

# Induced temporal variation at frequencies not in the stimulus: Evidence for a neural nonlinearity

**Anthony D. D'Antona**

Department of Psychology, University of Chicago,  
Chicago, IL, USA



**Steven K. Shevell**

Department of Psychology, University of Chicago,  
Chicago, IL, USA, &  
Department of Ophthalmology and Visual Science,  
University of Chicago, Chicago, IL, USA



The perceived color of a light depends on surrounding light. When the surround varies slowly over time, a central, physically steady light is perceived to vary also. This perceived temporal variation of the central region, however, is strongly attenuated when the surround varies faster than  $\sim 3$  Hz (R. L. De Valois, M. A. Webster, K. K. De Valois, & B. Lingelbach, 1986). The classical explanation is low-pass temporal filtering at a cortical stage that attenuates the neural representation of temporal frequencies capable of causing induced temporal variation. This theory assumes neural responses are linear, so only temporal frequencies in the stimulus are represented in the neural response. The current experiments revealed that temporal frequencies above 3 Hz are capable of inducing temporal variation. Specifically, with two temporal frequencies superimposed in the surround, the induced temporal variation in the uniform region is at the difference frequency of these two frequencies, even though this frequency is not physically present in the stimulus. The results are accounted for by a nonlinear neural process, which causes temporal variation at the difference frequency, and a following linear temporal filter.

Keywords: color appearance/constancy, temporal vision, color vision

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## Introduction

The neural representation of light from a location in visual space takes into account the spatial and temporal context of other light nearby. A well-known example is chromatic induction, in which the color in one area is influenced by surrounding light (De Valois, Webster, De Valois, & Lingelbach, 1986; Monnier & Shevell, 2003). One instance of induction is color contrast, in which the appearance of an area shifts away from the color in the surround (Krauskopf, Zaidi, & Mandler, 1986; Smith, Jin, & Pokorny, 2001; Zaidi, Yoshimi, Flanigan, & Canova, 1992). For example, a central square appears redder when viewed within a green-appearing surround than within an achromatic surround. In variegated natural environments, context plays an important role in determining color appearance.

Visual perception of temporally varying light is well studied (e.g. Bowker, 1983; Kelly, 1975; Lee, Pokorny, Smith, Martin, & Valberg, 1990; Pokorny, Smith, & Lutze, 1989), but comparatively little research examines how the properties of temporally varying surrounding light affect perceived temporal variation induced within a steady uniform region (De Valois et al., 1986; Kinney, 1965, 1967; Rossi & Paradiso, 1996). A consistent finding in earlier work is that the perceived modulation depth induced within a central region is severely attenuated at temporal inducing frequencies above about 3 Hz (D'Antona & Shevell, 2006; De Valois et al., 1986; Rossi &

Paradiso, 1996). This differs markedly from the perceived modulation depth of the temporally varying surround itself, which is first attenuated at a far higher temporal frequency (De Valois et al., 1986). Thus, perceived induced modulation seems to rely on a slower neural mechanism than perceived modulation of a physically varying light.

Temporally varying neural signals before the site of induction may be important for understanding how temporally varying light contributes to perception. Though induced modulation is attenuated above  $\sim 3$  Hz, physiological and psychophysical studies clearly demonstrate temporally varying neural signals can follow to much higher frequencies (Lee et al., 1990). Higher-frequency neural responses preceding the site of induction may have important consequences for induced temporal modulation, even though they are not directly perceived. For example, in brightness induction, higher temporal frequencies can contribute to perceived motion using a grating-induction stimulus (Blakeslee & McCourt, 2008).

The research here investigated whether neural mechanisms mediating induced temporal modulation were driven by a larger range of stimulus temporal frequencies than reported previously. Previous studies examine induced temporal modulation using one inducing temporal frequency at a time within a surround. These measured characteristics of induced temporal modulation would generalize to any temporal waveform by assuming a linear neural response. If the linearity assumption is invalid, however, then a temporal

frequency that induces no temporal variation when presented alone may induce temporal variation when a component of a more complex waveform. Consider, for example, a stimulus that is the superposition of two sine waves at frequencies  $f_1$  and  $f_2$  (rightmost graph, Figure 1A). It periodically reaches a peak at the difference frequency of its individual frequency components  $|f_2 - f_1|$ . Superposition of this frequency pair is the physical summation of two sine waves, so power is only at the two individual frequency components ( $f_1$  and  $f_2$ ). If this stimulus drives a nonlinear neural response, however, then the output from the nonlinearity can contain power at temporal frequencies not present in the stimulus. Two new temporal frequencies in a nonlinear response are the difference frequency  $|f_2 - f_1|$  and the sum frequency ( $f_1 + f_2$ ), which are shown in Figure 1B. In the case of induced temporal modulation, each frequency  $f_1$  and  $f_2$  presented individually may be too high to induce temporal modulation; when presented simultaneously, however, and with a nonlinearity preceding the site of induction,  $f_1$  and  $f_2$  result in a new lower-temporal-frequency component at the difference frequency. This difference frequency may be low enough to induce temporal modulation, even though each component in the stimulus is at a frequency too high to cause induction. This hypothesis was tested in three experiments.

## Methods

### Equipment and stimuli

All stimuli were displayed using a Macintosh G4 computer and a Sony color display (GDM-F520). The

cathode ray tube (CRT) monitor had a  $1360 \times 1024$  pixel display at a refresh rate of 75 Hz non-interlaced. The R, G, and B guns of the CRT were linearized using a 10-bit look-up table.

The spectral distribution of each CRT phosphor was measured at its maximal radiance using a PhotoResearch PR 650 Spectroradiometer. Equiluminant stimuli were specified in a MacLeod and Boynton (1979) ( $l, s$ ) chromaticity diagram (Figure 2A), modified so that the (arbitrary) unit of  $s$  was 1.0 for an equal-energy-spectrum (EES) 'white'. The Smith and Pokorny (1975) cone fundamentals were used to calculate L-, M-, and S-cone excitation.

Equiluminance for each observer was established using heterochromatic flicker photometry (HFP). Flicker settings were repeated in at least two sessions. The measurements were averaged and used to determine the relative radiance of the R, G, and B guns that produced equiluminance for each subject. Each observer also set a minimally distinct border (MDB) between equiluminant stimuli in order to verify that the S-cone isolation specified by the standard observer was appropriate.

The display consisted of a matching field and a test field (Figure 2B). The test field had a circular surround of diameter  $6^\circ$  and a concentric annular test ring with an inner/outer diameter of 2.25/3.25 deg. The region interior to the test ring was part of the surround. The observer judged the perceived temporal modulation within the test annulus.

The test annulus was separated from its circular surround by a 3 min. wide dark gap. Without the gap, the percept of flicker may be seen in the test annulus even without induced perceived temporal variation, as reported in previous work (De Valois et al., 1986). Flicker refers to a perceived temporal change in a region even though

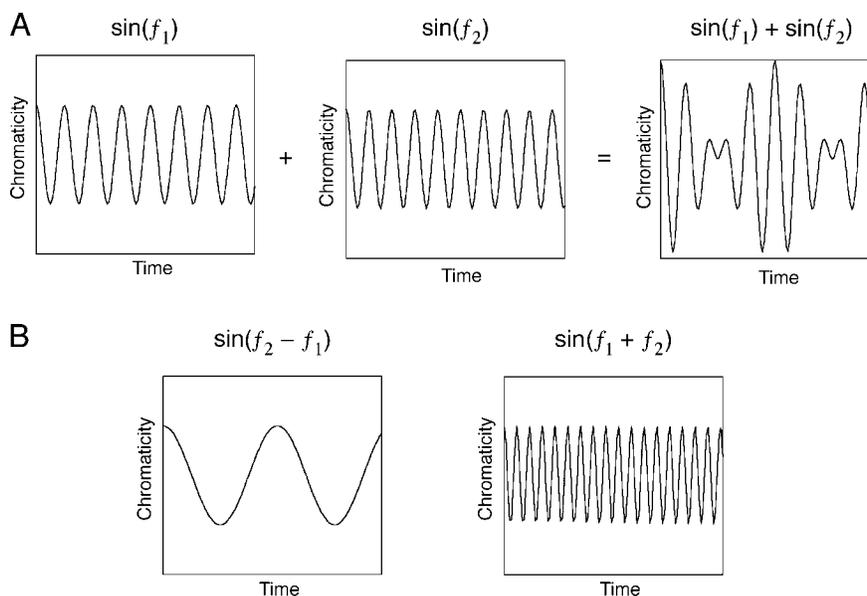


Figure 1. (A) Left, two sinusoidal waveforms at temporal frequencies  $f_1$  and  $f_2$ . Right, the superposition of these two waveforms. (B) Two new temporal frequencies,  $|f_2 - f_1|$  and  $(f_1 + f_2)$ , present in the output of a nonlinearity when the frequency-pair waveform is the input.

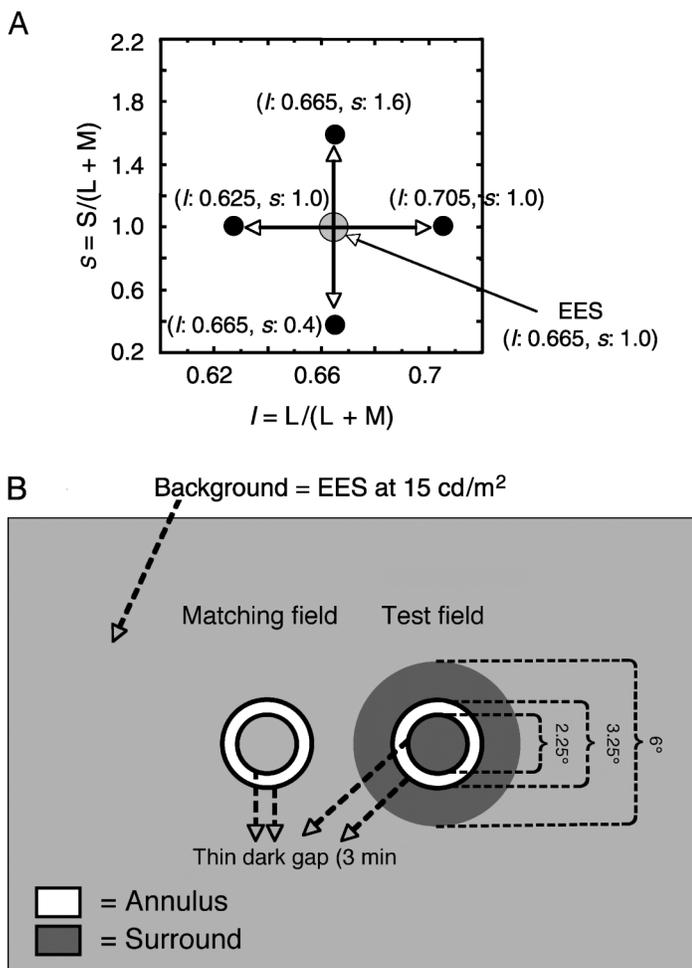


Figure 2. (A) MacLeod-Boynton chromaticity space used to specify the stimuli. The Equal-Energy-Spectrum (EES) stimulus has  $(l, s)$  coordinates of  $(0.665, 1.0)$ . Temporal modulation along an  $l$  direction varied between  $l$  values of  $0.625$  and  $0.705$  while  $s$  was constant at  $1.0$ . Temporal modulation along an  $s$  direction varied between  $s$  values of  $0.4$  and  $1.6$  while  $l$  was constant at  $0.665$ . (B) Spatial configuration of the stimulus. The annuli in both the test and the matching field had inner/outer radii of  $2.25^\circ/3.25^\circ$ . Both annuli were surrounded by thin dark gaps that were  $3 \text{ min}$  wide. The surround in the test field had diameter  $6^\circ$ . The luminance throughout the display was  $15 \text{ cd/m}^2$  (except for the dark gaps).

brightness or color remains steady (De Valois et al., 1986). Induced temporal variation refers to a perceived temporal change in brightness or color. Pilot experiments confirmed perceived flicker in the absence of induced temporal variation. The flicker made matching difficult because it introduced a separate and distracting percept in the annulus. The thin dark gap strongly reduced perceived flicker. The dark gap also helped perceptually delineate the annulus from its surround when chromatic variation was along only the  $s$  direction; without the gap, the border between the annulus and its surround was difficult to discern.

The matching field consisted of only an annular ring and a surrounding dark gap, which both had the same dimensions as their counterparts in the test field. This gap was added so that the edges of the test annulus and the matching annulus were the same. The background for both the matching and comparison fields, which filled the CRT screen, had  $(l, s)$  chromaticity  $(0.665, 1.0)$ , which was metameric to EES. The luminance throughout the display was  $15 \text{ cd/m}^2$  (except for the dark gaps).

Stimuli were modulated in color along one of two directions in color space. For the  $l$  axis, the modulation depth was 6% Michelson contrast,  $[(l_{\max} - l_{\min}) / (l_{\max} + l_{\min})]$ . The peak and trough  $l$  values associated with this contrast level were  $0.705$  and  $0.625$ , respectively. Modulation depth along the  $s$  direction was 60% Michelson contrast, with corresponding peak and trough  $s$  values of  $1.60$  and  $0.40$ . For both chromatic directions, temporal modulation within the surround was approximately sinusoidal (within the constraints of the CRT's refresh rate) at eleven different temporal frequencies:  $0.50, 0.75, 1.00, 1.50, 2.00, 3.00, 4.00, 5.00, 6.25, 7.50,$  and  $9.38 \text{ Hz}$ .

Six different frequency pairs also were presented in the surround. Each frequency pair consisted of two component frequencies:  $4.17$  &  $4.69, 4.17$  &  $5.00, 5.00$  &  $6.25, 6.25$  &  $7.50, 7.50$  &  $9.38,$  and  $5.00$  &  $7.50 \text{ Hz}$ . Each of the component frequencies was presented at half contrast in the frequency pair so that the maximum contrast of the pair was the same as the maximum contrast when a component frequency was presented individually. These six frequency pairs had difference frequencies of  $0.52, 0.83, 1.25, 1.25, 1.88,$  and  $2.50 \text{ Hz}$ , respectively.

## Procedure

On a given trial, temporal modulation along one chromatic axis was presented in the test-field surround. The task of the observer was to match the modulation depth perceived within the test annulus by adjusting the modulation depth (i.e. temporal contrast) of a physically varying light in the matching annulus. The matching light was always modulated sinusoidally at a frequency of  $2 \text{ Hz}$  (as in De Valois et al., 1986) along the same chromatic axis as the test's surround. Matching the induced modulation depth required matching the perceptual peak and trough of the induced temporal modulation to the perceptual peak and trough of the matching physical modulation.

The observer also had control of the chromaticity of the steady test annulus. At the beginning of every trial, the chromaticity was metameric to EES, but the observer could change this along the chromatic axis in question. The observer was given control of the test chromaticity for two reasons. First, in some cases the EES test annulus had no apparent temporal modulation, but its steady appearance clearly was different from EES (D'Antona & Shevell, 2006). In this case, the observer adjusted the

steady chromaticity of the test annulus along the chromatic axis so the color appearance of the test was the same as the EES background. Second, when perceived modulation was apparent, the test annulus sometimes had perceptual peaks and troughs that were asymmetric around the percept of an isolated EES light (e.g. the physically steady EES test annulus could appear to vary between gray and reddish, rather than between greenish and reddish). In this case, adjusting the modulation depth of the matching annulus alone could not simultaneously match the peak and trough perceived in the test annulus. By changing the chromaticity of the test annulus, the perceived peak and trough of induced modulation could be matched by physical temporal modulation in the matching annulus.

In a given session, measurements were taken for one of the two chromatic axes. Before starting a session, observers adapted to a dark monitor for three minutes. Subsequently, each temporal frequency and frequency pair was presented in random order and repeated five times within one session. Three sessions of each condition were run on different days.

## Observers

Three observers participated in each experiment. One was an author, and the other two were naïve observers.

Prior to data collection, the observers completed practice sessions as needed to produce repeatable measurements.

## Results

### Experiment 1: The magnitude of induced temporal variation from single frequencies and superimposed frequency pairs

Measurements of perceived temporal variation in the physically steady test annulus (left column, Figure 3) corroborated strong attenuation of induced modulation above approximately 3 Hz (cf. De Valois et al., 1986). Temporal variation induced from light modulated along the  $l$  [s] chromatic axis is shown in the top [bottom] panels. The magnitude and peak frequency of induction showed some variability across observers, but the overall results were similar.

The critical conditions used to test for a nonlinear neural process had a pair of temporal frequencies presented simultaneously in the surround (middle column). In these plots, the difference between the two temporal frequency components,  $|f_2 - f_1|$ , is on the horizontal axis. Note that two points are plotted at the

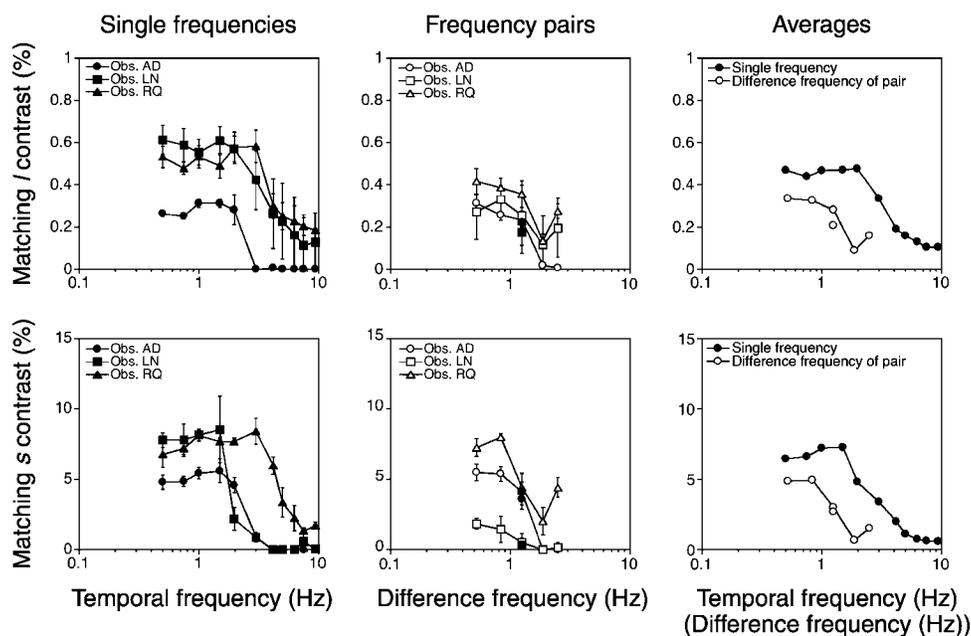


Figure 3. Perceived modulation-depth matching results from Experiment 1. The top and bottom rows show results for the  $l$  or  $s$  direction, respectively. The left and middle columns show results for the single-frequency and frequency-pair surrounds, respectively. The right column shows results for single-frequency and frequency-pair surrounds averaged over observers. Results for single frequency surrounds are plotted as a function of the surround temporal frequency, and results for frequency-pair surrounds are plotted as a function of the difference of the temporal frequencies in the surround. Error bars indicate 1 standard error of the mean.

1.25 Hz difference frequency: one on the line connecting the points, which is for frequency pair 5.00 and 6.25 Hz, and a separate filled symbol, which is for pair 6.25 and 7.50 Hz. Again, the magnitude of induction showed some variability across observers, but the overall shapes of the plots were similar.

Induction from single frequencies and frequency pairs were averaged across observers (right column, Figure 3). The shapes of the curves were similar for  $l$  and  $s$  inducing modulation for induction from single frequencies and frequency pairs (top and bottom right panels, Figure 3). Induction from pairs at a given frequency difference was weaker compared to a single-frequency stimulus at that difference frequency. Perceived induction from a single-frequency surround fell sharply above 3 Hz. With frequency pairs in the surround, the decline in perceived induced modulation began at 1 Hz. A possible explanation is that temporal induction from frequency pairs, due to a component at the difference frequency, is weaker than from a single stimulus at the difference frequency because frequency pairs have higher physical temporal frequencies. A linear low-pass temporal filter preceding the nonlinearity could attenuate these higher temporal-frequency components, and thus reduce the magnitude of induced modulation at the difference frequency. This possibility is considered later.

The steady offset chromaticity in the test annulus set by each observer is shown in Figure 4. The top and bottom rows show the  $l$  and  $s$  inducing modulations, respectively. The chromaticity of EES is shown by the dotted line in

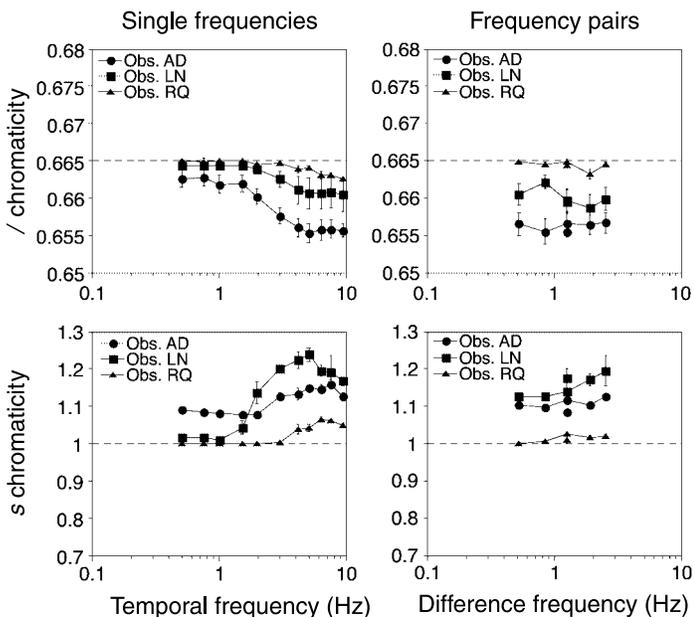


Figure 4. Steady test chromaticities set in Experiment 1. The top and bottom rows show results for the  $l$  or  $s$  direction, respectively. The left and right columns show results for the single frequency and frequency-pair surrounds, respectively. The dashed horizontal lines denote the EES chromaticity.

each panel. The shifts away from the EES value were consistent with a nonlinearity whose time-average response was different than the time-average of the physical stimulus (D'Antona & Shevell, 2006; Stockman & Plummer, 1998). The compensating offsets were most pronounced at high temporal frequencies, and in the direction of less  $l$  and greater  $s$ , relative to EES. Thus high temporal frequencies in the surround induced time-average chromatic shifts in the reddish and yellowish directions.

A nonlinear neural response would cause frequency pairs in the surround to induce temporal variation at their difference frequency. The nonlinearity and a subsequent low-pass filter, therefore, allow greater temporal induction from a pair of higher frequencies (e.g. 4.17 Hz and 5.0 Hz) than from either temporal frequency alone. The results showed this was the predominant finding. The magnitude of induction from each frequency pair was compared to the magnitude of induction from each temporal-frequency component of the pair when presented alone<sup>1</sup>. Each observer was tested with 6 frequency pairs on each chromatic axis (12 comparisons in all). For observers A.D. and R.Q., 10 of 12 comparisons had the greatest induced modulation with the frequency pair than for either component alone ( $p < 0.001$  for each observer by binomial test with  $p = 1/3$ ). For observer L.N., 7 out of 12 comparisons had this characteristic ( $p < 0.067$ ). This is clear evidence that the magnitude of induced temporal variation from frequency pairs is greater than from either temporal-frequency component presented alone, and therefore supports the hypothesis that a nonlinear neural response precedes a low-pass filter that limits the frequency of induced temporal modulation.

A small dip in the frequency pair measurements (Figure 3, middle panel) was found at difference frequency 1.88 Hz for both chromatic axes. This appears uncharacteristic of the overall shape. Note that the 1.88 Hz frequency pair was composed from component frequencies 7.5 and 9.38 Hz. This is the only frequency pair with a 9.38 Hz component, which is the highest temporal frequency used in the study. The dip at 1.88 Hz may be due to this high temporal-frequency component, which may be attenuated by an additional low-pass (linear) temporal filter preceding the nonlinear neural response. To test this possibility, an additional frequency pair at 4.41 and 6.25 Hz (difference frequency 1.84 Hz) was tested for one observer. This difference frequency was chosen to be near 1.88 Hz while being composed of lower frequency components than 7.50 and 9.38 Hz. The measurements from this new frequency pair are shown in Figure 5 along with the other frequency-pair measurements for this observer. The new 1.84 Hz difference frequency (filled symbol) is along the line connecting it to the other measurements, while the 1.88 Hz point is below the line. This suggests that the perceived magnitude of induction from the frequency pairs depends on both the component frequencies and the difference frequency of the pair.

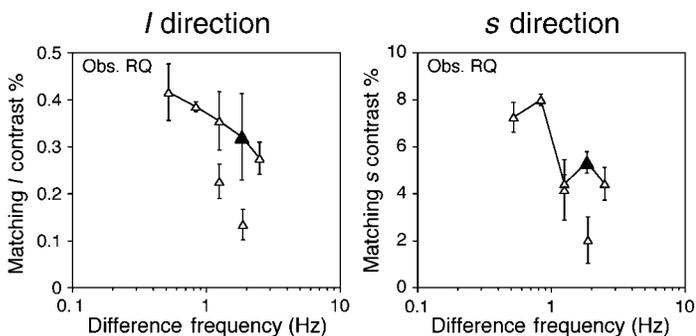


Figure 5. Matching results for frequency-pair surrounds for one observer with a new frequency-pair condition. The left and right figures show results for the *l* or *s* directions, respectively. Results for an additional difference frequency of 1.84 Hz (filled symbol) are on the line connecting the points, and results from the previously tested difference-frequency of 1.88 are below the line.

### Experiment 2: Perceived temporal frequency of induced temporal variation from frequency pairs

The magnitude of induced temporal variation from a pair of frequencies can be greater than from either of the component frequencies presented alone (Experiment 1). This super-additivity cannot be explained by different stimulus contrasts, since both types of stimuli, i.e. frequency pairs and single frequencies, had the same maximum contrast. We hypothesized that this super-additivity resulted from a nonlinearity in the neural processing stream preceding the site of induction. The nonlinearity would produce temporal variation at the difference frequency of the pair  $|f_2 - f_1|$ . Thus, if a nonlinearity is responsible for the observed super-additivity, then the induced temporal variation from a frequency pair should be perceived at the difference frequency. Experiment 2 tested this prediction by measuring the

perceived temporal frequency of induced temporal variation with frequency pairs in the surround. Only the test field, centered on the monitor screen, was presented in this experiment. For each of the two chromatic axes, there were two conditions with no physical modulation in the test annulus: the frequency-pair stimulus in the surround had a difference frequency of either (1) 0.83 or (2) 1.25 Hz, resulting from the superposition of 4.17 & 5.00 Hz or 5.00 & 6.25 Hz, respectively. The chromaticity of the test annulus was tailored for each observer and difference frequency by setting it to the steady offset chromaticity measured in the previous experiment (Figure 4).

In additional control conditions, the test annulus was modulated, rather than kept steady, at either 0.83 or 1.25 Hz. The surround was held steady.

Three observers adjusted the temporal frequency and phase of auditory clicks, which were generated by the computer, so that the clicks coincided with both the peaks and troughs of perceived modulation. In a single session, five measurements were made for each condition. Each session was completed three times by each observer.

The frequency of the auditory clicks set by each observer is shown in Figure 6 (*l* chromatic modulation in the left panel, *s* in the right panel). In the control conditions, sinusoidal physical modulation was present in the test annulus at a single temporal frequency. Observers set the perceived frequency of modulation very close to this temporal frequency, as expected. In the frequency-pair conditions, physical modulation was present only in the surround at a pair of temporal frequencies. Observers adjusted the clicks to correspond to the perceived peaks and troughs of induced temporal variation in the test annulus. The perceived frequency was always set very close to the difference frequency of the frequencies in the surround (Figure 6). This result is expected on the hypothesis that a nonlinearity causes the frequency pair to induce temporal variation at the difference frequency.

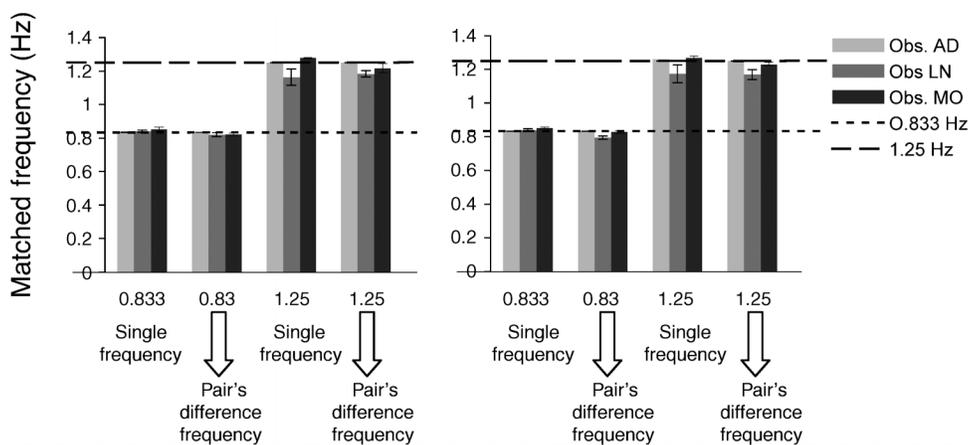


Figure 6. Perceived temporal frequency of test-annulus modulation. The left and right panels show results for the *l* or *s* direction, respectively. The horizontal dashed lines denote 0.83 Hz and 1.25 Hz.

### Experiment 3: Nulling of induced temporal variation at the difference frequency

Experiments 1 and 2 showed that a stimulus composed of both frequencies  $f_1$  and  $f_2$  in the surround induced temporal variation at the difference frequency  $|f_2 - f_1|$ . To provide further evidence of an induced temporal neural response at the difference frequency, Experiment 3 tested whether observers could null the induced temporal variation in the test area by adding real light in the test at the difference frequency in counter-phase to the induced modulation. Temporal nulling is a useful tool for measuring induction (Krauskopf et al., 1986; Zaidi et al., 1992) and may be an easier task than matching because of the lower demand on memory and the simpler criterion to null perceived temporal variation. It also provides a direct test of the hypothesis that the induced, temporally varying neural signal can be counterbalanced by physical light at the difference frequency.

The spatial configuration was the same as in Experiment 2. Four pairs of temporal frequencies were presented in the surround for each chromatic axis: 4.17 & 5.00, 5.00 & 6.25, 3.13 & 5.00, and 3.75 & 6.25 Hz, with respective

difference frequencies of 0.83, 1.25, 1.87, and 2.50 Hz. Observers were given control of the time-average (DC) level and the modulation depth of a temporally varying sine wave in the test annulus, which was at the difference frequency of the frequency pair in the surround. The observer first adjusted the test-annulus steady chromaticity, which initially was randomized, so the perceived chromatic excursions were approximately symmetric around the achromatic percept. Following this setting, a physically modulated sine wave at the difference frequency was presented within the test annulus at a random modulation depth. The observer adjusted the modulation depth of this sine wave to make the test annulus appear steady. Observers were able to switch back and forth between adjusting the time-average level and the modulation depth until the test annulus appeared both steady and achromatic. The phase of the sine wave could be  $0^\circ$  or  $180^\circ$  but otherwise was fixed to avoid overcomplicating the task. At  $0^\circ$  [ $180^\circ$ ] phase, arbitrarily indicated by a positive [negative] modulation depth, the peak [trough] of the sine wave corresponded to the peak of the frequency-pair modulation in the surround.

The nulling amplitudes (Figure 7, top row) and time-average (DC) shifts (Figure 7, bottom row) are shown for

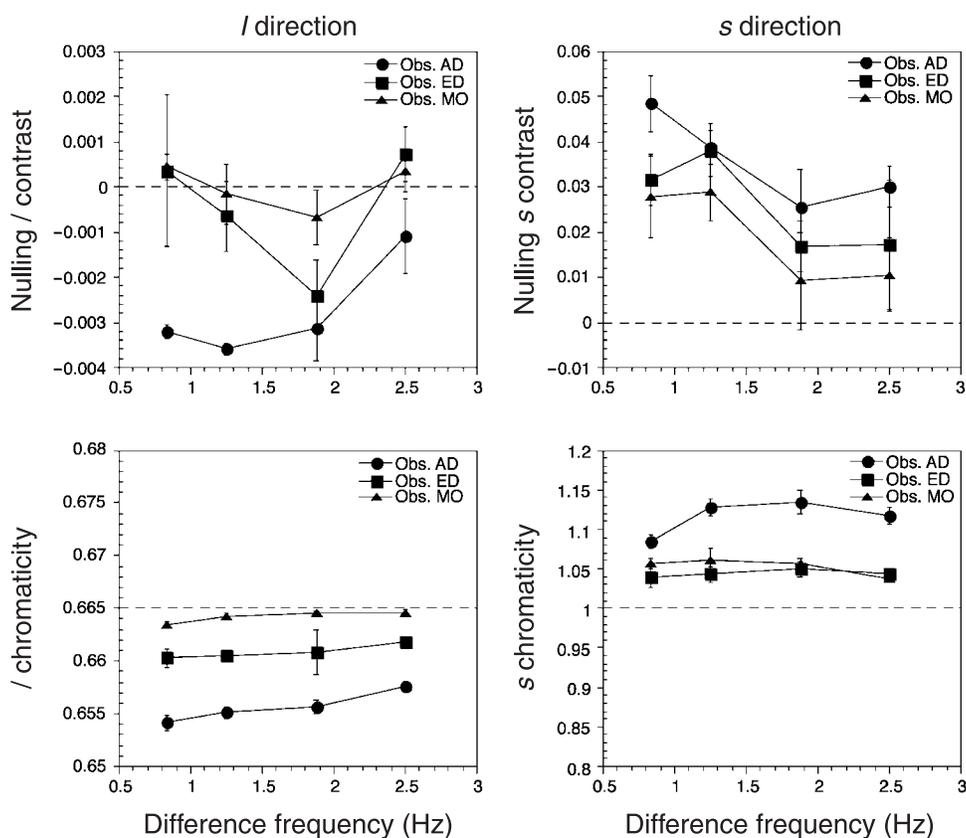


Figure 7. Nulling results from Experiment 3. The left and right columns show results for the *l* or *s* direction, respectively. The top and bottom rows show nulling amplitudes and time-average settings, respectively. In the top row, the dashed line indicates a zero nulling amplitude. Positive nulling amplitudes indicate that the peak of the nulling stimulus was in phase with the peak of the frequency-pair modulation in the surround; negative nulling amplitudes indicate that the trough of the nulling stimulus was in phase with the peak of the frequency-pair modulation in the surround. In the bottom row, dashed lines indicate the EES chromaticity value.

both the  $l$  (left column) and  $s$  (right column) directions of chromatic modulation. Along the  $s$  direction, nulling amplitudes (upper right panel) had consistent magnitudes and phases for all observers. Along the  $l$  direction (upper left panel), the phase of the nulling amplitudes was consistent across observers though the magnitude varied. Time-average settings differed from EES, indicating that the temporally varying surrounds caused time-average (DC) color shifts in the test annulus (lower panels).

## Discussion

Temporal modulation above  $\sim 3$  Hz within a surround has been thought not to induce temporal variation into a central area (De Valois et al., 1986), implying that a very limited range of temporal frequencies contributes to induction. This study shows this view is incomplete. While induced temporal variation does not occur above  $\sim 3$  Hz, induced temporal variation from superimposed pairs of temporal surround frequencies, each of which is well above 3 Hz, is perceived at the pair's difference frequency. This is consistent with a nonlinearity preceding the site of induction. Neural signals contributing to induction can encode a large range of temporal frequencies. These signals are transformed by a nonlinear neural response prior to the site of induction. A nonlinearity introduces new temporal frequencies into the inducing

signal that are not present in the physical stimulus. This signal, in turn, is temporally filtered prior to the site of induction, leaving only low-temporal-frequency modulation contributing to the induced percept.

The first stage of this model is a linear temporal filter representing neural filtering of the stimulus prior to the nonlinearity (Figure 8A, left). This filter passes temporal frequencies well above 3 Hz, as indicated by measurements of induced *steady* chromatic shifts resulting from high-frequency, temporally varying surrounds (D'Antona & Shevell, 2006). The second stage is a nonlinear response. The example shown here, which is used in simulations below, has different amplitudes above and below zero (Figure 8A, center). In principle, however, another nonlinear function could be used. The third stage of the model is a linear temporal filter representing the last stage of neural filtering prior to the site of induction (Figure 8A, right). This corresponds to a linear temporal filter of the sort suggested in earlier work (De Valois et al., 1986).

To illustrate the model, Figure 8B shows a waveform that is transformed at each stage. The initial waveform is a pair of temporal frequencies represented in general by

$$f(t) = DC[1 + c_1 \sin(2\pi f_1 t) + c_2 \sin(2\pi f_2 t)]. \quad (1)$$

This waveform is illustrated in the leftmost panel of Figure 8B, with an average level of 1.0, Michelson contrasts  $c_1$  and  $c_2$  of 0.3, frequency  $f_1$  of 6.0 Hz and

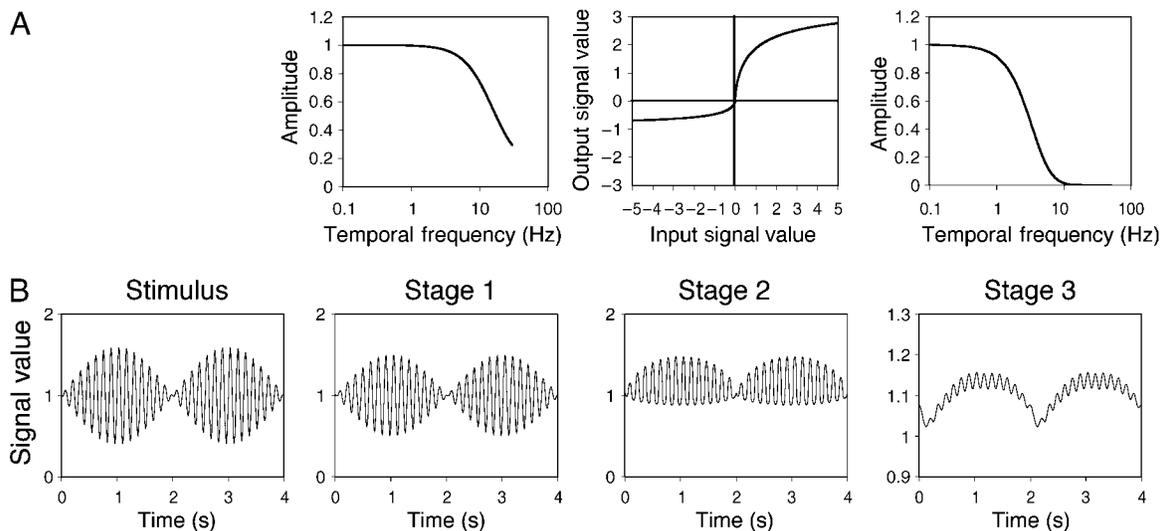


Figure 8. (A) A model to explain the results found in Experiments 1, 2, and 3. The first stage is a linear temporal filter with a cutoff well above 3 Hz. This represents neural filtering prior to the nonlinearity. The second stage is nonlinear. The zero value of the nonlinearity represents the time-average (DC) value of the input. This nonlinearity responds asymmetrically around the average level. The third stage is a linear temporal filter after the nonlinearity but before the site of induction. It attenuates temporal frequencies above 3 Hz. (B) A signal at various stages of the model. The signal at Stage 1 is nearly identical to the original stimulus because the temporal frequencies in the stimulus are little attenuated by the first filter. The signal at Stage 2 shows large distortion due to nonlinearity. The final signal (Stage 3) shows clear variation at the difference frequency  $|f_2 - f_1|$ . Higher temporal frequencies are attenuated by the second linear filter.

frequency  $f_2$  of 6.5 Hz. Stage 1 in Figure 8B shows this waveform after the first temporal filter. The waveform at this stage is nearly identical to the original stimulus because the first filter only slightly attenuates these temporal frequencies. Stage 2 illustrates the distortion from the nonlinearity. The average (DC) value was subtracted from the input to the nonlinearity in order to align the zero point of the nonlinearity with the average value of the input (the average value was later added back to the output of the nonlinearity shown in Stage 2). Prior to Stage 2 the waveform was symmetric around the DC level, but the nonlinearity causes the waveform to be quite asymmetric around the time-average value. This nonlinearity introduces new temporal frequencies in the waveform, including one at the difference frequency  $|f_2 - f_1|$ . Finally, the waveform at Stage 3 illustrates the influence of the second linear temporal filter, which strongly attenuates higher temporal frequencies. The resulting signal is a waveform with predominant temporal modulation at the difference frequency as well as a shift in the time-average value relative to the original stimulus.

Simulations from the model for various stimulus temporal waveforms are shown in Figure 9. The thin and thick solid lines show the first and second linear temporal filter, respectively (from Figure 8A). The horizontal

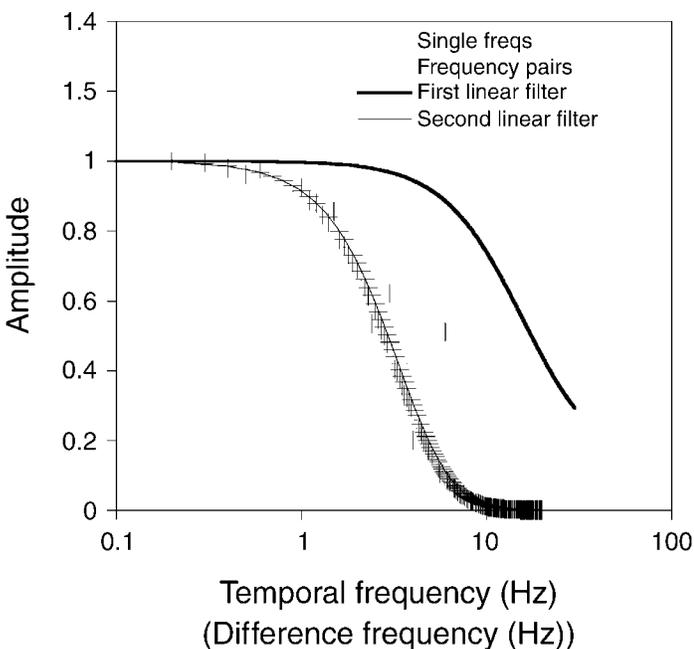


Figure 9. Simulations from the model for single-frequency and frequency-pair inputs. The continuous lines show the first and second linear filter. The horizontal and vertical dashes show the amplitude of the model's response for single-frequency and frequency-pair inputs, respectively. The curves were normalized to 1.0 at the leftmost frequency. The amplitudes for single-frequency and frequency-pair outputs virtually lie on top of the second filter (see text).

dashes show the model's response to single frequencies. The vertical dashes show the model's response to temporal frequency *pairs* in the stimulus with the lower temporal frequency fixed at  $f_1 = 6.0$  Hz, and the difference frequency,  $|f_2 - f_1|$ , varied along the horizontal axis. The relative units in the plots were normalized to 1.0 at the leftmost frequency. The figure shows that the modulation amplitude from both single frequencies and frequency pairs is controlled by the second filter because all three plots fall virtually on top of one another.<sup>2</sup>

This model provides one explanation for the experimental results, though others are possible. A necessary component of all such models is nonlinearity, because no linear model generates a neural response at the difference frequency. The nonlinearity in the model here was chosen as a simple and succinct way to generate a component at the difference frequency. A more biologically plausible model might incorporate rectifying nonlinearities, which are present in the responses of +L-M and +M-L parvocellular ganglion cells (Lee, Pokorny, Smith, & Kremers, 1994). This explanation alone, however, cannot account for the results here; additional modifications to the model would be needed to account for the induced temporal variation at the difference frequency that is not symmetric about the DC level of the stimulus (Figure 4 and bottom row of Figure 7). Such a model modestly increases biological plausibility at the cost of additional complexity. The model in Figure 8 accounts for the results as simply as possible.

Changes in color appearance during chromatic induction are affected by nonlinearity at high temporal frequencies (Anstis & Ho, 1998). For example, a spot flickering at 7.5 Hz between chromaticities that appear blue and yellow within a yellow-appearing surround appears more bluish than a steady achromatic spot at the same time-average chromaticity within the same surround (Anstis & Ho, 1998). These results can be understood by supposing the visual system weights higher contrast more strongly than lower contrast (and therefore in a nonlinear manner). Though the idea of nonlinear contrast weighting may be related to induced variation at the difference frequency of a pair of sinusoids in the surround, the results here require that the visual system weight asymmetrically the excursions around the DC level.

This study addressed the temporal properties of induction and the nonlinearity of neural responses from temporally varying surrounds. The results raise interesting questions for speculation. One question is whether there is a functional benefit of attenuating induced temporal modulation above 3 Hz when perceived modulation of the temporally varying surrounding light itself is not attenuated until much higher frequencies (De Valois et al., 1986). Some investigators propose that the low-temporal-frequency tuning of induction results from a filling-in process responsible for induction (Davey, Maddess, & Srinivasan, 1998; Rossi & Paradiso, 1996). On this view, the induced appearance change in the physically steady

center from the surround is the result of lateral spreading of neural activity originating at the border between center and surround. The temporal tuning of induction results from the time required for the spread of neural activity at the border to fill-in the field. This explanation implies that the low-temporal-frequency tuning of induction is a limitation of the biological mechanisms causing induced color changes.

Low-temporal-frequency tuning of induction may optimize a visual function. Consider, for example, an object moving in front of a chromatically variegated background. Without the low-temporal-frequency tuning of induction, the object would appear to change color rapidly if the chromatically variegated background induced high-temporal-frequency changes in the appearance of the object. Eliminating high-temporal-frequency color changes could contribute to the stable color appearance of the object.

A further question concerns the benefit of a nonlinearity preceding induction. The nonlinearity produces induced temporal variation at the difference frequency of the temporal-frequency pair in the surround, which allows many natural stimuli composed of more than one frequency to induce a temporal change in color. The nonlinear response may be useful for segmenting an object with perceived (induced) low-frequency variation and a DC offset from a higher-temporal-frequency background, even when the object and background have the same time-average chromaticity. A linear mechanism, even with high-frequency attenuation, would not induce a DC offset. This is a speculative function; a nonlinearity may serve other functional purposes.

In sum, temporal modulation in a steady central area can be induced with higher temporal-frequency (>3 Hz) surrounds than previously reported. The higher-temporal frequencies are represented in a neural stream that includes a nonlinear transformation prior to the site of induction. The nonlinearity causes low-temporal-frequency induced modulation from two or more higher temporal frequencies within a surrounding area. This nonlinearity may allow the visual system to exploit high-temporal-frequency information within the stimulus and low-temporal frequency changes in the induced percept without the unwanted consequence of high-temporal frequency induced color changes.

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Corresponding author: Anthony D'Antona.  
Email: [adantona@uchicago.edu](mailto:adantona@uchicago.edu).  
Address: Visual Science Laboratories, University of Chicago, 940 E. 57th Street, Chicago, IL 60637, USA.

## Footnotes

<sup>1</sup>The frequencies 4.17 and 4.69 used in the frequency pairs were not measured directly in isolation. Instead they were estimated by interpolating between the 4 Hz and 5 Hz stimuli, which were presented in isolation.

<sup>2</sup>A few vertical dashes representing the frequency pairs do not fall on the line for the second filter. This occurs when the output contains additional components not related to the difference  $|f_2 - f_1|$ . For example, the most noticeable excursion occurs when  $f_1 = 6.0$  Hz and  $f_2 = 12.0$  Hz because  $f_1$  itself contains a component at the difference frequency ( $f_1 = 6.0$  Hz and  $|f_2 - f_1| = 6.0$  Hz).

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