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Evidence for two interacting temporal channels in human visual processing

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Abstract

Previous studies have generally estimated that two independent channels underlie human temporal vision: one broad and low-pass, the other high, and band-pass. We confirm this with iso-oriented targets and masks. With orthogonal masks, the same high-frequency channel emerges but no low-pass channel is observed, indicating the high-frequency channel is orientation invariant, and possibly pre-cortical in origin. In contrast, orientation dependence for low frequencies suggests a cortical origin. Subsequent masking experiments using unoriented spatiotemporal-filtered noise demonstrated that high-frequency masks (>8 Hz) suppress low-frequency targets (1 and 4 Hz), but low frequencies do not suppress high frequencies. This asymmetry challenges the traditional assumption of channel independence. To explain this, we propose a two-channel model in which a non-orientation-selective high-frequency channel suppresses an orientation-tuned low-frequency channel. This asymmetry may: (i) equalise the over-representation of low temporal-frequency energy in natural stimuli (1/f power spectrum); (ii) contribute to motion deblurring.

Keywords: Temporal frequency; Channels; Masking; 1/f; Orientation; Filtering

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1. Introduction

As neural signals ascend the visual processing pathway they undergo a considerable transformation. For example, new tuning properties such as orientation selectivity emerge between the lateral geniculate nucleus (LGN) and primary visual cortex (V1), as does binocular integration (Hubel & Wiesel, 1962) and the conversion from cardinal to non-cardinal colour space (Johnson, Hawken, & Shapley, 2001). However, some aspects of ascending signals get lost rather than elaborated. For example, it has been shown that LGN units are sensitive to a higher range of temporal frequencies than are V1 units (Hawken, Shapley, & Grosof, 1996). This paper examines the relationship between orientation selectivity and temporal-frequency selectivity.

One phenomenon that is evident in V1 that is not typically observed in LGN is cross-oriented masking. This refers to a reduction in the firing-rate of otherwise optimally driven, orientation-selective V1 neurons due to the superposition of an orthogonal masking stimulus whose orientation fails to drive the masked neuron when presented alone (Bishop, Coombs, & Henry, 1973; Morrone, Burr, & Maffei, 1982). One early study concluded that cross-orientation masking is likely to result from intracortical processes due to its (reversible) extinguishment following a cortically applied pharmacological blockade of the major inhibitory neurotransmitter, gamma-aminobutyric acid (GABA) (Morrone, Burr, & Speed, 1987). However, recent studies call this interpretation into question. Psychophysical (Meier & Carandini, 2002) and single-unit neurophysiological studies (Allison, Smith, & Bonds, 2001; Freeman, Durand, Kiper, & Carandini, 2002) report that cross-oriented masking occurs in the presence of masks whose temporal modulation rate exceeds the typically reported high-frequency cut-off of V1 neurons of ≈15 Hz (Alitto & Usrey,

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2004; Allison et al., 2001; Burr, Morrone, & Maffei, 1981; Hawken et al., 1996).

These recent studies, then, suggest that cross-oriented masking may not be mediated by V1 units at all, but by other inhibitory processes. Non-V1 candidates for cross-oriented masking include extra-striate feedback to V1 (Allison et al., 2001) and pre-cortical inhibitory processes possibly involving thalamocortical synaptic depression (Freeman et al., 2002). Freeman et al. (2002) also note that LGN neurons are immune to both adaptation and cross-oriented masking, a correlation consistent with a pre-cortical site for cross-oriented masking.

Overall, however, the available evidence does not offer a clear picture of where cross-oriented masking originates. High temporal cut-off frequencies of up to 50 Hz have been reported in V1 units (Orban, Kennedy, & Maes, 1981), as have very robust stimulus phase-locking at rates of up to 100 Hz (Williams, Mechler, Gordon, Shapley, & Hawken, 2004). In addition, Freeman et al.'s (2002) claim that LGN neurons do not exhibit adaptation has been challenged in a recent demonstration of robust adaptation in LGN neurons (Solomon, Peirce, Dhruv, & Lennie, 2004). Therefore, claims that cross-oriented masking cannot originate in V1 are equivocal.

In this study, we use an alternative diagnostic cue- orientation- to assess whether pre-cortical mechanisms contribute to cross-oriented masking. The suitability of orientation stems from that fact that pre-cortical neurons exhibit poor orientation selectivity (Reid & Alonso, 1996; Shou & Leventhal, 1989) while many cells in V1 are sharply tuned for orientation (Hubel & Wiesel, 1962). Therefore, if temporal masking is indeed mediated by pre-cortical mechanisms, then we can expect that it will not be dependent upon the relative orientation of target and masking stimuli.

To preview the results, we find that the relative orientation of signal and mask does indeed affect the shape of the temporal masking function, but only for low (1 Hz) and not for high (15 Hz) temporal-frequency signals. These data suggest that there are two masking mechanisms, which differ in their orientation and temporal-frequency selectivity. One is an orientation-invariant, high-frequency mechanism, which appears to peak at 8–12 Hz and to suppress low temporal frequencies. It is possibly of pre-cortical origin (Freeman et al., 2002). The other is an orientation-selective mechanism tuned to lower temporal frequencies, possibly cortical in origin.

Because orientation appeared to distinguish between these two temporal-frequency mechanisms, we conducted an additional set of temporal masking experiments using spatio-temporally filtered dynamic noise stimuli. As these stimuli have no dominant orientation (unlike most previous studies), a different pattern of results from grating-based studies might be expected. These experiments showed, in contrast to the standard model in which temporal channels operate independently, that visual temporal-frequency channels interact in an asymmetric fashion. Specifically, high temporal-frequency channels appear to suppress those selective to lower frequencies, but not vice versa. We speculate that this asymmetric suppressive architecture may serve an equalising function to compensate for the preponderance of low temporal frequencies in natural image sequences (which have a 1/f power spectrum: (van Hateren, 1997)). Additionally, this temporal asymmetry may also be involved in the perceptual phenomenon known as motion deblurring (Burr, 1980).

2. Methods

2.1. Equipment

Stimuli were generated using a Macintosh G5 computer driving an ATI Radeon 9600 graphics card and displayed on a Mitsubishi Diamond Plus 93SB monitor with 800 × 600 pixel resolution running at 120 Hz vertical refresh rate. Matlab™ software was used to produce images and control stimulus presentation. All images were pre-drawn using 10-bit luminance resolution and stored in video memory. Stimuli were observed through a viewing chamber which prevented all ambient light from entering the visual field.

2.2. Stimuli

Viewing distance was 57 cm and the visual angle subtended by the illuminated visual field was 66° × 49.2°. A mean luminance of 91 cd m^{-2} was maintained throughout the stimulus sequence. The mask and target stimuli were circular (Experiments 1 and 2: diameter = 10.76° visual angle; Experiment 3: $\sigma = 0.25°$ visual angle) and concentrically located upon a small dark fixation point. The surround was a homogenous field of mean luminance.

2.2.1. Experiment 1

Target and mask stimuli each consisted of a temporally sinusoidal counterphasing luminance grating (4 cycles/°) of variable temporal frequency. Target grating orientation was held at 135°, and the orientation of the mask carrier was either 135° (iso-oriented condition) or 45° (cross-oriented condition). The exposure duration of each target/masking stimulus interval was 1 s (120 frames). Targets were presented at either 1 or 15 Hz. Mask frequencies were 1, 1.5, 2, 3, 4, 5, 6, 8, 10, 12, 15, 20, 24, and 30 Hz.

2.2.2. Experiment 2

Target and mask stimuli each consisted of independent 120 frame (1 second) sequences of spatially and temporally band-pass filtered 'noise'. The production of these stimuli comprised three stages. The first stage involved the generation of the raw, unfiltered noise stimuli. These were generated by computing two 120 frame 'stacks' of 256 × 256 pixel matrices (one stack each for target and masking stimuli). Pixels were assigned a random luminance value either side of mean luminance. The second stage involved filtering in spatial frequency (ω_{xy}) dimensions. This was done by applying a radial, one-octave wide band-pass filter which operated at a radial distance from the origin that was proportional to spatial frequency. This band-pass ω_{xy} filtering procedure reduced the complexity of the initial spatial waveform to its constituent sinusoidal spatial-frequency components between 2 and 4 cycles/°. The third stage involved applying a band-pass temporal-frequency (ω_t) filter to the spatially filtered noise sequences (Fig. 1). This was accomplished by extracting the sinusoidal components of the temporal-frequency (ω_t) dimension beyond the one-octave range defined by the temporal-frequency filter. Lower bound filter frequencies were 1, 4, 15, and 24 Hz for the target and 1, 1.5, 2, 3, 4, 5, 6, 8, 10, 12, 15, 20, 24, and 30 Hz for the masking stimuli. Both spatial and temporal-frequency filters operated ideally. The stimuli in Experiments 1 and 2 both were both enveloped within a square edged luminance transition,