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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 × 8.50 cm high rectangle by a 35.0 × 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 × 16.2° and 66.5 × 66.5° respectively at a viewing distance of 30 cm, 10.5 × 8.50° and 35.0 × 35.0° at 57 cm, and 4.35 × 3.52° and 14.5 × 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.