the same size and location as the adapted region (*aligned*), and when the test disk is significantly *inset* relative to the edges of the adapting disk (Fig. 1). The aligned condition has the potential to adapt both edge and uniform mechanisms. In the inset condition the edges of the adapter and the test do not overlap, but there could still be a sensitivity reduction due to adaptation in the uniform mechanism.

2.1. Methods

2.1.1. Subjects

Two psychophysically experienced subjects participated, one an author, and one naïve to the purpose of the experiment.

2.1.2. Apparatus

Stimuli were presented on a 22" iiyama HM204DT A CRT driven by an NVIDIA GeForce 8600 GT video card at a refresh rate of 75 Hz, in a moderately lit room. Display luminance was linearized using a Cambridge Research Systems Bits++ adapter with a 14-bit color lookup table. A UDT photometer was used to select the appropriate lookup table values for gamma compensation. A chinrest was used to maintain a viewing distance of 42 cm. Stimuli were generated and displayed using Matlab running the Psychophysics Toolbox, version 3 (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997) on a Windows XP computer. The same apparatus was used in all experiments.

2.1.3. Stimuli and procedure

The adapting and test stimuli consisted of a temporally flickering uniform disk centered on a gray background with a fixation dot at the center. Conditions varied along two dimensions: The diameter of the test disk and whether the test disk was aligned or inset relative to the adapting disk. We use the following shorthand (radius of adapter)/(radius of test) to summarize the degrees of visual angle each stimulus subtended (see Fig. 1). The aligned conditions were 2/2 and 10/10, and the inset were 4/2, 10/2, 12/10, and 15/10. During adaptation the luminance of the disks was modulated by a 6.25 Hz temporal square-wave (80 ms per frame) between black (2.3 cd/m²) and white (130 cd/m²), on a gray background (65 cd/m²). The black value was relatively high because the experiment was conducted with the room lights on. While this is somewhat unusual in vision experiments, we found it to be quite beneficial in this case, because otherwise adapting to large flickering disks caused significant visual strain and fatigue, changing visual thresholds over the course of a run.

Our paradigm is outlined in Fig. 2. Contrast thresholds were measured in two different kinds of sessions: *adapt* and *no-adapt*. In the adapt session subjects first view 9.1 s of flicker (not shown

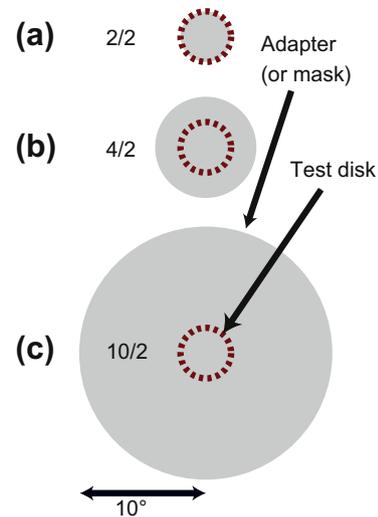


Fig. 1. Example spatial profiles of the adapting disk and test disk (test disk location denoted by dashed lines), with the corresponding stimuli shorthand names printed at left. (a) An aligned condition. (b–c) Inset conditions.

in Fig. 2). This *Pre-trial* flicker is meant to build up adaptation before any measurements are made. Subjects are instructed to fixate the dot at the center of the screen during this, and all subsequent parts of the experiment. After the pre-trial flickers the measurement trials start.

A measurement trial in an adapt session starts with 2.08 s of adapting flicker, which serves to maintain a constant state of adaptation. A white fixation dot is shown, which briefly flashes to black on the 2nd to last cycle of flicker to signal that the test is about to start. Next a gray screen is shown for 66 ms, followed by a green fixation dot and the test flickers. In a 2AFC task, subjects detect if 4 cycles of flicker are shown or just 1. When 1 cycle is shown it is at the same temporal location as the 3rd cycle in the 4-cycle sequence, to help equate visibility. The next measurement trial starts immediately; the subject has up to 2.08 s to respond to the 2AFC task from the previous trial while they adapt. 109 trials were collected each session and each session took 5.5 min.

To measure if adaptation reduced sensitivity we compared contrast thresholds for the adapt sessions to *no-adapt* sessions. In the no-adapt sessions no pre-trial flickers are shown. Instead of 2.08 s of adapting flicker between tests, 1 cycle of flicker was shown just before, and one just after the test flickers (total = 0.032 s). We included these flickers to make sure that any masking effects, such as meta-contrast masking, were present in both the adapt and no-adapt sessions.

Data were collected over multiple days. To prevent order effects both subjects were trained on the task until thresholds were consistent across multiple days, and training data were not used in analysis. To further protect against order effects, subjects completed the sessions in random order, except we tried to increase our ability to detect differences between adapt and no-adapt sessions. When a condition was selected that had both adapt and no-adapt sessions, both of those sessions were collected back to back (which was first was selected randomly on each day, though pilot tests showed that thresholds in no-adapt session were not shifted when preceded by an adapt session). An average of four sessions per subject were collected for each combination of condition and session type.

To measure contrast thresholds we adjust the magnitude of the test flickers using a variable stepsize staircase. The staircase was initialized at 30% Weber contrast, with a stepsize of 10% Weber contrast. After correct trials the flicker strength was reduced by

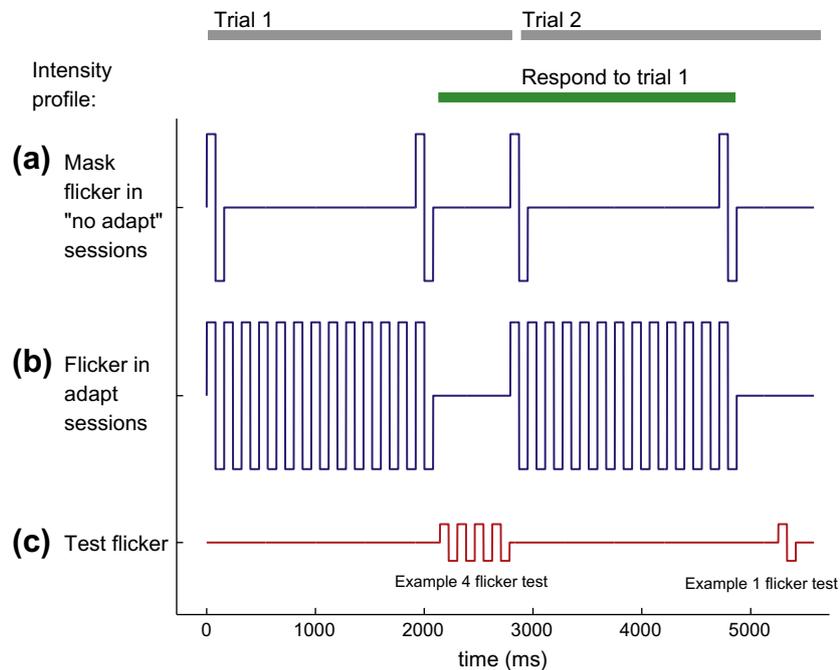


Fig. 2. Diagram of the paradigm used in experiment 1 (and 2), showing two example trials and two different session types. (a) Intensity profile of the “adapting” disk during no adapt trials (included to equate masking; minimal adaptation is expected). (b) Intensity profile used for the same disk in the adapt sessions, where maximal adaptation is desired. (c) Example intensity profile of the test disk near the beginning of the experiment where it is super-threshold. A no-adapt session would consist of (a) and (c), while an adapt session would consist of (b) and (c).

one stepsize; after incorrect trials it was increased by 2.7 times stepsize, and the stepsize was reduced by 20%. If the staircase reaches zero contrast then half of the last tested contrast is used instead and the stepsize is also reduced by 25%. After every four incorrect responses a single easy trial is introduced to keep the subjects’ attention and motivation from decreasing due to frustration. To ensure that thresholds were measured at steady state we discarded the first 20 trials of each session.

2.1.4. Analysis

We fit a Weibull curve to the data for each condition to estimate the contrast necessary to elicit 75% correct detection. A bootstrap analysis was used to estimate the 95% confidence intervals of this threshold, using the BCA method as implemented in Matlab R2010A. We allowed a lapse rate of up to 10% to address the curve fitting issues raised by Wichmann and Hill (2001).

2.2. Results

Contrast thresholds for the two subjects are shown in Fig. 3. Both show the same relative pattern of results. Contrast thresholds were much higher in the 2/2 (aligned) condition than in the 4/2 (inset) condition. Thresholds were quite similar for the 4/2 and 10/2 conditions, suggesting that adaptation drops off steeply as a function of distance between adapter and test edges, reaching asymptotic values by around 2° of separation for small test fields.

Larger test fields also showed a significant difference between the aligned (10/10) and inset (12/10; 15/10) conditions. Interestingly, the two inset conditions were quite similar to each other, suggesting that again, 2° of separation was sufficient to eliminate most of the sensitivity change, even for large test fields. Thus, it does not appear that the ratio of the size of adapter to test disk predicts the change in threshold. Instead, it is the absolute change in size that matters, and only a couple degrees difference is necessary. Any edge-selective mechanisms tuned to scales larger than 2° should have been adapted even in the 12/10 condition. Thus,

detection in the 12/10 condition must be driven by very small-scale spatial contrast mechanisms responding to the flicker immediately along the edge of the test disk. This is why thresholds in the 15/10 condition are no better: both conditions spare the small-scale edge detectors equally.

We also found evidence of adaptation in our inset conditions, though much weaker. Our no-adapt sessions were designed to duplicate any short-term masking effects caused in the adapt sessions, while inducing minimal flicker adaptation. We consistently found lower thresholds than in the corresponding inset adapt sessions, and though the differences were small, they exceeded the 95% confidence intervals in all cases (except for the 4/2 condition for subject AR). Thus, mechanisms that are sensitive to uniform flicker also adapt.

Subjects maintained fixation throughout the experiment. Since we did not use an eye tracker, we do not know the frequency and magnitude of eye movements, though both subjects were experienced psychophysical observers so it is fair to expect these errors to be small. Furthermore, any effects would have been constrained to the smaller adapting and test stimuli, where eye movements could have reduced adaptation by reducing alignment in the 2/2 condition, or increased adaptation by reducing the distance between edges in the unaligned 4/2 condition. In the 10/2 condition, only implausibly large eye movements would have caused significant alignment between adapt and test edges, and yet the thresholds are very close to the 4/2 conditions, suggesting that eye movements did not influence our results.

3. Experiment 2: adapting to edge flicker

Experiment 1 showed that small (2°) changes in scale (and thus alignment) between adapter and test drastically change the level of adaptation. Thus it is possible that the edges (that is, the spatial contrast component) of the adapter cause most of the reduction in sensitivity. To test this, in experiment 2 we use an adapter that targets edges, while leaving the interior untouched, to see if this

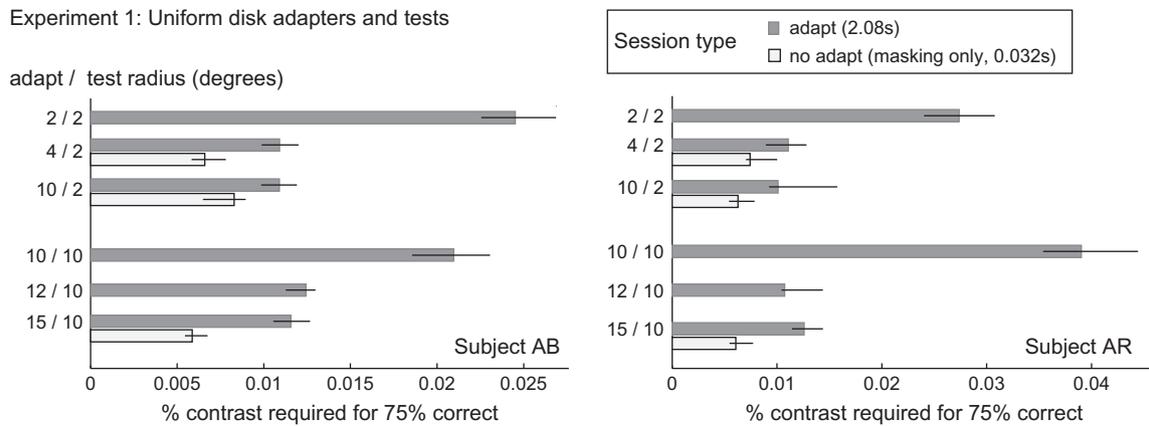


Fig. 3. Results for two subjects in experiment 1. Error bars denote 95% confidence intervals.

causes significant adaptation for uniform disk tests that stimulate both the adapted edges and the unadapted interior. All methods, apparatus, and procedures are the same as in experiment 1.

3.1. Stimuli

The new adapter (*polar checkerboard*, Fig. 4) was designed to modulate local contrast across the test disk's edge, while leaving global contrast constant. It consisted of a checkerboard with a circular border between the inner and outer checks. This border was aligned with the outer edge of the test disk. On each successive frame the identity of the black and white checks was switched, creating local flicker along the border, while holding global luminance and contrast constant. The check radius was varied across conditions to vary the scale of the contrast modulation across the test edge. The conditions are summarized with the following shorthand (check radius, measured from the adapting edge)/(radius of the test disk). Thus summarized, the conditions were 4/10 (6° radius hole in the center), 8/10, and 10/10 (no hole).

3.2. Results

For both subjects the 4/10 adapt sessions had significantly higher thresholds than in the no-adapt sessions (Fig. 5), but the effect was quite small. The 4/10 condition should have reduced sensitivity of any edge mechanisms with receptive fields of 4° in radius or less, including the small-scale detectors that appeared to dominate thresholds in experiment 1. Thus, it appears that when these mechanisms are adapted, other mechanisms (such as uniform

mechanisms) can serve to detect flicker, resulting in little change in contrast thresholds.

Going from 4/10 to 8/10 (reducing the size of the hole in the adapter), and then to 10/10 (eliminating the hole) minimally increased thresholds, suggesting that adapting any larger scale contrast mechanisms (should they exist) did not reduce sensitivity.

4. General discussion

Experiment 1 shows that adapting uniform mechanisms but not edge mechanisms only slightly reduces flicker sensitivity. Experiment 2 shows that the reverse also holds: adapting edge mechanisms but not uniform mechanisms also reduces sensitivity only slightly. Thus both mechanisms play an important role in flicker adaptation. Large threshold changes were only seen in the aligned conditions in experiment 1, which would have adapted both edge and uniform mechanisms, suggesting that both mechanisms must be adapted to significantly reduce flicker sensitivity. This matches Tyler's suggestion that flicker sensitivity thresholds are determined by whichever mechanism is most sensitive to that flicker.

The fact that flicker detection remains when only one mechanism is adapted indicates that flicker detection does not depend on the proper interplay of edge and uniform mechanisms – each one in isolation serves quite well. This may have relevance to theories of surface perception that depend on the filling-in of uniform regions from edge signals (e.g. Grossberg and Todorović (1988) to name but one prominent example).

One subject (AR) observed in the second experiment that the test flicker percept in the 4/10 condition had one of two distinct forms: at high contrast the entire test disk was seen to flicker, with a clearly defined edge, while at low contrast, a somewhat ill-defined region in the center 6° radius of the test disk flickered, with no clear boundary. This corresponded to the region that was not modulated by the adapting checkerboard. This implies that uniform regions can be perceived without edge signals to contain them. While just speculation, it does suggest that the paradigm and stimuli used in this experiment may be useful to test and evaluate models of filling in.

Our results are compatible with but extend the predictions of Green (1981). He reported that full-field flicker did not reduce sensitivity to moving gratings that were 4 cycles/degree and higher. While motion is not the same as stationary flicker, one might predict from this absolutely no adaptation in the inset conditions in experiment 1, since our stimulus could have been detected from high spatial frequencies alone (which Green suggests are not adapted by flicker). Note, however, a 4 cycle/degree grating has very little in the way of uniform regions (7.5 arcminutes which is

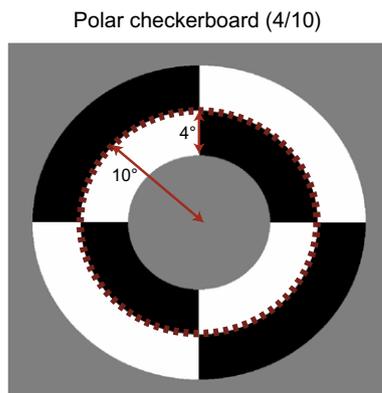


Fig. 4. Polar checkerboard (4/10 condition).

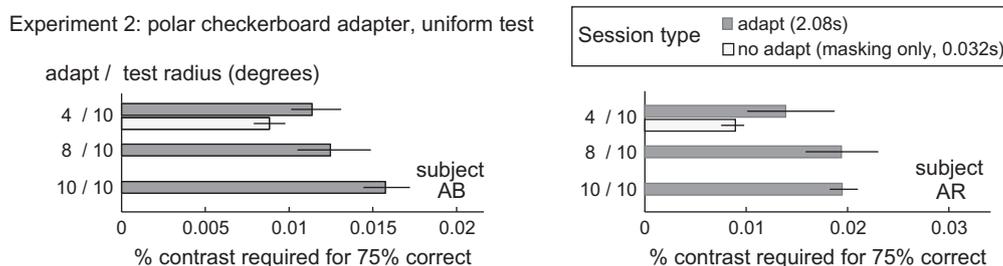


Fig. 5. Results for two subjects in experiment 2. Error bars denote 95% confidence intervals.

comparable to the range of spatial summation found in Sinai, Essock, and McCarley (1999). Gratings of higher frequency have even smaller uniform regions that may result in uniform spatial summation mechanisms contributing minimally to grating detection above 4 cycles/degree. Even in our 10/2 condition, however, the central test disk was 4° in diameter and thus will activate uniform mechanisms that could be adapted by uniform flicker. Green's results predict that if our test disk was reduced to 1/8th of a degree in diameter, uniform flicker might no longer cause any adaptation.

Green did find significant adaptation for gratings below 4 cycles/degree. We explain this by positing that those gratings were wide enough to stimulate a sufficient number of uniform mechanisms to provide a useful detection signal (prior to adaptation). For these larger gratings (lower spatial frequency) Green found more adaptation than we did in the inset conditions of experiment 1, probably because he used sine wave gratings, which would have only stimulated edge mechanisms tuned to a narrow range of spatial scales. Thus, uniform mechanisms would have contributed relatively more of the signal in his paradigm.

Our work also suggests another interesting line of research. Given the evidence that flicker adaptation is at least partially cortical, one could extend our paradigm to test if both mechanisms have cortical components by testing for interocular transfer of adaptation. D'Antona, Kremers, and Shevell (2011) have found evidence that the perception of flicker magnitude has a monocular and binocular component, which can be distinguished by a minimal binocular contribution at high (12.5 Hz) flicker rates. If these are the same mechanisms we tested, then our paradigm should also show some dependence on flicker rate when testing for transfer between eyes. Such work would help constrain the neural underpinnings of the mechanisms studied here.

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