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Flicker adaptation or superimposition raises the apparent spatial frequency of coarse test gratings

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ABSTRACT

Independent channels respond to both the spatial and temporal characteristics of visual stimuli. Gratings <3 cycles per degree (cpd) are sensed by transient channels that prefer intermittent stimulation, while gratings >3 cpd are sensed by sustained channels that prefer steady stimulation. From this we predict that adaptation to a spatially uniform flickering field will selectively adapt the transient channels and raise the apparent spatial frequency of coarse sinusoidal gratings. Observers adapted to a spatially uniform field whose upper or lower half was steady and whose other half was flickering. They then adjusted the spatial frequency of a stationary test (matching) grating on the previously unmodulated half field until it matched the apparent spatial frequency of a grating falling on the previously flickering half field. The adapting field flickered at 8 Hz and the spatial frequency of the gratings was varied in octave steps from 0.25 to 16 cpd. As predicted, adapting to flicker raised the apparent spatial frequency of the test gratings. The aftereffect reached a peak of 11% between 0.5 and 1 cpd and disappeared above 4 cpd. We also observed that superimposed 10 Hz luminance flicker raised the apparent spatial frequency of 0.5 cpd test gratings. The effect was not seen with slower flicker or finer test gratings. Altogether, our study suggests that apparent spatial frequency is determined by the balance between transient and sustained channels and that an imbalance between the channels caused by flicker can alter spatial frequency perception.

1. Introduction

It is well known that adaptation to a grating can distort perceived spatial frequency. Test gratings of higher spatial frequency than the adapting pattern appear to be even finer, and gratings of lower frequency than the adapting pattern appear to be even coarser, than they really are (Blakemore, Nachmias, & Sutton, 1970; Blakemore & Sutton, 1969). No shift is perceived if the test spatial frequency either matches the adapting frequency or differs from it by more than two octaves.

This spatial frequency shift has been explained as follows. A test grating of some particular spatial frequency arouses a distribution of activity in frequency selective channels. Adaptation to some other spatial frequency selectively depresses the sensitivity of a group of channels without changing their characteristic frequency. This skews the distribution of activity and the ratio of responses made to the same test grating, and this causes a change in perceived spatial frequency. This explanation assumes that channels are "labeled" in such a way that activity in a given channel somehow signals a particular spatial frequency.

Channels can be tuned to temporal as well as to spatial frequencies. Watson and Robson (1981) hypothesized that each channel was a "labeled line", which means that the visual system can perfectly identify the input signal by the identity of the channel signaling the input. Based on this hypothesis, if two stimuli were signaled by two different channels, even when the stimuli were barely detectable (at threshold), as long as they were detected, they could also be perfectly discriminated. In other words for these two stimuli, the discrimination threshold and absolute threshold should be equal. Conversely, if two stimuli were signaled by the same channel, discriminating the two should be more difficult than simply detecting them. Therefore the discrimination threshold should be higher than the absolute thresholds. From their data and this hypothesis, they concluded that there should be (at least) two distinct channels in the temporal frequency domain, one tuned to high temporal frequency and one tuned to low temporal

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frequency. Using the same logic and more temporal frequency conditions, Mandler and Makous (1984) concluded three temporal frequency channels were needed to explain their data. More recently, Cass and Alais (2006) showed that there were two temporal frequency channels, tuned to 5 Hz and 15 Hz, and that the high temporal frequency channel can suppress the low temporal frequency channel but the low temporal frequency channel does not suppress the other channel.

It has been also shown that spatial and temporal properties of our visual system are closely related and can sometimes interact. There is evidence that there are two types of spatiotemporal channels. Some channels are "transient", tuned to high temporal frequency and low spatial frequency. These channels are considered critical in motion perception. Other channels are "sustained". These channels have an opposite tuning to the transient channels; tuned to low temporal frequency and high spatial frequency (e.g., Anderson & Burr, 1985; Kulikowski & Tolhurst, 1973; Legge, 1978). For example, Kulikowski and Tolhurst (1973) found two contrast sensitivities for stationary pattern detection and flicker detection, the former being temporally low-pass and the latter being temporally band-pass with its peak at around 5–6 Hz. The relative contribution of the two channels depends on the pattern's spatial frequency, and the "form analyzer" is more responsive at higher spatial frequency than the "movement analyzer". Anderson and Burr (1985) found the peak of bandpass transient channels at around 10 Hz, depending on spatial frequency. Transient channels are dominant over sustained channels at low spatial frequency (such as 0.1 cpd) but sustained channels become dominant as the spatial frequency increases (such as 10 cpd).

These psychophysical channels are probably embodied in primary visual cortex (V1). Many monkey/cat V1/area 17 cells have band-pass or low-pass spatial frequency tunings (De Valois, Albrecht, & Thorell, 1982; Foster et al., 1985; Ikeda & Wright, 1975; Mazer et al., 2002) as well as temporal frequency tunings (bandpass and lowpass; Foster et al., 1985; Hawken, Shapley, & Grosof, 1996; Ikeda & Wright, 1975), and these are consistent with the human psychophysical contrast sensitivity data (Hawken, Shapley, & Grosof, 1996). Singh, Smith, and Greenlee (2000) studied spatiotemporal tunings of areas V1 to MT with fMRI techniques and concluded that V1 activity fits the psychological data best. LGN cells, however, are mostly low-pass in spatial tunings (Kaplan & Shapley, 1982) and are tuned to a higher range of temporal frequencies than V1 cells (Derrington & Lennie, 1984; Foster et al., 1985; Hawken, Shapley, & Grosof, 1996). Temporal tuning curves are not much different between P cells and M cells in the LGN: broadly tuned up to 10 (P) or even 20 (M) Hz (Derrington & Lennie, 1984). Foster et al. (1985), who used high contrast stimuli to examine the temporal tuning of cells in LGN and V1, showed the population peak activity at 16 Hz for LGN and 10 Hz for V1. Therefore psychophysical data (Anderson & Burr, 1985; Kulikowski & Tolhurst, 1973) favor V1 cells as the candidate neural basis for the psychological channels. Recent studies showed that the spatial tuning of individual V1 cells is dynamic in nature, with their peak shifting from low to high spatial frequencies with longer latencies (Bredfeldt & Ringach, 2002; Mazer et al., 2002). This may be the result of mixed inputs from M and P cells in LGN.

The close relationship between spatial and temporal properties implies that spatial manipulations can affect temporal perception and vice versa. For example, when a grating was flashed up briefly, its apparent spatial frequency increased (Georgeson, 1985; Kulikowski, 1975; Tynan & Sekuler, 1974). This effect was restricted to low spatial frequency gratings, indicating the involvement of transient channels, which are tuned to low spatial and high temporal frequency. Other temporal modulations of a grating can affect apparent spatial frequency in various ways (Kelly, 1966; Kulikowski, 1975; Richards & Felton, 1973; Virsu & Nyman, 1974). Kulikowski (1975) examined the role played by pattern and movement channels in producing illusory spatial frequency doubling of a counterphase flickering grating.

Conversely, spatial frequencies can affect the perceived temporal frequency of sinusoidal flicker (Bowker, 1982). Apparent flicker rate was higher for counterphase-flickering gratings than for spatially-uniform fields of the same temporal frequency, and this effect increased with increasing spatial frequency especially at low flicker rates. On the other hand, Smith and Edgar (1990) reported the opposite effect: the perceived temporal frequency of the counterphase grating decreased with increasing spatial frequency. Either way, these studies showed that the spatial properties of a stimulus affected temporal perception. All in all, strong interactions have been shown between spatial and temporal perception.

We shall now examine the effect of flicker adaptation on perceived spatial frequency of test gratings, and the ability of the transient/sustained channels hypothesis to explain the results.

2. Experiment 1: flicker adaptation raises apparent spatial frequencies

In this experiment, we examined the effect of flicker adaptation on apparent spatial frequency. We argue from the transient/sustained channels hypothesis that exposure to fast flicker should selectively adapt the transient channels leaving the sustained channels intact. Since the transient channels signal low spatial frequency as well as high temporal frequency, adapting out these channels by means of flicker would have the same effect as a low spatial frequency adaptor; both would cause an increase in the apparent spatial frequency of coarse gratings.

2.1. Method

2.1.1. Apparatus and stimuli

The stimuli were generated by a Picasso Image Synthesizer and displayed on a Tektronix 608 electrostatic-deflection monitor with a P31 (green) phosphor. The display was masked down to a 10.5 cm wide $\times$ 8.50 cm high rectangle by a 35.0 $\times$ 35.0 cm white cardboard surface illuminated at approximately the same mean level and hue. Viewing distance was 30, 57, or 137.5 cm depending on the spatial frequency condition. The display and mask subtended 20.0 $\times$ 16.2° and 66.5 $\times$ 66.5° respectively at a viewing distance of 30 cm, 10.5 $\times$ 8.50° and 35.0 $\times$ 35.0° at 57 cm, and 4.35 $\times$ 3.52° and 14.5 $\times$ 14.5° at 137.5 cm. A small black dot in the center of the display served as a fixation point. The duration of the stimuli and their spatial frequency, contrast, position, and temporal frequency were controlled by digital-to-analog converters (National Instruments analog output board (NB-AO-6)) under the control of a MacIntosh II. Viewing was binocular with natural pupils, and the observer's head was held in position by a chin rest. The Picasso and the monitor were calibrated to be linearized prior to the experiments. The mean luminance of the display was kept at 10 cd/m^2. We explored spatial frequencies over a six-octave range, from 0.25 to 16 cpd.

2.1.2. Observers

Five observers were run. All had normal or corrected-to-normal visual acuity and were practiced in psychophysical observations. All but one (DG) were naïve about the purpose of the experiments. The research was conducted in accord with the Code of Ethics of the World Medical Association (Declaration of Helsinki). The observers gave their informed consent.

2.2. Procedure

Each trial began with 60 s[1] (for the first trial of a session) or 5 s (top-up) adaptation to a spatially uniform field whose upper or lower half flickered sinusoidally at 8 Hz. This condition will be referred to as the flicker condition. In the baseline condition, the uniform adapting field was static with no temporal modulation. During the test interval the uniform field was replaced by two static vertical sinusoidal gratings, one above the other. Both gratings had the same mean luminance as the adapting field; their physical contrast was 1 log unit (10 times) above the baseline contrast threshold measured in a separate experiment. The spatial phase relationship between the two gratings was randomly varied. The spatial frequency of the standard grating that replaced the flickering half field was held constant at 0.25, 0.5, 1, 2, 4, 8 or 16 cpd on different trials. Each standard grating had a minimum of 5 cycles to ensure that its spatial frequency was tolerably well-defined (Regan, 1989), but this made it necessary to vary the viewing distance to obtain the desired range of spatial frequencies. The viewing distance was 30 cm (0.25 cpd), 57 cm (0.5–4.0 cpd) or 137.5 cm (8.0–16.0 cpd) on different trials. Observers used a knob to adjust the spatial frequency of the comparison grating that replaced the static field until it appeared to match the standard grating. To avoid eye-movement artifacts, observers were instructed to fixate on the dot in the center of the display throughout the trial. Six matches were made at each spatial frequency in both baseline and flicker conditions.

2.3. Results

The mean of six spatial frequency matches was taken as the point of subjective equality (PSE). We express the effects of flicker adaptation in terms of the increase in apparent spatial frequency in the flicker condition relative to the baseline condition with adaptation to a static field. The apparent spatial frequency shift was determined by the following formula:

$$\text{Apparent spatial frequency shift} = 100 * (\text{post-flicker PSE} - \text{baseline PSE})/(\text{baseline PSE}) \times (\%)$$

The same formula was used throughout this paper. The mean spatial frequency shift for the 5 observers is shown in Fig. 1 as a function of the standard spatial frequency. Results clearly show the predicted apparent spatial frequency shift. Flicker adaptation raised the apparent spatial frequency by up to 11%. The effect was biggest for the lowest standard spatial frequency (0.25 cpd) and decreased monotonically with increasing standard spatial frequency, falling to zero above 4 cpd.

Observers reported that the grating that followed the flickering field appeared to have a lower contrast than the grating that followed the static field. Given the documented dependence of perceived spatial frequency on perceived contrast (Georgeson, 1980, 1985), it is reasonable to question whether the apparent spatial frequency shift we observed was brought about by flicker adaptation per se or merely by a flicker-induced reduction in apparent contrast. To test for this, we made pilot measurements of the apparent *contrast* of the test gratings in the flicker condition (Experiment 2). We used these data to adjust the physical contrast of the test gratings so that they matched in apparent contrast, and ran Experiment 1 again as Experiment 3. If the apparent spatial frequency shift in Experiment 1 was brought about by apparent contrast change, then matching the apparent contrast of the gratings should eliminate the effect. On the other hand, if the effect was caused by flicker adaptation per se, the apparent spatial frequency shift should persist.

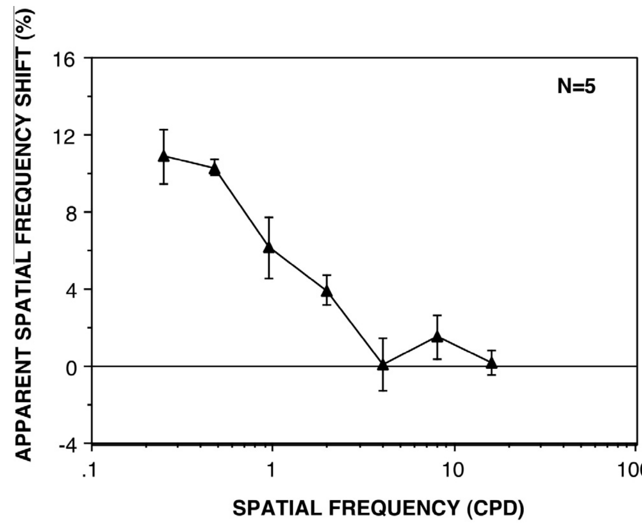

Fig. 1. Changes in apparent spatial frequency produced by adaptation to 8 Hz flicker. The zero line indicates no difference in spatial frequency, and points falling above this line indicate an apparent increase in spatial frequency following flicker adaptation. Each point is the mean of 6 spatial-frequency matches x 5 observers. Standard error bars are shown.

3. Experiment 2: flicker adaptation reduces apparent contrast

3.1. Methods

Two observers who participated in Experiment 1 also participated in Experiment 2. After the initial 60 s of adaptation to a uniform field with flicker in either the upper or lower half of the display, 10 test-readapt cycles were presented. During each test interval the standard grating had a fixed contrast of 1 log unit above threshold, but the contrast of the comparison grating, which replaced the flickering field, was one of 10 contrast levels spanning the range from 1 log unit above the detection threshold in the baseline condition to 1 log unit above the detection threshold in flicker condition. Observers chose the grating with the higher contrast. A psychometric function was fit to the% "comparison" data. The matched contrast, or PSE was taken to be the level that was reported higher than the standard contrast 50% of the time.

3.2. Results

We calculated the apparent contrast change using the following formula:

$$\text{Contrast compensation} = 100 * (\text{post-flicker PSE} - \text{baseline PSE})/\text{baseline PSE}\ (\%)$$

In this experiment, the comparison grating whose contrast was variable was on the flicker-adapted side, unlike in Experiment 1. Therefore, if the post-flicker PSE was higher than the baseline PSE, that suggests that the apparent contrast was *decreased* via flicker adaptation since it means that the observers had to compensate for the reduced apparent contrast by increasing the physical contrast of the comparison. Contrast compensations are shown in Fig. 2 for two observers. As stated above, the greater these values are, the greater the contrast reduction via flicker adaptation. Fig. 2 shows that apparent contrast reduction was marked,

[1] Pilot work showed that longer adaptation time did not change the extent or duration of the aftereffect.

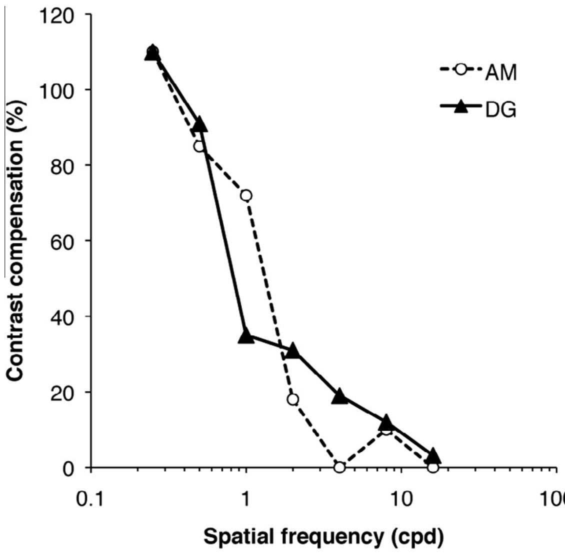

Fig. 2. Contrast compensation, or the increase in physical contrast of the comparison grating after flicker adaptation in order to match the standard grating, is shown. Open circles are data from observer AM and filled triangles are from observer DG (one of the authors).

especially for the test gratings of lower spatial frequencies (0.25–1 cpd). For higher spatial frequencies, the apparent contrast reduction was little to moderate.

4. Experiment 3: apparent spatial frequency shift with matched apparent contrast

4.1. Methods

The two observers who participated in Experiment 2 also participated in Experiment 3. The flicker condition of Experiment 1 was repeated at all seven spatial frequencies with the test gratings matched in apparent contrast based on the results of Experiment 2. Other conditions and procedures were identical to Experiment 1. Observers adjusted the spatial frequency of the comparison grating that replaced the static field until it appeared to match the standard grating.

4.2. Results

Apparent spatial frequency shifts with gratings matched in apparent contrast are presented in Fig. 3, along with the original results obtained with the gratings matched in physical contrast (i.e., Experiment 1). Although adaptation to flicker did reduce the apparent contrast of the test grating (Fig. 2), the spatial frequency shift was only slightly smaller when the gratings were matched in apparent contrast. The difference in spatial frequency shift in Experiment 1 and this experiment did not reach significance (AM: $F(1, 70) = 1.682$, $p > .05$: DG: $F(1, 70) = 0.243$, $p > .05$). Therefore, the increase in spatial frequency following adaptation to a flickering field was not due simply to a reduction in apparent contrast, although such reduction was found to occur.

5. Experiment 4: superimposed flicker raises apparent spatial frequencies

In Experiment 1 and 3, we confirmed that adapting to 8 Hz flicker increased the apparent spatial frequency of low-frequency gratings. This effect can be called the *successive* effect of flicker on spatial frequency. In Experiment 4, we explored the *simultaneous* effect of flicker: the effect of superimposed flicker on the apparent spatial frequency of a grating (see Fig. 4).

5.1. Methods

5.1.1. Apparatus and Stimuli

All stimuli were presented on a 19″ CRT monitor (SONY CPD-G400; Sony Corporation, Tokyo, Japan) controlled by an Apple Mac-Pro (Apple Inc., California, USA). Viewing distance was 52 cm. A chin rest was used to maintain the viewing distance. The experiment was run in a darkened room.

All stimuli were generated using the MATLAB (The MathWorks) programming environment with Psychtoolbox (Brainard, 1997; Pelli, 1997) routines. Standard gratings and comparison gratings were 40° wide × 4° high sinusoidal grating strips presented in the upper or lower half of the display at 3° eccentricity. A fixation point was provided at the center of the display. The contrast of the comparison grating was fixed at 20%. Spatial frequency conditions of the standard grating were 0.5 and 4 cpd. The standard grating of 40% contrast was presented as 50% transparent, superimposed on a luminance flicker of the same size. The luminance flicker was

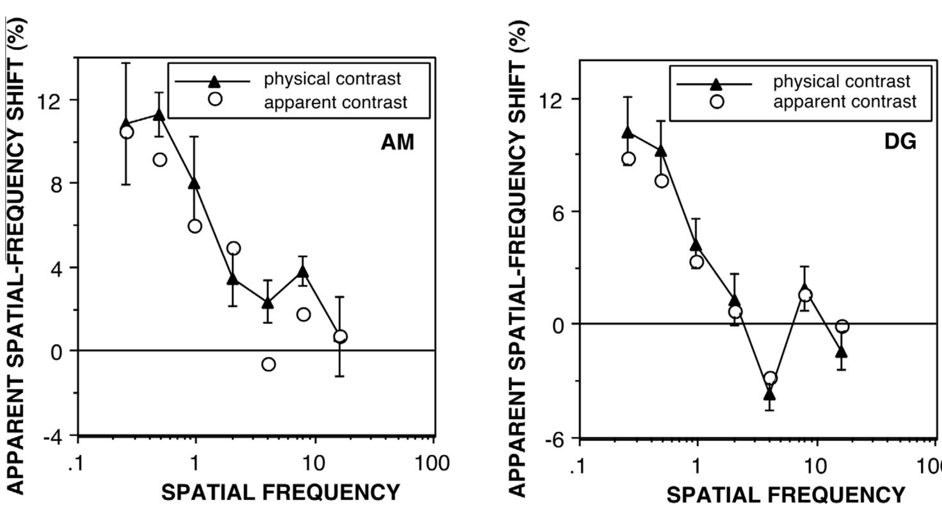

Fig. 3. Changes in apparent spatial frequency following flicker adaptation with the test gratings matched in either apparent or physical contrast. Results are shown for 2 observers. Each point is the mean of 6 spatial-frequency matches. Standard error bars are shown for the original data obtained with the gratings matched in physical contrast. Using the physically matched or subjectively matched contrast made no significant difference.

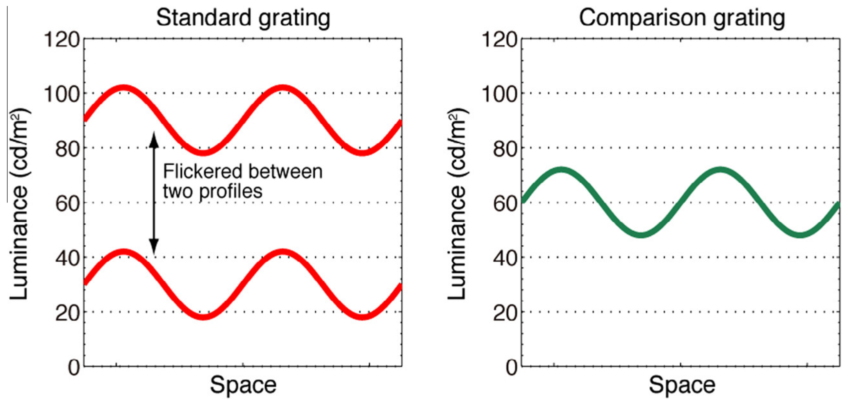

Fig. 4. Luminance profiles of standard (flickering) grating (on left) and comparison (static) grating. The standard grating flickered at 0.5 Hz or 10 Hz, but the comparison grating did not change over time. Note that since the amplitude of each grating (i.e., luminance difference between lightest and dimmest point in a grating) was kept constant, the Michaelson contrast of the standard grating changed.

modulated at 100% contrast in temporal square-wave fashion. The mean luminance of the resulting grating varied between 30 and 90 cd/m^2; the contrast varied between 40% and 13% because the luminance difference between the lightest and dimmest point was kept constant. Flicker rate conditions were 0.5 or 10 Hz. In addition to these two conditions, there was a baseline condition, where the standard grating was superimposed on a static mean-luminance gray. The rest of the display was uniform gray at a mean luminance level of 60 cd/m^2.

5.1.2. Observers

Four naive observers participated. All had normal or corrected-to-normal visual acuity. Observers were unaware of the purpose of the experiment.

5.1.3. Procedure

The method of adjustment was used for Experiment 4. The standard and comparison gratings were presented in the upper and lower halves of a display, positioned above and below the central fixation point. Locations of the gratings were counterbalanced across sessions. Observers adjusted the spatial frequency of the comparison grating (the one without the superimposed flicker) by key press until both gratings appeared to have the same spatial frequency. Adjustment step size was 2.5% of the standard spatial frequency. Initial spatial frequency of the comparison grating and the phase of both gratings were randomized. Sixteen matches were made for each condition.

5.2. Results

As in previous experiments, the apparent spatial frequency shift was calculated based on the PSE from flicker and baseline conditions. Average spatial frequency shift data from four observers are presented in Fig. 5. Independent *t*-tests revealed that only the 0.5 cpd/10 Hz condition showed a shift significantly greater than 0% (no illusion) [0.5 cpd/0.5 Hz condition ($t(3) = 0.43$, $p = .69$); 0.5 cpd/10 Hz condition ($t(3) = 4.98$, $p < .05$); 4 cpd/0.5 Hz condition ($t(3) = -1.02$, $p = .38$); 4 cpd/10 Hz condition ($t(3) = 0.92$, $p = .43$)]. This suggests that with a fast flicker superimposed, coarse gratings appear to have higher spatial frequency.

6. Discussion

Experiments 1–4 showed that flicker can affect apparent spatial frequency. In Experiment 1 we showed that adapting to 8 Hz

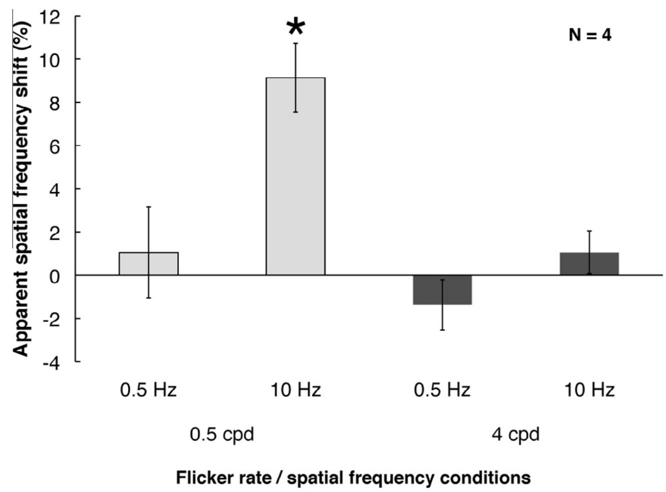

Fig. 5. Post-flicker apparent spatial frequency shift (PSE difference from baseline condition). Average across four observers. Error bars are ±1 SE. Light gray bars for 0.5 cpd grating and dark gray bars for 4 cpd grating. Only 0.5 cpd/10 Hz condition showed the significant increase from 0% shift (* = $p < .05$).

luminance flicker could increase the apparent spatial frequency of a subsequent test grating. In Experiments 2 and 3, we confirmed that the apparent spatial frequency shift seen in Experiment 1 was due to flicker adaptation, and was not simply the byproduct of an apparent contrast reduction. Experiment 4 showed that a superimposed luminance flicker could increase the apparent spatial frequency of a grating. All of these effects were seen only with coarse (0.5–1 cpd) gratings, not with fine gratings (>4 cpd).

These results are consistent with a model of spatiotemporal interaction in which low spatial frequency channels have band-pass temporal frequency selectivity and high spatial-frequency channels have low-pass temporal selectivity (Anderson & Burr, 1985; Kulikowski & Tolhurst, 1973; Legge, 1978). The low-pass shape of Fig. 1 curve shows us the spatial tuning of the mechanism that is adapted-out by flicker. The adaptation effect (Fig. 1, see also Fig. 6) is prominent in the low spatial frequency range and almost nonexistent in the >4 cpd range. That suggests the channels that were knocked-out are most responsive to low spatial frequencies and contribute little to the appearance of high (>4 cpd) spatial frequency gratings. This spatial tuning fits the known properties of the transient channels well (Anderson & Burr, 1985; Kulikowski & Tolhurst, 1973; Legge, 1978).

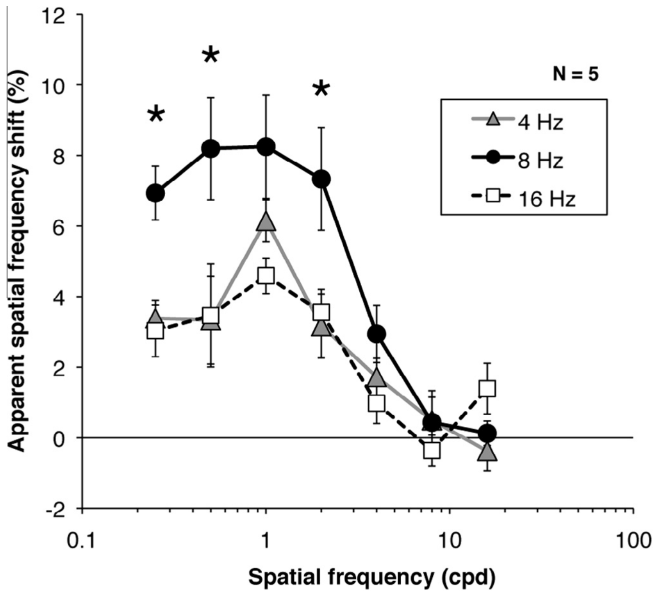

Fig. 6. Apparent spatial frequency shift after adapting to three different flicker rates; 4 Hz (triangles), 8 Hz (circles) and 16 Hz (squares). Average of five observers. Each observer made four matches per condition. 8 Hz flicker produced a greater illusion than the other two flicker rate conditions. Asterisks show the conditions where the 8 Hz adaptation effect is significantly stronger.

The observed shifts in apparent spatial frequency can be explained as follows: Adaptation to flicker desensitizes transient channels tuned to low spatial frequencies but leaves sustained channels tuned to higher spatial frequencies unchanged. The coarse test gratings would normally activate both transient and sustained spatial frequency channels, but flicker adaptation would reduce the activity of the transient compared to the sustained channels. The spatial frequency of these gratings is therefore perceived as higher because the balance of activity has been upset, with the peak activity occurring at a higher spatial frequency after adaptation. Flicker adaptation does not alter the perception of finer test gratings (>4 cpd) because adaptation does not change the pattern of activity within sustained channels tuned to high spatial frequencies/low temporal frequencies.

We have characterized our flicker experiments as a temporal adaptation that gives a spatial aftereffect. But one might object that flickering the adapting field serves merely to raise its effective contrast. A flickering field that alternates between black and white has a higher mean contrast than a steady mid-gray static field, so it may act simply like a high-contrast, zero-spatial frequency adapting field. We have addressed this objection by flickering the adapting field at different rates (4, 8, 16 Hz). Using the same method as in Experiment 1, we reran the 8 Hz condition and added the 4 and 16 Hz conditions, and obtained the results shown in Fig. 6 (5 observers, 4 readings per datum point).

The results shown in Fig. 6 are consistent with those in Experiment 1, Fig. 1; the apparent spatial frequency shift was greater for low spatial frequencies, declining and disappearing towards higher spatial frequencies. At first glance the three curves in Fig. 6 appear to have a band-pass shape, having peaks at around 0.5–1 cpd, but they do not differ significantly from the low-pass data of Experiment 1. ANOVA revealed the main effects of both flicker rates [$F(2, 8) = 17.01$, $p < .05$] and test spatial frequencies [$F(6, 24) = 13.26$, $p < .05$]. Also, a significant interaction was found [$F(12, 48) = 2.57$, $p < .05$]. Post-hoc analysis of the interaction (Bonferroni, $p = .05$) showed that at low spatial frequencies, 8 Hz gave a stronger effect than 4 Hz and/or 16 Hz, shown by asterisks in Fig. 6. The most relevant finding here is that the aftereffects also peaked for an adapting flicker frequency of 8 Hz and declined for both slower and faster flicker rates (4 and 16 Hz). If only the higher contrast of the flickering field relative to the static field was important, then all three flicker rates should have given the same results. These temporal band-pass results show that the temporal properties of the adaptor were indeed important, and the flicker did not act merely like a high-contrast version of a static adapting field.

That 8 Hz adaptation gives a stronger effect than 4 Hz or 16 Hz adaptation also tells us about the temporal tuning of our "transient" channels that were knocked out by adaptation. The channels are temporally tuned to 8 Hz and are less sensitive to lower or higher frequencies. In addition to the spatial tuning revealed by Experiment 1 (Fig. 1), these channels are spatially low-pass and temporally band-pass with a peak at 8 Hz. These quantitatively fit the previous psychophysical data of transient channels well (Anderson & Burr, 1985; Kulikowski & Tolhurst, 1973; Legge, 1978). As for physiological candidates, the 8 Hz peak activity is a better fit to V1 population data (10 Hz) than to LGN population data (16 Hz) (Hawken, Shapley, & Grosof, 1996).

Is there an alternative explanation to our proposed channel imbalance following adaptation? If some of the channels' tuning shifted towards the adaptor frequency instead of away, this could explain the repulsive effect of apparent spatial frequency (Gilbert & Wiesel, 1990; Kohn & Movshon, 2004). For example, Kohn and Movshon (2004) examined the directional aftereffect of movement, and showed that the direction tuning of MT neurons was narrower and shifted towards the adaptor direction. They argued that this *attractive* tuning shift of MT neurons corresponded to the perceptual *repulsive* effect, i.e., motion direction aftereffect. Our spatial frequency aftereffect, however, likely involved neurons in V1. The spatial frequency tuning of V1 neurons has been shown to shift after spatial frequency adaptation (Movshon & Lennie, 1979; Saul & Cynader, 1989), but the shift was in a repulsive direction, not an attractive direction. If, like Kohn and Movshon (2004), we assume that each neuron's response has a fixed label regardless of adaptation, a repulsive tuning shift should not give the known perceptual spatial frequency aftereffect. On the other hand, the overall reductions in responsivity of V1 neurons are well observed (Movshon & Lennie, 1979; Saul & Cynader, 1989), and can explain the repulsive aftereffect. We suggest that our flicker-adaptation-induced spatial frequency shift also caused by the reduction of responsivity of neurons/channels that signal high temporal frequency/low spatial frequency, not the tuning shift of those channels.

Results from Experiment 4 showed that flicker affected the spatial frequency perception not only successively but also simultaneously. Virsu and Nyman (1974) and Nyman and Rovamo (1980) reported similar results. They found that counterphase-flickering a coarse grating at 8 Hz increased its apparent spatial frequency. Our results further indicate that the effect of flicker can be generalized for a different type of flicker, not just counterphasic or monophasic. Virsu and Nyman (1974) argued from their data that the temporal modulation changed the selectivity of spatial-frequency-selective channels.

There have been a number of studies on the effects of spatially-uniform flicker. A single-channel 'labeled-line' model cannot predict the results of masking and adaptation studies involving spatially-uniform flickering fields. Such flicker affects the appearance of low spatial frequencies only, confirming that low spatial frequencies are processed by channels sensitive to temporal change.

A spatially uniform field flickering at 20 Hz was found to mask wide flickering bars (60 min) but not narrow flickering bars (5 min) (Stromeyer, Zeevi, & Klein, 1979). This selectivity of masking was taken as evidence that wide and narrow bars are detected by different mechanisms. The authors suggested that wide bars, which contain more energy at low spatial frequencies, were detected by transient channels and narrow bars were detected by sustained channels. Unfortunately, the temporal tuning of this masking was not studied.

Breitmeyer, Levi, and Harwerth (1981) found that reaction times and visual persistence to stationary sinusoidal gratings increased with increasing spatial frequency, and a 6 Hz flickering field mask increased both measures for test gratings below 4 cpd. Their flickering mask also increased contrast thresholds for detecting flicker at test spatial frequencies below 8 cpd, and slightly decreased detection thresholds for patterns below 2 cpd. They concluded that 6 Hz flicker strongly masked the activity of channels tuned to low spatial frequencies, but left channels tuned to higher spatial frequencies relatively unaffected. They suggested that the increase in reaction time and response persistence with spatial frequency indicated a transition from short latency, low spatial frequency transient channels (<4 cpd) to long-latency, high spatial frequency sustained channels.

Green (1981) found that adaptation to a spatially uniform flickering field raised the contrast threshold for detecting low spatial frequency gratings drifting or counterphase flickering at the same temporal frequency as the adapting stimulus. However, the temporal tuning of this effect was quite broad. Adaptation to a 2.5, 7.5, or 15 Hz flicker raised thresholds for gratings of drift rates between 0.6 and 20 Hz. The threshold elevation curves were low-pass in shape with an upper cutoff at 4 cpd. Similar results were obtained when flicker thresholds rather than absolute detection thresholds were measured. Green concluded that flicker adaptation desensitizes a transient system but has no effect on a separate sustained system. Legge (1978) found a similar spatial frequency tuning for the transient channel.

At first glance, our effects of superimposed flicker may not easily fit our hypothesis: One might expect that superimposed fast flicker would activate the low spatial frequency tuned channel and shift the peak activity toward lower frequencies. The result was, however, the opposite. The results are unexpected but seem to be consistent with previous masking studies.

Spatial frequency selective masking effects are known. A superimposed masking grating reduces the detectability of a test grating. This masking effect is the strongest when the two gratings have the same spatial frequency and gets weaker as the difference in spatial frequencies goes up to 2 octaves (e.g., De Valois & Switkes, 1983).

Spatial frequency specific masking also affects suprathreshold percepts. Gelb and Wilson (1983) examined the apparent spatial frequency of difference of Gaussians (DOG) when masked by single frequency gratings. They showed that the apparent spatial frequency of DOG increased when masked by a grating whose spatial frequency was 1.5 octaves lower than the DOG or 1 octave above it. With a lower spatial frequency mask, the apparent spatial frequency shifted upwards.

According to the transient/sustained hypothesis, temporal and spatial frequencies are processed by overlapping mechanisms, so for the visual system the high temporal frequency input should be almost equivalent to, or indistinguishable from, the low spatial frequency input. Therefore, in Experiment 4, superimposing the fast luminance flicker on a low spatial frequency grating was almost like superimposing a low spatial frequency mask on the grating. Consequently, as in Gelb and Wilson (1983), the spatial frequency of the grating appeared to be higher.

Stromeyer, Zeevi, and Klein (1979) suggest that coarse and fine bars may preferentially stimulate transient and sustained mechanisms, respectively. They found that background flicker selectively interrupts the detection of a coarse bar, not a fine bar. This shows that simultaneous presentation of fast flicker, which is optimal for transient channels, inhibits the transient channel's ability to signal spatial frequency information. Likewise, our superimposed flicker should also inhibit transient channels, and the resulting imbalance between transient and sustained channels should shift the perceived spatial frequency of a test grating upwards. In short, the transient/sustained channels paradigm can predict our results in Experiment 4.

Recently, Putzeys et al. (2012) demonstrated the strong effect of superimposed noise on spatial frequency perception. They used low-pass filtered and high-pass filtered one-dimensional spatial noise as maskers, and superimposed them on a test grating. They found an assimilative effect: when a grating was presented together with a masker that had broad spatial frequencies lower than the grating, the apparent spatial frequency of the grating was judged lower than veridical, and vice versa. They attributed this strong (±30%) spatial frequency shift to the suboptimal broadly-tuned decoders, that were unable to single out the target spatial frequency signal from the noise signals from encoders. The results of this study are not consistent with ours: we found that superimposing spatially uniform flicker made test gratings look higher in spatial frequency.

This discrepancy may be related to the spatial frequency of the test gratings. The spatial frequencies of our test gratings (0.5 and 4 cpd) were selected to stimulate both transient and sustained channels. We assumed that the imbalance between these channels would only affect spatial frequency perception when they were both sufficiently active; we found no spatial frequency shifts at 4 cpd. Putzeys et al. (2012) used a single spatial frequency of 5.5 cpd, which was higher than our highest spatial frequency and might have been too high to adequately stimulate the transient channel. Also, since their apparent spatial frequency shift was far stronger than our modest ~10% shift, we speculate that the underlying mechanisms are fundamentally different.

We now turn to computational models of visual pattern detection. Goris et al. (2013) propose a two-stage neural population model, in which the first stage *encodes* visual stimuli, such as gratings, with an array of linear, spatial frequency-tuned neurons in V1 (see Blakemore & Campbell, 1969). Linearity is then lost owing to squaring and gain control mechanisms (Carandini & Heeger, 2012). The second stage is a *decoder* that takes perceptual decisions based upon maximum-likelihood. In other words it decides what stimulus is most likely to have produced the observed pattern of neural firing. Goris attributes adaptation to gratings (Blakemore & Campbell, 1969) to an encoding (first stage) effect, while the spatial frequency assimilation effect (Putzeys et al., 2012) is due to a limitation in the decoder (second stage). Our flicker-adaptation effect should have the same underlying mechanism as the standard spatial frequency adaptation effect (Blakemore & Campbell, 1969), namely the encoding stage of the model of Goris et al. (2013). It is more difficult to place the superimposed effect in the context of this model because the temporal nature of the spatial encoders is not specified. Uniform flicker should be encoded by a totally different set of encoders from the ones that encode the target gratings, therefore the decoders should have no trouble telling those signals apart and perception should be veridical. Because it is difficult to attribute the errors to the decoding stage, we only assume by exclusion that it should also occur at the encoding stage.

Altogether, our results are consistent with the perception of spatial frequency being mediated by the balance between transient channels tuned to high temporal and low spatial frequency, and sustained channels tuned to low temporal and high spatial frequency. By adapting out (Experiments 1 and 3) or by masking (Experiment 4) transient channels through high contrast fast flicker, we can tip the balance to create the apparent shift in spatial frequency.

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