Cover Page

1) Title of the paper:

Temporal nulling of induction from spatial patterns modulated in time

2) authors' affiliation and address:

IRCCyN-IVC, (UMR CNRS 6597), Polytech' Nantes
Rue Christian Pauc, La Chantrerie, 44306 NANTES, France.
Tel : 02.40.68.32.47
Fax : 02.40.68.30.66

3) e_mail address:

Florent.Autrusseau@polytech.univ-nantes.fr

4) Journal & Publisher information:

Visual Neuroscience
Cambridge University Press
http://www.journals.cambridge.org/jid_VNS

5) bibtex entry:

```
@inproceedings{Autrusseau2006vns,
    Author = {F. Autrusseau and S. Shevell},
    Booktitle = {Visual Neuroscience  },
    Month = {Sept},
    Pages = {479-482},
    Publisher = {Cambridge University Press},
    Title = {Temporal nulling of induction from spatial patterns modulated in time},
    Volume = {23},
    Year = {2006}}
```

doi:10.1017/S0952523806233534

VNS23(3) 23353 1/4 05/22/06 13:34 pm

log no. VNS23353

Visual Neuroscience (2006), **23**, 1–4. Printed in the USA.

DOI: 10.1017/S0952523806233534

Temporal nulling of induction from spatial patterns modulated in time

FLORENT AUTRUSSEAU[1,2] AND STEVEN K. SHEVELL[1]

[1]Visual Science Laboratories, University of Chicago, Chicago, Illinois
[2]Polytech'Nantes, IRCCyN, Nantes, France

(Received June 20, 2005; Accepted April 25, 2006)

Abstract

Temporally varying chromatic-inducing light was used to infer receptive-field organization. Time-varying shifts in color appearance within a test field were induced by a surrounding chromatic pattern; the shifts were then nulled by adding a time-varying stimulus to the test area so the observer perceived a steady test. This method measured chromatic induction without requiring an observer to judge the color appearance of the test. The induced color shifts were consistent with a $+s/-s$ spatially antagonistic neural receptive field, which also accounts for color shifts induced by static chromatic patterns (Monnier & Shevell, 2003, Monnier & Shevell, 2004). The response of this type of receptive-field, which is found only in the visual cortex, increases with S-cone stimulation at its center and decreases with S-cone stimulation within its surround. The measurements also showed a negligible influence of temporal inducing frequency in the range 0.5–4 Hz.

Keywords: chromatic induction, temporal nulling, $+s/-s$ spatially antagonistic receptive field

Introduction

A cortical, spatially antagonistic receptive field can account for chromatic assimilation and contrast, depending on the properties of the contextual inducing light (Monnier & Shevell 2003, 2004). This type of receptive field implies large induced color shifts, as illustrated in Fig. 1. The two test rings in the figure, linked by the horizontal bar, appear different but are physically identical. A $+s/-s$ spatially antagonistic receptive field explains the test's appearance shift toward the contiguous chromaticity and away from the non-contiguous chromaticity. This study extends previous work by testing whether this spatially antagonistic cortical receptive field also accounts for induced color percepts with temporally varying inducing patterns and also by assessing temporal properties of the neural pathway mediating the color shifts.

We measured how temporal variation in a surrounding area affected the appearance of the test ring. An important feature of the design was that the observer judged only whether the test ring appeared steady over time; no judgment of color was required (Krauskopf et al., 1986). There were two aims of the study. First, the cortical receptive field inferred from asymmetric color matching (Monnier & Shevell, 2004) implies that temporal modulation very near the test should result in induced assimilation (that is, a shift in test appearance in phase with the appearance of the temporally varying inducing light). Similarly, temporal variation some distance from the test should result in induced contrast (out of phase with the inducing light). These predictions were tested using a temporal nulling method, in which the observer set a temporally varying light within the test area to null the perceived change in appearance induced by temporal variation in a surrounding region. A judgment of discrimination between a steady and temporally varying percept is a threshold judgment, and thus a Brindley (1970) class A observation; asymmetric color matching, as used in previous work, is not.

Second, the amplitude of induced color change from nearby and more remote inducing light was compared as a function of temporal frequency of inducing light. Whereas the temporal properties of the S-cone pathway are controversial and complex (Wisowaty & Boynton, 1980; Yeh et al., 1995; Cottaris & De Valois, 1998; Smithson & Mollon, 2004), the expectation for chromatic induction is a sharp fall off above 3 Hz for *induced* temporal variation (DeValois et al. & Lingelbach, 1986). Both psychophysical and physiological evidence reveals that some levels of the S-cone pathway can follow temporal variation to more than 10 times this frequency (Stockmanet al., 1993; Yeh et al., 1995), which strongly suggests the temporal fall off of induction is constrained at a cortical level (De Valois et al., 1986).

Materials and methods

A $+s/-s$ receptive-field of the size described in previous work (Monnier & Shevell, 2004; Shevell & Monnier, 2005), with peak sensitivity near 1 cpd, implies that temporal modulation in a region near the test field drives the neural response to light within the test

Address correspondence and reprint requests to: Florent Autrusseau, Polytech' Nantes, IRCCyN, Rue Ch. Pauc, La Chantrerie, BP 50609, 44306 Nantes Cedex 03. France. E-mail: Florent.Autrusseau@univ-nantes.fr

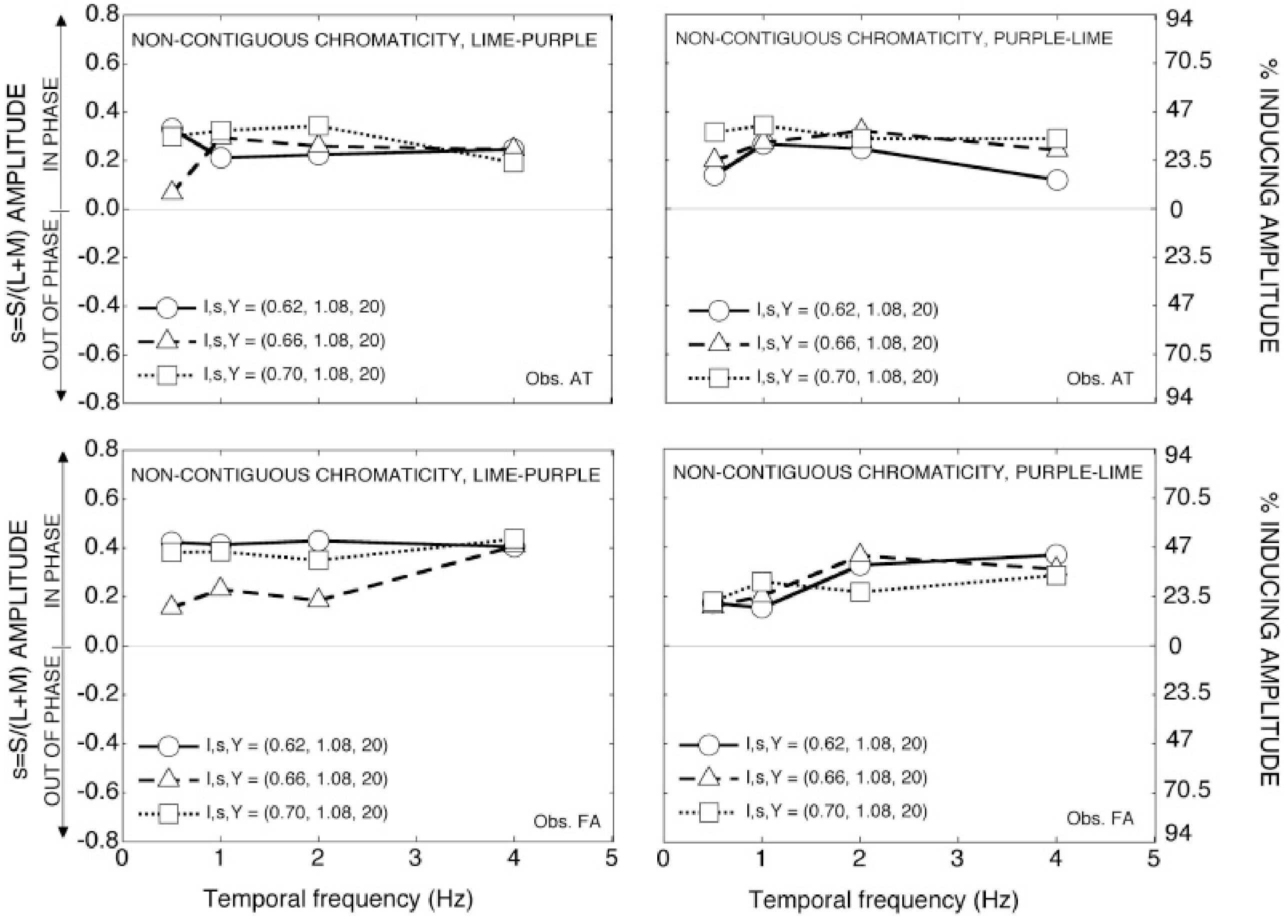

Fig. 3. Test-field nulling modulation as in Fig. 2 but with *non*-contiguous-chromaticity temporal modulation.

et al., 1986) may limit induced temporal variation more strongly than adaptation to a steady field, though again a comparison across different observers does not allow a firm conclusion.

The experiments here showed also that increasing temporal frequency from 0.5 to 4 Hz did not appreciably affect the induced color shifts. Based on chromatic induction from a time-varying *uniform* surround (De Valois et al., 1986), a sharp drop off in induced temporal variation was anticipated above 3 Hz. One possibility is that the drop off frequency increases with the spatial frequency of the stimulus (3.3 cycles per degree was used here), as found for induced temporal-variation of brightness (Rossi & Paradiso, 1996).

Acknowledgments

This research was supported by NIH grant EY-04802. Publication supported in part by an unrestricted grant to the Department of Ophthalmology and Visual Science from Research to Prevent Blindness.

References

Cottaris, N.P. & De Valois, R.L. (1998). Temporal dynamics of chromatic tuning in Macaque primary visual cortex. *Nature* **395**, 896–900.

DeValois, R.L., Webster, M.A., De Valois, K.K. & Lingelbach, B. (1986). Temporal properties of brightness and color induction. *Vision Research* **6**, 887–897.

Krauskopf, J., Zaidi, Q. & Mandler, M. (1986). Mechanisms of simultaneous color induction. *Journal of the Optical Society of America A* **3**, 1752–1757.

MacLeod, D.I.A. & Boynton, R.M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America* **69**, 1183–1185.

Monnier, P. & Shevell, S.K. (2003). Large shifts in color appearance from patterned chromatic backgrounds. *Nature Neuroscience* **6**, 801–802.

Monnier, P. & Shevell, S.K. (2004). Chromatic induction from S-cone patterns. *Vision Research* **44**, 849–856.

Rossi, A.F. & Paradiso, M.A. (1996). Temporal limits of brightness induction and mechanisms of brightness perception. *Vision Research* **36**, 1391–1398.

Shevell, S.K. & Monnier, P. (2005). Color shifts from S-cone patterned backgrounds: Contrast sensitivity and spatial frequency selectivity. *Vision Research* **45**, 1147–1154.

Smithson, H.E. & Mollon, J.D. (2004). Is the S-opponent chromatic sub-system sluggish? *Vision Research* **44**, 2919–2929.

Stockman, A., MacLeod, D.I.A. & Lebrun, S.J. (1993). Faster than the eye can see: Blue cones respond to rapid flicker. *Journal of the Optical Society of America A* **10**, 1396–1402.

Yeh, T., Lee, B.B. & Kremers, J. (1995). Temporal response of ganglion cells of the Macaque retina to cone-specific modulation. *Journal of the Optical Society of America A* **12**, 456–464.

Wisowaty, J.J. & Boynton, R.M. (1980). Temporal modulation sensitivity of the blue mechanism: Measurements made without chromatic adaptation. *Vision Research* **20**, 895–909.

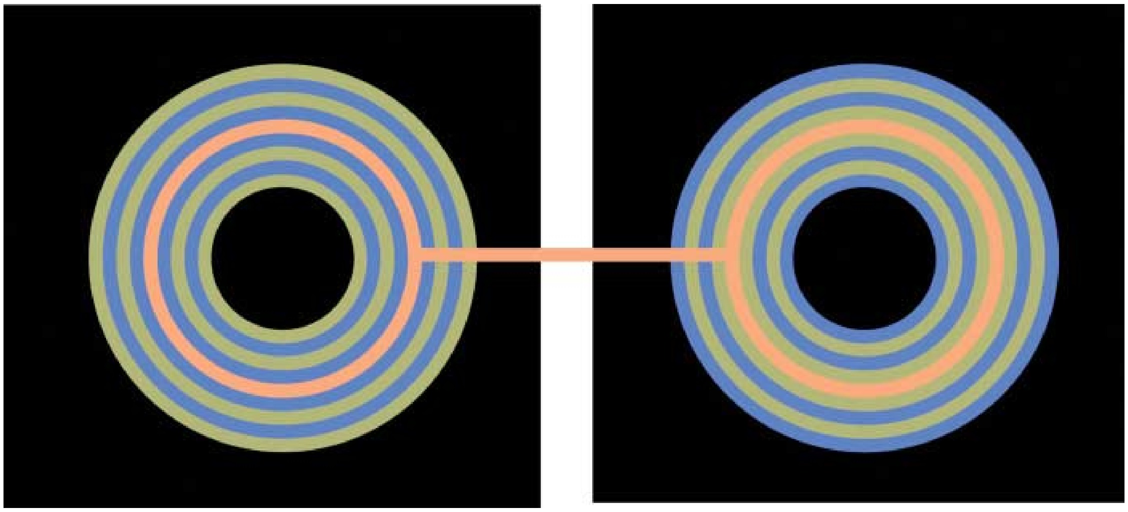

Fig. 1. Induction from a chromatic pattern. The two test rings (connected by a horizontal bar) are physically identical.

area in-phase with the modulating light. This would cause time-varying chromatic assimilation from the nearby light into the test area. On the other hand, temporal modulation within the receptive-field surround inhibits the cell's response, so the test's percept would change inversely with the surrounding modulation (time-varying chromatic contrast). In the experiments here, the chromatic induction was nulled by adding a time-varying light within the test area. The phase and amplitude of this light were adjusted by the observer so there was no perceived temporal variation in the test.

The surround was composed of concentric circles temporally alternating between two chromaticities (Fig. 1). The whole stimulus was composed of a test ring flanked on each side by 4 concentric circles, alternating between chromaticities initially appearing "purple" and "lime." The left pattern in Fig. 1 is called the purple-lime pattern (purple-appearing chromaticity adjacent to the test ring) and the right pattern the lime-purple pattern (lime-appearing chromaticity adjacent to the test). Both purple-lime and lime-purple patterns were used in the experiments. For each pattern, either the contiguous or non-contiguous chromaticity, but not both simultaneously, was modulated temporally.

The pattern's inner and outer diameters were, respectively, 1.8 deg and 4.5 deg, and the spatial frequency was 3.3 cycles per degree.

The stimuli were specified in a cone-based two-dimensional chromaticity space (MacLeod & Boynton, 1979) characterized by relative L-cone to M-cone stimulation $[l = \mathrm{L/L{+}M}]$ and relative S-cone stimulation $[s = \mathrm{S/(L + M)}]$. The unit of s is arbitrary and normalized here to 1.0 for equal energy white. The inducing chromaticities differed in only S-cone stimulation: l, s, Y of 0.66, 0.16, $15\mathrm{cd/m}^2$ for the lime circles, and l, s, Y of 0.66, 2.00, $15\mathrm{cd/m}^2$ for the purple circles.

In various conditions, either the contiguous or noncontiguous chromaticity was temporally varied sinusoidally between S/(L+M) of 0.16 and 2.00. L/(L+M) was held constant at 0.66. The observer's task was to adjust the test ring's sinusoidal modulation amplitude in the s direction, and its phase (in-phase or out-of-phase with the inducing light), in order to null the perceived temporal modulation in the test ring induced by the time varying part of the surround. Unlike Monnier and Shevell's experiments, no color judgment was required. Observers were encouraged to report any cases for which a satisfactory null could not be achieved (7% and 12% for observers A.T. and F.A., respectively).

The three test-ring chromaticities appeared white, green, or pink when viewed alone. Their l, s, Y chromaticities were respectively 0.62, 1.08, 20 cd/m2; 0.66, 1.08, 20 cd/m2; and 0.70, 1.08, 20 cd/m2. Four temporal inducing frequencies were tested: 0.5, 1, 2, and 4 Hz.

Three observers took part in this study. All had normal acuity as well as normal color vision as tested by the Ishihara plates and Rayleigh matching. Each observer completed training sessions before the data collection began. Each stimulus was presented three times to the observer in separate experimental sessions. Because of measurement variability, results from one of the observers are not reported. The median standard error for both observers A.T. and F.A. was 0.08. The corresponding value for the third observer, whose results are not reported, was 0.15 (90%ile standard error 0.30).

Results

Contiguous-chromaticity temporal modulation

Temporal variation of the contiguous chromaticity was predicted to shift test appearance in-phase with the inducer (assimilation), so the required nulling modulation to make the test appear steady should be out-of-phase with the inducer. The required nulling amplitude for the three test chromaticities is plotted in Fig. 2 for temporal frequencies of 0.5, 1, 2 and 4 Hz. In these plots, a negative amplitude (left vertical axis) represents test-field modulation out-of-phase with the inducing light (i.e., chromatic assimilation). Each row shows results for a different observer.

The results show the required test-field nulling modulation was out-of-phase with the inducing light (that is, induced assimilation), as predicted, for 46 of the 48 measurements (Fig. 2). For naïve observer A.T., all 24 measurements for both types of background (purple-lime and lime-purple), three chromaticities of test, and four temporal frequencies of the contiguous-chromaticity temporal modulation were out-of-phase ($P < 0.000001$ by sign test). For author F. A., 22 of 24 measurements were out-of-phase ($P < 0.00002$). (Even the results from the highly variable observer were out-of-phase for 22 of 24 measurements [$P < 0.00002$].)

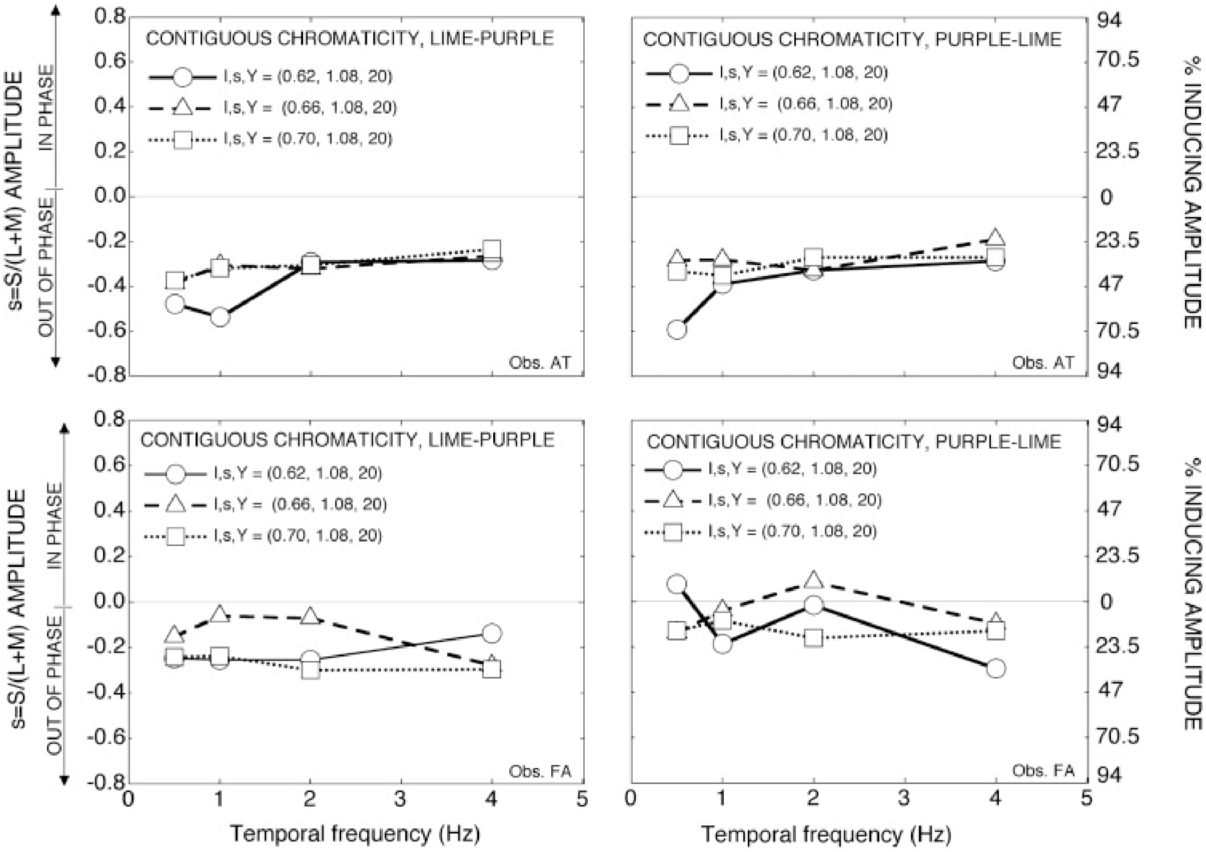

Fig. 2. The test-field nulling modulation with contiguous-chromaticity temporal modulation (inducing amplitude 0.85). The nulling amplitude in the S/(L+M) direction (left vertical axis) is plotted as a function of temporal frequency, for three test-ring chromaticities (open circles, triangles and squares). The results are shown also in terms of the percentage of the inducing-light amplitude (right vertical axis). The left and right panels show results with purple-lime and lime-purple background patterns, respectively. Each row shows results for a different observer.

Non-contiguous chromaticity variation

Temporal variation of the noncontiguous chromaticity was predicted to shift the test's appearance out-of-phase with the inducer (chromatic contrast) so the required nulling modulation in the test should be in-phase with the inducer. In plots, a positive amplitude (left vertical axis, Fig. 3) represents test-ring modulation in-phase with the inducing modulation. The results for each observer show the required test-ring nulling amplitude was in-phase for all of the 24 measurements, as predicted ($P < 0.000001$ for each observer). (Results from the highly variable observer were consistent with the in-phase prediction for 20 of 24 measurements [$P < 0.001$].)

On average over both observers, the results show approximately the same inducing magnitude for both nearby and more remote inducing-light temporal modulation. The average contiguous-chromaticity and non-contiguous-chromaticity S/(L + M) nulling amplitudes were 0.20 and 0.23, respectively, which correspond to 23.5% and 27% of the inducing-light amplitude.

Discussion

The results showed that contiguous-chromaticity temporal modulation required an out-of-phase nulling modulation of the test ring, implying assimilation from the inducer, and that non-contiguous-chromaticity modulation required in-phase modulation of the test ring, implying induced contrast. This is precisely the temporal variation in the test's color appearance expected for a $+s/-s$ spatially antagonistic receptive field, which previously was inferred from asymmetric color matching to a test ring within a steadily presented patterned background (Monnier & Shevell, 2003, Monnier & Shevell, 2004).

Chromatic induction measured here by nulling modulation was consistent in sign with previous experiments that used asymmetric color matching, but what about inducing magnitude? A quantitative comparison of the magnitude of induction from steady *versus* temporally-modulated inducing patterns unfortunately is not possible because it would require comparing results across different observers from each study. This is not appropriate given the small number of subjects used here. Note, however, there is no evidence to suggest less induction from a steady than a temporally varying field, as might be expected because of adaptation to a steadily presented background pattern: a greater magnitude of induction with a time varying than steady background was not found (cf. Monnier & Shevell, 2003).[a] Cortical temporal filtering (De Valois

[a]Recall that temporal modulation of the contiguous chromaticity in the lime-purple pattern, for example, had as extremes the lime-purple pattern shown in Fig. 1 (right panel) and a uniform purple surround. The nulling amplitude in this case should be compared to the difference between asymmetric matches with a steady lime-purple background and a steady uniform purple background. Similar reasoning applies to other comparisons of temporally-modulated *versus* steady chromatic induction.