Temporal frequency and chromatic processing in humans: An fMRI study of the cortical visual areas

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Psychophysical sensitivity to isoluminant chromatic modulation declines at temporal frequencies beyond 4 Hz, whereas chromatically opponent cells of the afferent visual pathway (long- to middle-wavelength (L–M) cone-opponent or short-wavelength (S) cone cells) show responses at much higher temporal frequencies, indicating a central limitation in temporal processing capacity. Here, we sought to localize this limit in cortical retinotopic visual areas. We used fMRI to investigate responses of lateral geniculate nucleus and cortical visual areas in humans to isoluminant chromatic modulation as a function of temporal frequency (2–12 Hz). Our results suggest that L–M cone-opponent and S-cone signals are processed in LGN up to 12 Hz. In all visual areas except MT (middle temporal) and V3a, S-cone responses declined steeply with temporal frequency, implying that psychophysical sensitivity loss to blue–yellow modulation might occur early within these areas. While V1 showed robust L–M responses up to 12 Hz, there was a progressive falloff of responses with temporal frequency as information is transferred from V1 to higher areas (V2, V3, and V4), suggesting that, in humans, temporal limitation in perception of red–green chromatic modulation likely results from limited processing capacity of higher ventral extrastriate areas.

Keywords: color vision, temporal frequency, isoluminance, cone-opponent, visual areas, retinotopy, fMRI


Introduction

There are multiple afferent pathways in the primate visual system. The long- (L) to middle-wavelength (M) cone-opponent ([L–M]) parvocellular (PC) pathway originates in the midget ganglion cells of the retina and forms the basis of detection of red–green color contrast and plays a role in high acuity spatial vision. A short-wavelength (S) cone system forms the substrate for contrast detection along a blue–yellow dimension and is associated with the koniocellular (KC) pathway. Finally, the magnocellular (MC) pathway, originating in the parasol ganglion cells, is thought to form the basis of a luminance channel responsible for photometric tasks such as flicker photometry and detection of luminance flicker (Kaiser, Lee, Martin, & Valberg, 1990; Kremers, Lee, Pokorny, & Smith, 1993; Lee, 2011; Lee, Martin, & Valberg, 1988; Lee, Pokorny, Smith, Martin, & Valberg, 1990). Spatial and temporal characteristics of these pathways, in both retina and lateral geniculate nucleus (LGN), have been extensively studied employing electrophysiological methods (e.g., Blakemore & Vital-Durand, 1986; Derrington, Krauskopf, & Lennie, 1984; Derrington & Lennie, 1984; Dreher, Fukuda, & Rodieck, 1976; Lee, Valberg, Tigwell, & Tryti, 1987). Retinal ganglion cells of the afferent pathways respond up to luminance modulation frequencies that match or exceed the human critical fusion frequency (20–50 Hz at photopic levels depending on retinal illuminance; Lee et al., 1990). Equivalent studies in the LGN appear to show similar temporal frequency tuning properties, although comparison of data is
complicated by the different luminance levels used in different studies (Derrington & Lennie, 1984; Lankheet, Lennie, & Krauskopf, 1998a, 1998b; Levitt, Schumer, Sherman, Spear, & Movshon, 2001).

Psychophysical data have shown that while humans are capable of detecting luminance modulation at high temporal frequencies, detection sensitivity of isoluminant chromatic modulation falls off rapidly above 4 Hz and is only possible up to ca. 10–15 Hz (Kelly, 1983; Swanson, Ueno, Smith, & Pokorny, 1987). Retinal ganglion cells respond to chromatic modulation at higher temporal frequencies (Lee, Martin, & Valberg, 1989b; Lee et al., 1990); temporal tuning in LGN to chromatic modulation has not been systematically studied, but data that are available (Derrington et al., 1984; Lankheet et al., 1998a, 1998b) indicate good responses at frequencies of 15–20 Hz or more. Although some degree of temporal filtering in the LGN cannot be excluded, responsiveness to high temporal frequencies in the primary visual cortex (V1) is more restricted (Foster, Gaska, Nagler, & Pollen, 1985; Hawken, Shapley, & Grosof, 1996). Nevertheless, responses can still be obtained to well beyond 10 Hz. Similarly, restricted frequency response characteristics have also been observed for the extrastriate visual areas (Foster et al., 1985; Gegenfurtner, Kiper, & Levitt, 1997; Levitt, Kiper, & Movshon, 1994), although neurons of area MT (middle temporal) respond well to higher frequencies (Lui, Bourne, & Rosa, 2007; Priebe, Cassanello, & Lisberger, 2003). However, all these studies have been primarily concerned with achromatic or luminance-only modulation; temporal tuning properties of chromatically responsive cells have received little attention (Hawken, Shapley, Mechler, & Ringach, 1997).

Functional MRI has been used previously to determine response properties of the human visual areas to luminance and chromatic stimuli; such studies aimed at locating cortical specialization for processing temporal change. There is evidence that, when presented with high cone contrasts, LGN responses are robust to both achromatic and chromatic stimuli (L–M cone-opponent and S-cone) at frequencies up to 10 Hz (Kastner et al., 2004; Mullen, Dumoulin, & Hess 2008; Mullen, Thompson, & Hess, 2010; Schneider, Richter, & Kastner, 2004). As for the cortical areas, the primary visual cortex (V1) also shows robust responses at higher frequencies for L–M cone-opponent and luminance stimuli (Engel, Zhang, & Wandell, 1997; Jiang, Zhou, & He, 2007; Kastner et al., 2004; Kleinschmidt, Lee, Requardt, & Frahm, 1996; Liu & Wandell, 2005; Mullen, Dumoulin, McMahon, de Zubicaray, & Hess, 2007; Mullen et al., 2010; Singh, Smith, & Greenlee, 2000; Wade, Augath, Logothetis, & Wandell, 2003); an MEG study has also shown strong responses at 8–10 Hz (Fawcett, Barnes, Hillebrand, & Singh, 2004). There have been incidental observations suggesting that the S-cone response decreases with increasing frequency in V1, although this may be contrast-dependent (Liu & Wandell, 2005). Further, there is some evidence suggesting that extrastriate areas have different frequency tuning characteristics as compared to V1, with areas in the ventral pathway preferring low frequencies and dorsal areas responding equally well to low and high frequencies (Liu & Wandell, 2005; Tootell et al., 1995; Wade et al., 2008). As for specialization for time-varying stimuli, Tootell et al. (1995; Liu & Wandell, 2005) have proposed a common functional network comprising visual areas V3a and MT, despite these areas being quite far apart on the cortical surface. The proposed network is believed to be responsible for processing high-frequency information; chromatic components may not be encoded efficiently there, however. Although these previous fMRI studies have investigated how the striate and extrastriate areas process chromatic modulation, here our specific goal was to ascertain neural loci limiting the temporal processing of chromatic information.

In this study, we used fMRI to characterize the temporal frequency response properties of LGN and cortical retinotopic visual areas. We measured fMRI responses in LGN and cortical visual areas as a function of temporal frequency, with selective stimulation of the chromatic (L–M cone-opponent, S-cone) and luminance pathways. We confirmed that, even though the response amplitudes in LGN were smaller than those in cortical visual areas, there was no systematic decline in chromatic and luminance responses as a function frequency. In the cortex, the limit to temporal resolution is imposed further on than the primary visual cortex (V1), although temporal filtering of S-cone signals may begin at this site. It was shown that, based on the temporal frequency response profiles, cortical visual areas can be grouped into clusters.

**Methods**

**Subjects**

Six healthy volunteers (3 females and 3 males; mean age: 24 ± 4 years) participated in the study. All subjects had normal visual acuity and were color normal; normalcy for color vision was checked by the Farnsworth-Munsell 100-Hue Test. Informed written consent was obtained from subjects prior to participation in each experimental session. All experimental procedures strictly conformed to the institutional guidelines and were approved by the institutional review board.

**Visual display system**

Visual stimuli were generated using the VSG ViSaGe system (Cambridge Research Systems, Rochester, UK) and projected by a SANYO, PLC-XT 11 LCD projector.
(pixel resolution: 1024 × 768; frame rate: 80 Hz; mean luminance: 126 cd/m²) onto a translucent screen mounted on top of the MRI head coil seen through a 45° tilted mirror (Schäfer and Kirchhoff, Hamburg, Germany) by the subject. The visual display subtended a visual angle of approximately 28° horizontally and 21° vertically. For retinotopic mapping experiments, the visual stimuli were generated using a stand-alone software tool based on the Microsoft DirectX library (StimulDX, Brain Innovation, Maastricht, The Netherlands).

**Calibration**

The LCD projector system was calibrated for luminance and chromaticity by defining gamma curves and spectral properties separately for each of the three RGB color channels. For gamma correction within the scanner, we used a fiber optic cable and a digital luminance meter (Mavo-Monitor USB, GOSSEN Foto- und Lichtmesstechnik, Nürnberg, Germany) and followed the procedures as described by Strasburger, Wustenberg, and Jancke (2002) to determine the relationship between the digital input value and the output level of the LCD meter. In that procedure, a fiber optic cable allows the luminance meter to be outside the scanner room; attenuation of each primary by the fiber optic cable was separately checked and corrected. The luminance values were entered manually into the VSG gamma calibration software. The chromaticity of the projector output was calibrated with a PR-650 Spectra Colorimeter (PhotoResearch, Chatsworth, MA) using a mirror arrangement. The CIE chromaticity coordinates for the R, G, and B primaries were then entered into the VSG software before the gamma-corrected lookup tables (LUTs) were generated. The temporal characteristics of the LCD projector were verified using a photodiode whose signal was led through an operational amplifier to a digital oscilloscope (TDS 2024B, Tektronix, Beaverton, OR). The rise and fall times of the LCD projector were sufficiently fast to faithfully present visual stimuli at frequencies up to 12 Hz.

**Visual stimuli**

**Spatial profile:** The stimuli were contrast-reversing circular sine-wave gratings spanning a diameter of 21°, with a central cross (1° in diameter) to maintain fixation. To minimize the influence of cortical magnification, we used an approximately M-scaled stimulus with a spatial frequency of 4 cpd at the center, scaled across eccentricity to 0.16 cpd at the perimeter (e.g., Figure 1a).

**Temporal profile:** Grating contrast was modulated sinusoidally at different frequencies, with the start and end of a block of a given frequency equal to the mean luminance and chromaticity for that condition. In each cycle, the contrast of the grating was modulated at one of the six different temporal frequencies. The order in which these were presented was pseudorandomized within each cycle.

![Figure 1](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932800/) Spatial layout of the pathway-selective stimuli and experimental paradigm. Circular sine-wave gratings with spatial frequency scaled with eccentricity to compensate for cortical magnification were used. Stimuli to selectively stimulate the (a) L–M cone-opponent, (b) luminance (L+M), and (c) S-cone pathways are shown. Stimuli were modulated sinusoidally around the mean chromaticity and luminance. (d) An experimental run, for stimulation of an individual pathway, commenced with a control period followed by six cycles. Each cycle consisted of six stimulus blocks and a control block. In each stimulus block, the contrast of the grating was modulated at one of the six different temporal frequencies. The order in which these were presented was pseudorandomized within each cycle.
block, the stimuli were held at the same contrast, i.e., the contrast step for that particular condition was abrupt.

Pathway-selective stimuli: Three types of stimuli, “L–M,” “L+M,” and “S,” were designed to stimulate the L–M cone-opponent (Figure 1a), luminance (L+M) (Figure 1b), and S-cone (Figure 1c) postreceptoral pathways, respectively; the abbreviation “L+M” is used to refer to luminance modulation, since it is thought that S-cones do not contribute to luminance (Smith & Pokorny, 1975). The L–M and S-cone stimuli were isoluminant, i.e., varied in their chromatic content only, whereas in the L+M stimulus, only the luminance was modulated. We calibrated our stimuli using the red, green, and blue spectral emissions of the LCD projector and the Smith and Pokorny’s 10° cone fundamentals (Smith & Pokorny, 1975; Smith, Pokorny, Davis, & Yeh, 1995). Cone fundamentals were multiplied with the emission spectra, resulting in the calibration matrix. The matrix values represent the spectral absorptions of the S-, M-, and L-cones to red, green, and blue lights, respectively. Using these cone excitation values, we computed the chromaticity values for the pathway-selective stimuli. The resulting mean CIE chromaticity coordinates for the L–M, luminance, and S conditions were (0.51, 0.47), (0.51, 0.47), and (0.26, 0.22), respectively. We also carried out preliminary experiments in which stimuli for all conditions were modulated around equal-energy white. These stimuli had lower cone contrasts (<10%) and evoked fMRI signals were weaker and less reliable, especially in LGN and extrastriate visual areas. However, the pattern of results was very similar to those presented here; the legitimacy of using different mean chromaticities for the different conditions is taken up in the Discussion section. In the present experiments, the L–M cone-opponent, luminance, and S-cone stimuli had a mean luminance of 126 cd/m², and modulation of the LCD primaries was modified to give a mean cone contrast of 29%, calculated as the vector length (square root of the sum of squares) of the individual cone contrasts (Liu & Wandell, 2005). Individual isoluminance setting for the chromatic stimuli was obtained for each observer with the minimum motion technique (Anstis & Cavanagh, 1983) inside the scanner, using the same experimental setup. We found that for all subjects tested isoluminance values were close to those of the standard CIE observer.

Experimental design

Each subject participated in three experimental runs lasting 10 min each. In a typical run, one of the three stimulus gratings (L–M, L+M, or S) was shown at six different temporal modulation frequencies (2, 4, 6, 8, 10, and 12 Hz) using a block design paradigm (Figure 1d) similar to that used by Henriksson, Nurminen, Hyvarinen, and Vanni (2008).

Each experimental run commenced with a 24-s control period (data from the first 12 s were discarded in the analysis), followed by six stimulus cycles. Each cycle (96 s) consisted of six stimulus blocks (12 s each) and a control block (24 s). In each stimulus block, we presented contrast-reversing gratings at one of the given temporal frequencies. The order in which these frequencies were presented was pseudorandomized within each cycle and balanced across the experimental run. During the control blocks, no stimulus appeared and a blank screen was shown with the same mean chromaticity and luminance as each grating stimulus. Each run lasted 600 s (300 functional volumes, TR = 2 s). A small fixation cross was present throughout the run.

To maintain fixation, the volunteers were instructed to fixate on a contrast-modulated central cross present during the stimulus and control blocks of the experimental run. The fixation cross was luminance modulated (2 Hz sinusoidal) with a 50% Michelson contrast. At random intervals, its luminance was set to zero, resulting in a black cross; to keep subjects alert, their task was to count the occurrence of these black crosses during the entire experimental run. All subjects detected more than 95% of these (black cross) events.

Magnetic resonance imaging (MRI)

All imaging studies were performed on a 2.9-T scanner (Magnetom Tim Trio, Siemens, Erlangen, Germany) using a 12-channel receive-only phased-array head coil.

Anatomical data: A high-resolution T1-weighted 3D data set (MPRAGE, 1 × 1 × 1.1 mm³) was acquired in each retinotopic session. These images were used to reconstruct the cortical surfaces for mapping and visualization purposes. At the beginning of each main experimental session, T1-weighted 3D FLASH images (1 × 1 × 1 mm³) were acquired. These anatomical images served to coregister the functional data with the high-resolution MPRAGE data acquired in the retinotopic session.

Functional data: A T2*-sensitive gradient-echo echo-planar imaging (EPI) technique with an in-plane resolution of 2 × 2 mm² (repetition time TR: 2000 ms, echo time TE: 36 ms, flip angle: 70°, acquisition matrix: 96 × 96) was used to acquire functional volumes. Twenty-two consecutive sections of 4-mm thickness, approximately perpendicular to the calcarine fissure, covered early as well as higher visual areas in the occipital lobe.

MRI data processing and analysis

Data analysis was performed using BrainVoyager QX 1.10 (Brain Innovation, Maastricht, The Netherlands). The anatomical volumes (MPRAGE) acquired in the retinotopic sessions were first interpolated to a 1 × 1 × 1 mm³ isovoxel resolutions. Subsequent processing steps included correction for intensity nonuniformity, AC–PC transformation, and finally transformation of the data to a standard stereotaxic space (Talairach transformation) for
reconstructing the cortical surfaces at the white–gray matter boundary. The surface reconstructions for each hemisphere were then inflated. Anatomical volumes acquired during the main experimental sessions were automatically aligned to MPRAGE data from the retinotopic sessions. Preprocessing of the functional data included deletion of the initial six volumes (to allow the longitudinal magnetization to reach a steady state), 3D motion correction (also including intra-session alignment), slice-time correction, temporal high-pass filtering (3 cycles/run), linear trend removal, and spatial smoothing with a Gaussian kernel (full width at half-maximum $4 \times 4 \times 4$ mm$^3$). After the preprocessing, functional data were coregistered to the anatomical volume (FLASH) acquired at the beginning of the same session and, subsequently, transformed into Talairach space.

### Identification of visual areas

Retinotopic mapping was performed for each of the six subjects in separate scanning sessions.

**Localization of LGN:** The stimulus for identification of the LGN was constructed from high-contrast checkerboard patterns flickering at 8.33 Hz (Figure 2a). It was presented in a block design comprising periods of 12-s activation and 18-s controls. During the control phase, a gray screen with luminance equal to the average of the black and white checks was presented. A GLM analysis of the data was performed to obtain activation maps in response to checkerboard stimulation. Statistical maps of $t$-values were visualized (Figures 2b and 2c) at Bonferroni-corrected threshold level of $p = 0.001$. Regions of interest (ROIs) were constructed based on the statistically significant voxels in the appropriate anatomical location (Kastner et al., 2004; Schneider et al., 2004). We identified the peak voxel within the LGN region (i.e., the voxel having the maximal correlation with the presentation of the stimulus) and from that chose a maximum cluster spread range of 10 voxels (mm) on each dimension ($x, y,$ and $z$). An ROI was defined as the set of all voxels within this cubic range whose activity in response to the checkerboard stimulus was above threshold ($p = 0.001$). The mean Talairach coordinates of the two LGNs across all subjects are given in Table A1 (see Appendix A).

**Delineation of cortical visual areas:** Standard phase-encoded retinotopic mapping procedures were employed to map the visual field eccentricities (expanding rings) and to distinguish boundaries separating the visual areas (polar angle mapping) (DeYoe et al., 1996; Engel et al., 1994). We also obtained maps of the horizontal and vertical meridian by using meridian-specific stimuli that alternated in a block design to further confirm the delineation of visual areas (Figure 3a).

**Mapping of area MT (middle temporal):** The human motion-sensitive area was mapped (Figure 3b) by comparing responses to stationary white dots with those to a motion stimulus that consisted of white dots moving radially outward on a gray screen. This stimulus is known to produce a clear MT response (Tootell et al., 1995).

### Region-of-interest (ROI) analysis

To estimate the strength of the fMRI response within each of the retinotopically mapped visual areas (ROIs), we performed a general linear model (GLM) analysis separately for each subject. To do so, we first extracted the mean fMRI time course of a given ROI and experimental run, for each of the three stimulus conditions (L–M, L+M, and S), by averaging over the ROI’s voxels. The time course was then normalized to $z$ values and the GLM with six predictors (corresponding to six temporal frequencies) and a baseline (control block) was fit to the normalized time course. The time course of the predictors was obtained from the stimulation protocol and had been convolved with the double-gamma hemodynamic response function (Boynton, Engel, Glover, & Heeger, 1996). In the GLM equation, each predictor time course is associated with a beta weight $\beta$, quantifying its statistical contribution to the ROI time course. The six beta weights in this context reflect the strength of the fMRI response at
the six different temporal frequencies (2, 4, 6, 8, 10, and 12 Hz).

Statistical analysis

For each ROI, we calculated the mean fMRI response amplitude across all subjects as a function of temporal frequency for the three stimulus types (L–M, L+M, and S). Repeated-measures ANOVAs and planned comparisons were performed for each stimulus type separately to study the effects of frequency, area, and their interaction.

Cluster analysis

We hypothesized that cluster analysis of the temporal response profiles of cortical visual areas will reveal a functional organizational structure, within the dorsal and ventral cortical streams, in correspondence with the visual field map clusters (Wandell, Dumoulin, & Brewer, 2007). To capture the temporal profiles, we first calculated response amplitudes as a function of temporal frequency for each subject, visual area, and stimulus type. Next, we fitted second-order polynomials (McKeeff, Remus, & Tong, 2007) to the data such that the first- and second-order terms in the equation allowed us to effectively capture the linear (slope) and nonlinear (curvature) trends present in the temporal frequency response profiles across visual areas. A hierarchical cluster analysis was then performed on the mean first- and second-order coefficients of the polynomials fitted to the frequency response data corresponding to eight cortical visual areas (MT, V3a, V3d, V2d, V1, V2v, V3v, and V4) and three stimulus conditions (L–M, L+M, and S). Cluster analysis was performed using the SPSS 16.0 statistical package. We used the within-group linkage procedure for combining clusters and the squared Euclidean distance for the distance measure. The output of the hierarchical cluster analysis is represented as a dendrogram.

Results

Temporal frequency tuning profiles for each visual area were obtained by plotting the mean fMRI response amplitudes—averaged across subjects (twelve hemispheres)—as a function of frequency, for L–M cone-opponent, luminance (L+M), and S-cone stimulus conditions. To better visualize whether visual areas differed in their temporal response properties, mean response amplitudes were normalized to the response evoked by the lowest frequency, i.e., 2 Hz. We analyzed response profiles for the LGN, the primary visual cortex (V1), and areas of the ventral (V2v, V3v, and V4) and dorsal (V2d, V3d, V3a, and MT) visual pathways.

Temporal frequency response profiles for LGN and V1

Figure 4 provides a comparison of response profiles for the LGN and V1, separated by stimulus condition. Both mean and normalized fMRI responses are shown in Figures 4a–4c and Figures 4d–4f, respectively. Two-way
repeated-measures ANOVAs were performed on the data set from each of the plots in Figures 4a–4c, to assess whether fMRI response strength reliably varied across areas (LGN versus V1) or temporal frequencies. The analysis revealed that in each ANOVA there was a main effect of brain area, i.e., a significant difference in overall response amplitudes between LGN and V1 (L–M: $F = 320.60, p < 0.001$; L+M: $F = 199.13, p < 0.001$; S: $F = 100.06, p < 0.001$). For the L+M and S-cone conditions, there was also a significant main effect of frequency (L+M: $F = 4.86, p = 0.013$; S: $F = 20.93, p < 0.001$) and a significant interaction between visual areas and frequency (L+M: $F = 5.23, p = 0.013$; S: $F = 28.96, p < 0.001$). For the S-cone condition, there was a significant frequency effect in V1 only (LGN: $F = 1.44, p = 0.25$; V1: $F = 45.36, p < 0.001$).

The interaction effects in the luminance and S-cone conditions indicate that frequency response profiles differ across visual areas; subsequent one-way ANOVAs across frequency revealed a significant frequency effect for both LGN and V1 in the luminance condition (LGN: $F = 3.95, p = 0.004$; V1: $F = 7.20, p = 0.002$). For the S-cone condition, there was a significant frequency effect in V1 only (LGN: $F = 1.44, p = 0.25$; V1: $F = 45.36, p < 0.001$).

In general, response amplitudes were smaller in LGN than in V1, for all three stimulus conditions. From visual inspection of the data, it appears that the most prominent change in response across visual areas occurs for the S-cone stimulus. For the L–M stimulus, both the LGN and V1 showed no change in response strength with frequency. In the case of the luminance stimulus, the LGN showed variable responses with frequency, whereas in V1 response strength dropped from 2 to 4 Hz, followed by approximately constant amplitude up to 12 Hz. For the S-cone stimulus, in LGN there is little systematic change in response across frequency. However, there was a consistent decrease in response strength with frequency in V1; this was further confirmed by the statistical analyses. Liu and

Figure 4. Temporal frequency response profiles for the LGN and V1. Mean fMRI responses, averaged over six subjects (12 hemispheres), are plotted as a function of frequency for individual visual areas. Subplots show frequency response profiles for (a) L–M cone-opponent, (b) L+M (luminance), and (c) S-cone stimuli, respectively. Error bars indicate ±SEM. The lower row of subgraphs (d–f) shows the same data normalized relative to the response evoked by the lowest frequency, i.e., 2 Hz. There was a significant difference between LGN and V1 (L–M: $F = 320.60, p < 0.001$; L+M: $F = 199.13, p < 0.001$; S: $F = 100.06, p < 0.001$). For the L+M and S-cone conditions, there was also a significant main effect of frequency (L+M: $F = 4.86, p = 0.013$; S: $F = 20.93, p < 0.001$) and a significant interaction between visual areas and frequency (L+M: $F = 5.23, p = 0.013$; S: $F = 28.96, p < 0.001$). For the S-cone condition, there was a significant frequency effect in V1 only (LGN: $F = 1.44, p = 0.25$; V1: $F = 45.36, p < 0.001$).
Wandell (2005) have previously reported that such differential responses between low and high frequencies occur with low cone-contrast S-cone stimuli, although, at high cone contrast (>25%), both low and high frequencies elicited equally strong responses in V1. Possible reasons for this discrepancy are taken up in the Discussion section.

**Temporal frequency tuning in ventral visual areas (V2v, V3v, and V4)**

Going up the visual pathway, Figure 5 next provides a comparison of temporal frequency response profiles for the ventral visual areas (V2v, V3v, and V4), separated by stimulus condition. The V1 response profiles repeated in these plots serve as a reference. As in the previous graph, both mean and normalized fMRI responses are shown in Figures 5a–5c and Figures 5d–5f, respectively. Overall response amplitudes for all three stimulus conditions declined progressively across ascending visual areas starting from V1, which is reflected in terms of a main effect of area in the two-way ANOVAs (L–M: $F = 43.05$, $p < 0.001$; L+M: $F = 30.47$, $p < 0.001$; S: $F = 5.98$, $p = 0.002$). For the L–M condition, the response profiles varied across visual areas, especially for V3v and V4. There was a drop in response amplitude from 2 to 4 Hz, followed by near-constant response amplitude up to 12 Hz. This drop at 4 Hz becomes more marked through the ventral areas. Statistical analyses showed a significant overall main effect of frequency and a significant interaction between visual areas and frequency for the L–M condition (frequency effect: $F = 4.79$, $p = 0.008$; interaction: $F = 8.57$, $p < 0.001$). From the graph, it is seen that the change across frequency is limited to higher areas. For the luminance (L+M) stimulus, response patterns across ventral visual areas were all very similar to those of V1, also showing a drop in response amplitude at 4 Hz, followed by an approximately constant amplitude up to 12 Hz (frequency effect: $F = 4.89$, $p = 0.01$) and no interaction ($F = 1.03$, $p = 0.40$). Finally, for the S-cone stimulus condition, all ventral areas showed reliable effects of frequency and some evidence of differences in response profiles across visual areas. For all areas, responses declined steeply with frequency leading to a

![Figure 5](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932800/)
significant main effect ($F = 34.55, p < 0.001$). Shape of the response profiles also varied across visual areas, as seen from the significant statistical interaction ($F = 4.34, p = 0.01$). Subsequent one-way ANOVAs performed to investigate the nature of frequency profiles suggested that there was a reliable modulation in response amplitude as a function of frequency for the S-cone stimulus in every single ventral area. Area V2v showed a nonsignificant trend for L–M stimulus ($F = 1.6, p = 0.21$), and area V4 showed a nonsignificant trend for the luminance (L+M) stimulus ($F = 2.39, p = 0.09$).

**Temporal frequency tuning in dorsal visual areas (V2d, V3d, V3a, and MT)**

Figure 6 provides a comparison of frequency response profiles for the dorsal visual areas (V2d, V3d, V3a, and MT), separated as before by stimulus condition. The V1 response profiles in these plots again serve as a reference. Mean and normalized fMRI responses are shown in Figures 6a–6c and Figures 6d–6f, respectively. Overall response amplitudes for all three stimulus conditions varied across visual areas, and there was a main effect of area in the two-way ANOVAs (L–M: $F = 22.95, p < 0.001$; L+M: $F = 14.29, p < 0.001$; S: $F = 10.94, p < 0.001$). The plots indicate that response profiles of MT and V3a differed substantially from other dorsal areas, whose response patterns were similar to their ventral counterparts. The response of dorsal areas to L–M stimulus showed no reliable main effect of frequency ($F = 1.97, p = 0.148$) but revealed a highly significant interaction ($F = 11.98, p < 0.001$). Whereas for the luminance (L+M) condition the main effect of frequency was nonsignificant ($F = 2.63, p = 0.098$) and the interaction was significant ($F = 9.23, p < 0.001$), both the frequency effect and interaction were significant in the case of the S-cone condition (frequency: $F = 14.62, p < 0.001$; interaction: $F = 39.12, p < 0.001$). Because of the latter, we performed additional one-way ANOVAs to investigate in which of the areas the frequency response varied. In these, all areas showed reliable modulations in the response amplitude as

![Figure 6](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932800/)
a function of frequency for the luminance condition. While area V2d showed a nonsignificant trend for the L–M stimulus ($F = 2.75$, $p = 0.07$), area V3a showed a nonsignificant trend for the S-cone stimulus type ($F = 2.42$, $p = 0.10$).

**Properties of shape of temporal frequency response profiles**

As described above, the shapes of the frequency response profiles vary across visual areas. While in many areas there is a monotonic increase or decrease in response amplitude with frequency, some other areas show nonmonotonic relationships. We characterized the shape properties of the response profiles quantitatively by fitting second-order polynomials to the data obtained for each visual area, stimulus type, and subject. First- and second-order term coefficients of the fitted polynomials allowed us to effectively capture the linear (slope) and nonlinear (curvature) trends, respectively. The sign of the slope and curvature value is also important: a positive sign indicates an increase in response amplitude across frequency, i.e., high-pass behavior, and a negative sign indicates a decline of response (low-pass behavior). For the curvature value, a positive sign indicates that the frequency response profile shows a minimum, whereas a negative sign indicates band-pass characteristics. The results of polynomial fittings are shown in Figures 7a–7c, for L–M, luminance (L+M), and S-cone conditions, respectively. For the L–M stimulus type, visual areas showed both linear and minor nonlinear trends in their frequency response profiles. The slopes in ventral areas V3v and V4 were large and negative and statistically significant, reflecting a decline in response with frequency. Similarly, dorsal areas V2d and V3d showed significant negative slopes. Among these, areas V3v, V4, and V3d also showed small but significant positive curvature values. Unlike the other areas, there was a monotonic increase in response amplitude with frequency in area MT, indicated by a significant positive slope. As for the luminance (L+M) stimulus, areas V2d and V3d showed significant negative slope values and a significant positive curvature for V2d. For MT, in contrast, the slope was significantly positive. Unlike in the L–M and luminance (L+M) conditions, for the S-cone stimulus type the response profiles across visual areas could be summarized just by their slope values. Statistically significant negative slopes in ventral areas V1, V2v, V3v, and V4 and dorsal areas V2d and V3d indicated that the response amplitudes decreased with frequency. The slope value for area V3a was positive, though nonsignificant. As with the two other stimuli conditions, there was an increase in response amplitude with frequency in area MT, which is indicated by a positive significant slope value. The analysis of slope and curvature for frequency response profiles across visual areas further confirmed the results obtained using the ANOVAs in the previous sections.

**Cluster analysis of cortical visual areas**

In the previous section, we summarized the frequency response profiles across cortical visual areas by the estimated first- and second-order coefficients of polynomial fitting. To find regularities in these tuning-type coefficients, they were subsequently used in a hierarchical cluster analysis to group visual areas according to the similarity in their response profiles. It is expected that grouping of visual areas based on their frequency response properties will reveal a functional organizational structure within the visual cortex. The clustering was based on the slope and curvature coefficients obtained for all three stimulus conditions; the result is shown in Figure 7d as a dendrogram. Visual areas V1, V2, V3, and V4 formed one main cluster with two subclusters, one composed of areas V1 and V2v and the other by V3d, V3v, V2d, and V4. That main cluster, in combination with V3a, formed another cluster as opposed to an independent cluster comprising area MT only. These clusters of visual areas with different functional specialization for temporal frequencies show a good correspondence with visual field map clusters proposed by Wandell, Brewer, and Dougherty (2005).

**Discussion**

We measured fMRI responses in LGN and cortical visual areas as a function of temporal frequency of the stimulus. The purpose was to compare the frequency response profiles across multiple visual areas of the visual pathway, with the goal of understanding the possible origin of the temporal limit in processing chromatic information. We selectively stimulated chromatic (L–M cone-opponent and S-cone) and luminance (L+M) pathways, at frequencies ranging from 2 to 12 Hz. The stimuli used had matched cone contrast to allow for comparison of fMRI responses across conditions in the different visual areas.

**Temporal tuning in LGN**

L–M cone-opponent responses in LGN were more vigorous than those to L+M and S-cone modulations, as has been reported by other authors (Mullen et al., 2008, 2010). L–M responses were maintained up to 12 Hz and S-cone and luminance responses also persisted up to this frequency. This is again similar to earlier results (Mullen et al., 2008, 2010), although others (Kastner et al., 2004) report an increase in luminance response with frequency; however, this difference may be more apparent than real, for the most obvious increase in the latter authors’ report was from 0.5 to 7.5 Hz, intermediate frequencies not being tested; the lowest frequency in the other reports was 2 Hz.
Figure 7. (Left) Summary of the shape properties of the frequency response profiles for the cortical visual areas. Second-order polynomials were fitted to the response profiles obtained for each visual area, stimulus type, and subject. Mean value of the first-order coefficients (slope values; gray) and second-order coefficients (curvature values; black) of the fitted polynomials across visual areas are shown for (a) L–M, (c) Luminance (L+M), and (e) S-cone conditions, respectively. *p < 0.05 and **p < 0.005, significance level as calculated by a one-sample t-test comparing the mean values with zero. (Right) Cluster analysis for these coefficients. The dendrogram depicts the output of the hierarchical cluster analysis as applied to the coefficients obtained from polynomial curve fitting to the response profiles. Visual areas are clustered based on the properties of shape of their frequency response profiles to all three stimulus conditions (L–M, L+M, and S).
Comparison of the temporal response of electrophysiological and fMRI recordings from the afferent pathways (and cortex) is complicated by the fact that retinal illuminance differs between different studies, and many studies only used luminance modulation. Temporal response at different luminance levels has been studied in ganglion cells (Lee et al., 1990). However, Derrington and Lennie (1984) measured the temporal response of LGN cells to luminance modulation at ca. 1400 td and found a similar temporal response to ganglion cells at 2000 td (Lee et al., 1990). In another detailed LGN study (Levitt et al., 2001), retinal illuminance can be estimated to have been a few hundred trolands (based on display luminance, in the absence of a specified pupil diameter); the achromatic temporal response of PC and MC cells appears similar to that of ganglion cells at the equivalent illuminance. Temporal tuning to chromatic modulation has also been most extensively studied in ganglion cells, but data that are available suggest similar properties in LGN at an equivalent illuminance (Lankheet et al., 1998a, 1998b). Different fMRI studies have also used different luminance levels; most have used displays with luminances of 30–50 cd/m², but those of Kastner et al. have used higher levels (Kastner et al., 2004; Schneider et al., 2004) as did the present study (127 cd/m²); 30–50 cd/m² would correspond to a few hundred trolands. Taking retinal and LGN physiological data as a whole, PC cells at and above this retinal illuminance would appear to respond to frequencies above the modulation frequency at which chromatic modulation is no longer perceived (10–15 Hz). If there is any low-pass filtering of the retinal signal in the LGN, it is above this frequency range.

Recent fMRI studies in LGN using chromatic modulation (Mullen et al., 2008, 2010) set mean stimulus chromaticity about the white point. This limits maximum achievable cone contrast for the L–M stimulus (typically <10%). In our experiments, the colors were modulated about nonwhite mean chromaticities that depended on the pathway to be isolated. This approach yielded a maximum cone contrast of 29% for the L–M cone-opponent stimulus, with the goal of obtaining reliable fMRI responses even at high frequencies in all visual areas. In terms of the goal of these experiments—the loss of psychophysical chromatic sensitivity at high temporal frequencies—mean chromaticity does not affect psychophysical results; for example, Swanson et al. (1987) used an orange mean chromaticity to achieve higher cone contrast, as was the case here.

As in the data of Mullen et al. (2010), our fMRI results show low-pass frequency tuning for luminance stimuli, which does not resemble the frequency response patterns exhibited by either the MC or PC pathways, which typically have a band-pass characteristic (Derrington & Lennie, 1984; Lee et al., 1990). Mullen et al. also found a low-pass response pattern with fMRI measurements at low luminance contrasts, which might favor selective MC pathway activation. This difference between fMRI and physiological results is puzzling, and as pointed out by the above authors, the relation between BOLD response and neural activity is a complex one; spiking activity may not be the main driver of the BOLD signal. An additional complication is that maintained activity levels in the thalamus (and its input) may be high, and any response consisting of a modulation of firing without changing mean rate might not affect the BOLD signal. Finally, the more vigorous LGN response to L–M than to luminance or S-cone stimuli is likely to be attributable to the higher numerosity and larger volume of cells in the PC layers compared to the MC layers or to cells in the KC layers. In these experiments, we could not resolve the sublaminae of the LGN. It is possible to do so using high-resolution fMRI (Schneider et al., 2004); it may be possible to selectively investigate temporal tuning in the PC and MC layers using this technique.

**Temporal frequency response in primary visual cortex (V1)**

In V1, we observed robust L–M and luminance (L+M) responses for frequencies up to 12 Hz. A number of other studies have explored temporal frequency as a parameter (Engel et al., 1997; Jiang et al., 2007; Kleinschmidt et al., 1996; Liu & Wandell, 2005; Mullen et al., 2007; Singh et al., 2000; Wade et al., 2008) and found robust responses up to 10 Hz or above. However, studies that have specifically investigated temporal tuning have yielded mixed results. Mullen et al. (2010) reported data similar to ours, but Singh et al. (2000) found a more high/band-pass frequency tuning. One reason for this (Mullen et al., 2010) may be the 2-cpd spatial frequency used. Kastner et al. (2004) also reported a high-pass temporal frequency dependency but using square-wave reversing check patterns, which have a broad temporal frequency spectrum. However, low temporal frequency square-wave modulation contains much energy in a higher frequency range, which might be expected to enhance responses at such frequencies. Sinusoidal modulation provides a more frequency-specific stimulus. As mentioned above, one critical parameter might be the spatial structure of the stimulus. In an early study using Ganzfeld stimuli (Kleinschmidt et al., 1996), responses to full-field red–green modulation were found to be much more vigorous than with luminance stimuli. This differs from the results of Mullen et al. (2010) and those here, in which red–green and luminance responses were of similar magnitude, but both these latter studies used spatially patterned stimuli. The gratings used in our experiments approximated an M-scaled stimulus and are likely to have provided optimum spatial frequencies at different eccentricities. This might point to a more critical role of spatial structure in evoking BOLD responses for luminance rather than chromatic stimuli. Spatial structure is known to strongly affect psychophysical sensitivity to luminance.
modulation at low temporal frequency (Kelly, 1969), either due to static contrast effects or as a consequence of fixational eye movements. In any event, there is no indication of temporal filtering of the [L–M] signal below 10 Hz in V1, whereas psychophysical sensitivity has decreased markedly at this frequency. For S-cone modulation, the current study differs from that of Mullen et al. (2010) in finding marked low-pass filtering. However, other studies (Liu & Wandell, 2005; Mullen et al., 2007) have found a decrease in S-cone response with temporal frequency, although the former study only found a decrease at low S-cone contrast; however, the study from Liu and Wandell (2005) used the 2-deg rather than the 10-deg luminosity function (Vx) for calibration, which may have introduced a luminance artifact in the S-cone stimulus at high contrast. It should be noted that, in common with the observations of Mullen et al. (2007, 2010), responses to low-frequency S-cone modulation were almost comparable to those to [L–M] modulation; these authors suggested that this represents an amplification of the S-cone signal in V1 relative to LGN, where S-cone responses are weak.

Electrophysiological data have shown that V1 neurons respond to luminance (L+M) stimuli up to 12 Hz or more but exhibit attenuation of response by about 20 Hz (Foster et al., 1985; Hawken et al., 1996). This is lower than in LGN neurons (Lankheet et al., 1998a, 1998b), but comparison may be difficult because of differences in mean luminance levels between different studies. There is little information available on the temporal tuning of L–M opponent cells in V1; the few recordings that are available (Hawken et al., 1997) suggest a response up to at least 10 Hz. Based on our and other fMRI results in humans, area V1 is not responsible for the psychophysical loss of high-frequency L–M chromatic information.

While no single-unit data on the temporal tuning of cells in macaque V1 to S-cone input are available, recently Johnson, Van Hooser, and Fitzpatrick (2010) have provided evidence that S-cone responses exhibit a steep falloff at frequencies above 8 Hz in tree shrew. An additional complication is the possibility of multiple populations of S-cone-driven cells existing in V1. Many cells in V1 appear to receive some degree of S-cone input, for the clear segregation of cone inputs into afferent pathways is not maintained in the cortex (Lennie, Krauskopf, & Sclar, 1990). On the other hand, some cortical cells resemble LGN and retinal ganglion cells in strength of their S-cone opponent signal (J. Alonso, personal communication). It is unclear whether such different populations might display different temporal tuning.

The L–M cone-opponent and S-cone pathways are thought to have developed at different times and for different purposes in evolution, and their retinal substrates remain anatomically and genetically distinct (Mollon, 1991). It had been suggested that the phylogenetically ancient S-cone pathway is temporally sluggish (Brindley, du Croz, & Rushton, 1966), but it now seems clear that this is rather a result of cortical attenuation of high temporal frequency signals. It has also been suggested that the S-cone pathway has long response latency (Smithson & Mollon, 2004) as compared to the L–M pathway. These latter authors suggested that macaque V1 neurons receive S-cone signals with a delay in comparison to L–M, due to a delay in arrival of S-cone signals in V1 related to the small diameter of the axons of the S-cone pathway between LGN and V1. However, it is unclear how this, by itself, could contribute to the high-frequency attenuation of the S-cone signals. In any event, our fMRI results here are in agreement with psychophysical data, implying that the sensitivity loss to high-frequency blue–yellow chromatic information has neural origins beginning in the primary visual cortex (V1).

**Temporal frequency responses in extrastriate visual areas**

In our fMRI results, luminance modulation (L+M) evoked responses to temporal frequencies up to 12 Hz in all areas. Our results are broadly consistent with previous fMRI reports using luminance modulation (Kastner et al., 2004; Liu & Wandell, 2005; Toottell et al., 1995; Wade et al., 2008); we concentrate here on a comparison with studies that have also used chromatic modulation (Liu & Wandell, 2005; Mullen et al., 2007, 2010; Wade et al., 2008). Similar to the results in those studies, our findings suggest that the frequency response in the case of both luminance and L–M stimulation goes through increasing levels of filtering as information passes from V1 to V2, V3, and V4. The significant negative slope values obtained from the frequency response profiles in V4 for both L–M and S-cone stimuli suggest V4’s specialization for low-frequency chromatic information. The major difference with one previous study (Mullen et al., 2010) is the significant decline in S-cone response with temporal frequency in extrastriate visual areas (V2, V3, and V4), both ventrally and dorsally (V2 and V3), as well as V1.

The size of area V4 in our experiment was relatively large, so it is possible that some parts of area VO and V8 were included in our topographical definition of V4 (Brewer, Liu, Wade, & Wandell, 2005; Wandell et al., 2005). It was previously suggested that ventral visual areas (V4, VO) play a critical role in color perception and are highly selective for low temporal chromatic modulation (Liu & Wandell, 2005; see also Jiang et al., 2007). Another body of evidence obtained from fMRI data on object processing in ventral pathways suggests that temporal limitations in object recognition performance may be caused by the progressive loss in the temporal processing capacity across ventral visual areas (McKeeff et al., 2007). Here, area V4 showed peak responses at considerably lower stimulation rates compared to earlier areas along the ventral pathway. It is known that color contributes in form perception and object recognition; although for processing of such complex features,
temporal information may not be so important. Hence, it is plausible that the color-selective areas such as V4/VO filter out the temporal content present in the visual information prior to provision of input to higher areas in the ventral visual cortex. Current results support a decrease in temporal resolution in ventral visual areas.

While responses in V3a were relatively constant up to 12 Hz, there was a significant increase in response amplitude with temporal frequencies in area MT for all stimulus conditions; a very similar result was reported by Mullen et al. (2010), who also found significant responses to [L–M] and S-cone modulations in MT. Strong responses to frequencies around 8 Hz have been reported previously (Kastner et al., 2004; Liu & Wandell, 2005; Tootell et al., 1995; Wade et al., 2008). In line with a previous report on repetitive transcranial magnetic stimulation (rTMS) combined with fMRI (McKeefry, Burton, & Morland, 2010), the observed robust selectivities of V3a and MT imply that these areas are important for the analysis of motion, irrespective of the chromatic content present in the stimuli. Delivery of rTMS to V3a and MT induces measurable behavioral deficits in perceiving the speed of moving stimuli designed for L–M, luminance, and S-cone pathways. There are suggestions that visual areas V3a and MT form parts of a common functional network specialized for the analysis of motion (Liu & Wandell, 2005). In our results, MT showed significant luminance (L+M) and L–M responses. It has recently been suggested (Lee & Sun, 2009) that the nonlinear, frequency-doubled response of MC cells (Lee, Martin, & Valberg, 1989a) is a means of enhancing motion signals for chromatic red–green [L–M] targets close to isoluminance. This may correspond to the unsigned chromatic motion signal described by Dobkins and Albright (1995). The L–M fMRI response we observed in area MT may arise from this source. There have been reports of S-cone signals being detectable in MT (Wandell et al., 1999) and we also observed such signals. However, the possibility of a luminance artifact contributing to this response cannot be ruled out. Since stimuli in these experiments covered both foveal and extrafoveal regions, it is difficult to construct equal-luminance stimuli involving short wavelengths.

As with V1 cortical neurons, neurons in extrastriate areas (V2, V3, and MT) exhibit considerable diversity in temporal tuning, with responses peaking between 3 and 6 Hz in single cell studies (Foster et al., 1985; Gegenfurtner et al., 1997; Levitt et al., 1994; Priebe et al., 2003). These measurements used achromatic stimuli only. Based on behavioral observations, Gegenfurtner and Hawken (1996) proposed the presence of two streams, distinct mostly in their way of coding temporal attributes of the visual input. They suggested that a “slow” channel has a high sensitivity for color but does not code the velocity of the moving patterns veridically. On the other hand, a “fast” channel has a high sensitivity to luminance-varying stimuli. Area MT was thought very likely to be forming the neural substrate for the fast channel, whereas area V4 was hypothesized to be involved in the slow motion mechanism. In light of these previous findings, V3a (in part) and MT temporal frequency responses in our study support the notion that they are part of a “fast” motion pathway, whereas the V4 responses can be related to the “slow” pathway.

Hierarchical cluster analysis of visual areas based on their temporal frequency response characteristics offers an objective way of looking at the data. We found three main clusters: areas V1, V2, V3, and V4 formed one large cluster, and areas V3a and MT each formed two independent clusters. Functionally, these clusters show different specialization for temporal signals and correspond with the visual field map clusters proposed by Wandell et al. (2005, 2007). Wandell et al. (2005) suggested that visual maps are arranged in clusters where neurons underlying those maps serve a common computational goal. It is argued there that these visual field map clusters share resources, such as circuitry coordinating the timing of neural signals or temporally storing local calculations. In our experiments, we could not separate area V3b from V3a, which together form an independent visual field map cluster (Wandell et al., 2005). Similarly, area MT is also known to have its own visual field map. Our results support these previous observations of visual field map clustering.

### Appendix A

#### Table A1

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Table A1. Talairach coordinates. Mean coordinates and estimated number of voxels are shown for retinotopically mapped visual areas.
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