

Pupillary Response to Chromatic Flicker

Patrick Drew^{1,3}, Rory Sayres¹, Katsumi Watanabe¹, and Shinsuke Shimojo^{1,2}

California Institute of Technology,
Division of Biology / Computation and Neural Systems

¹Division of Biology / Computation and Neural Systems
M/C 139-74
California Institute of Technology
Pasadena, CA 91125

² Human and Information Science Laboratory
NTT Communication Science Laboratories,
Atsugi, Kanagawa, 243-0198 Japan.

³ Neurosciences Department
Brandeis University
Waltham, MA 02454

Contact:
Shinsuke Shimojo
sshimojo@its.caltech.edu

Key Words: pupil, flicker, photosensitive, chromatic

Abstract

There is significant evidence for higher-level cortical control of pupillary responses to visual stimuli, suggesting that factors other than luminance changes may induce a pupillary response. In the present study, the pupillary responses to equiluminant flickering stimuli in a range of 3-13 Hz were examined. Flicker stimuli included color-black (luminance-modulated) and color-color (hue-modulated) flicker. Equiluminance was determined both by objective luminance measures as well as by subjective, perceptual equiluminance for each subject. For both objectively and subjectively equiluminant flicker, significant, sustained pupillary constrictions were recorded. The magnitude of these responses was sensitive to both color and frequency parameters; Red-Blue color-paired flicker consistently produced the strongest constrictions. These responses occurred even when the flicker was of a lower luminance, both physically and perceptually, than a preceding nonflickering color, indicating that chromatic rather than luminance-sensitive mechanisms are involved in this response. Interestingly, the color- and frequency-sensitivity of constriction parallels those of flickers which maximally stimulate photosensitive epileptic patients, raising the possibility that chromatic response may be a factor in photosensitivity.

Introduction

The pupil serves as a gain control device for the visual system. It responds to luminance changes in the environment, and this response is largely governed by a well-characterized subcortical projection through the pretectum to the accessory oculomotor nucleus (Lowenfeld, 1993).

However, in addition to this luminance sensitivity, pupillary responses have been found for a number of other stimuli, including single changes in color and pattern, as well as onset of coherent motion (Kohn and Clynes, 1969; Young and Alpern, 1980; Barbur *et al.*, 1992). Change in pupil size has also been implicated in such higher-level behaviors as attention (Hess and Polt, 1960, 1964) and social signaling (Niedenthal and Cantor, 1986). Additionally, it was found that a single flash of color on a white background produced a pupillary constriction response made of several distinct components, including transients related to flash onset and offset as well as a sustained component (Kimura and Young, 1995).

The role of the pupil as a gain control may have some clinical and social significance. Unusual luminance-contrast gain control has been linked to photosensitivity, in which afflicted individuals are abnormally sensitive to particular forms of photic stimulation and which can result in seizure attacks (Doose and Waltz, 1993; Porciatti *et al.*, 2000). A particularly notorious incident involving photosensitivity happened in 1997, when over 700 children in Japan were hospitalized after exposure to patterned red-blue flicker on a children's television cartoon show (Ishida *et al.*, 1998). Particular color and frequency parameters have been shown to be favorable at inducing seizure-like symptoms in clinical settings (Takahashi and Tsukahara, 1976).

The role of the pupillary response in regard to non-luminance-related changes such as transient chromatic exchanges is not clear. Kimura and Young (1995, 1996, 1999) draw parallels between the pupil action spectra to single flashes on a colored background and the spectral sensitivity curve of the psychophysical chromatic channel. These parallels imply a close relationship between pupillary response and color perception. Previously, Troelstra (1968) used the pupillary response as a measure of brightness enhancement, examining the pupil's response to a temporally-modulated light stimulus.

A further exploration of the role of these responses is clearly valuable. For instance, if the pupil responds transiently to individual changes, yet most natural visual scenes feature myriad individual changes of this nature, how does the pupil respond to these sequences of changes? How does a non-luminance-driven pupillary response extend to dynamic, constantly-changing stimuli? The present study attempts to address these questions by investigating flickering stimuli which are temporally modulated over relatively long periods of time (6 seconds) and which have been shown to have unusual effects on some people. Notably, the dangerous excitatory effects on photosensitive patients.

Preliminary studies performed in our laboratory indicated a sustained pupillary constriction in response to a flickering stimulus. The amplitude and duration of this response appeared to be sensitive to color and frequency parameters, with some overlap between those parameters producing the strongest constrictions and those most likely to produce seizure activity in photosensitive patients. These preliminary findings were based on flicker in which the color

components of flicker were perceptually equiluminant. The presence of constrictions raised the question of whether this response was due to small physical luminance changes between perceptually isoluminant colors in the flicker. In order to establish whether this response was due to the action of luminance channels, we performed two experiments: one in which the stimulus had the same physical luminance throughout, and one in which the flickering components were perceptually equated, yet of a lower mean luminance than a preceding solid color.

Materials and Methods

Subjects

Subjects were 6 healthy volunteers, 3 male and 3 female, between the ages of 18 and 28. Subjects were screened for photosensitivity and personal or familial history of epilepsy. The study was approved by the Human Subjects Committee; all subjects gave their informed consent prior to their inclusion in the study.

Stimulus

The stimulus was presented on a 16" NEC RGB monitor operating at a resolution of 1152 pixels x 870 pixels and a refresh rate of 76 Hz. The monitor was placed 19 cm in front of the subjects' eyes, for a visual angle of 58° by 53°. For a given color/frequency combination, the subject was presented with a stimulus loop composed of 5 trials; each trial followed the sequence of six seconds of stable control color, followed by six seconds of full-screen flicker, followed by six seconds of control color. The control color for a given condition was a fusion between the color components of flicker: for instance, for red-blue flicker, the control color was purple. For luminance-modulated flicker such as red-black flicker, the control color was the same as the flickering color, although lower in luminance so that the time-averaged luminance of flickering and non-flickering stimuli were both 3.6 cd / m². All stimuli were generated in

MATLAB“ (The MathWorks, Inc, Natick, MA), using the extensions provided by the high-level Psychophysics Toolbox (Brainard, 1997) and low-level VideoToolbox“ (Pelli, 1997).

Flicker stimuli were presented at three frequencies 3.16, 6.33, and 12.6 Hz, corresponding to a color change every 12, 6, and 3 frames, respectively. At each frequency, eight different color combinations were used, grouped into two categories: hue-modulated (color-color) flicker, which included red-blue, blue-green, red-green, and blue-yellow flicker; and luminance-modulated (color-black) flicker, which included red-black, blue-black, green-black, and white-black flicker.

Two experiments are reported here. In the first experiment, the flicker was of equal physical luminance to the preceding solid color: both stimuli had a time-averaged luminance of 3.6 cd/m². For hue-modulated flicker (e.g. red-blue flicker), this meant that both components of flicker (e.g., red and blue) as well as the stable fusion color (e.g., purple) were at 3.6 cd / m². For luminance-modulated flicker, the stable fusion color was at 3.6 cd / m² while the flicker components alternated between < 0.1 cd / m² for black, and ~7.5 cd / m² for the color. Thus control colors and flicker had the same time-averaged luminance.

In the second experiment, the flicker components were perceptually equiluminant as determined by a minimum-motion criterion (Anstis and Cavanaugh, 1983), relative to a red ((x, y, Y) = (0.58, 0.35, 3.6)). In order to address possible concerns that small luminance differences between colors might be a possible factor mediating pupillary response, the flicker was also of a lower physical and perceptual luminance than the stable control color which both preceded and followed it. Specifically, the stable color was the combination of the RGB values in a software color table of the flicker components: for instance, for red-blue flicker, red ((x, y, Y) = (0.58, 0.35, 3.6)) and blue (for one subject, (x, y, Y) = (0.15, 0.08, 3.7)) combined to generate a purple ((x, y, Y) = (0.24, 0.13, 7.3)) approximately twice the luminance of either the red or blue. For luminance-modulated flicker, the stable color was identical to the non-black color of the flicker.

Procedure

Pupil sizes were recorded by video pupillometry techniques. The display was controlled by a Power Macintosh 7300/200 and the subjects were instructed to observe it passively. Head movements were constrained during experiments by the use of a chinrest. During experiments, the left eye was illuminated by the monitor, while the right eye was illuminated through the use of an IR LED and shielded from the display by a mirror. This mirror was oriented 45 degrees to the monitor, used to reflect the image of the eye into an IR CCD camera, which input into a digital video recorder, which also received timing information about stimulus onset and offset. During rest periods between tests, room lights were turned on in order to prevent the rod dominance due to dark adaptation.

The diameter of the right eye video was sampled off-line using the ViewPoint™ eye-tracking software (Arrington Research, Mesa, AZ) at a rate of 20 Hz. Size of constriction was defined as the difference between the minimum pupil diameter during the flicker period and the mean pupil diameter during the preceding control period, for each trial.

Results

Experiment 1 investigated pupillary responses to flicker whose components were equal in physical luminance to each other as well as a preceding stable color. For all conditions, significant pupillary constrictions were found during flicker. Waveforms of the pupillary responses obtained for Experiment 1 are presented in Figure 1. As can be seen by the average traces for each condition, the size of constriction depended on both color and frequency of the stimulus. The dependence of amplitude of constriction in relation to these parameters is plotted in Figure 2. In general, size of constriction decreased with increasing frequency, and also for hue-modulated as opposed to luminance-modulated flicker. Red-Blue and Blue-Green flickers produced the strongest constrictions, with decreases in diameter of up to 38.3% and 52.8% and mean constrictions of 24.0% and 24.7%, respectively. A two-way ANOVA on size of constrictions revealed main effects

of color ($F(7,35) = 50.1, p < 0.01$) and frequency ($F(2,10) = 54.75, p < 0.01$), as well as an interaction between color and frequency ($F(14,70) = 4.81, p < 0.01$).

In order to test the possible effect of small luminance effects in the observed response, Experiment 2 was performed in which luminance decreased with flicker onset. As with Experiment 1, significant constriction responses were found for all conditions. Figure 3 shows sample waveforms obtained in this experiment, while Figure 4 plots the color- and frequency-dependence of the strength of constriction. In this experiment, constrictions were generally smaller in amplitude than those in Experiment 1, indicating constrictions were weakened by a luminance-driven dilation response in Experiment 2. As a notable exception, some trials at 13Hz yielded dilation in response to flicker onset, which would be expected if luminance-driven channels dominated this response, since luminance is decreasing by nearly a factor of 2 with flicker onset. Most notably, the difference between Red-Blue and other colors in efficacy at generating responses became striking. Constrictions by Red-Blue were significantly larger than any other color flicker (one-tailed t-test: $p < 0.02$) at 3 and 6 Hz, though not at 13Hz. A two-way ANOVA on size of constrictions again revealed main effects of color ($F(7,35) = 17.9, p < 0.01$) and frequency ($F(2,10) = 64.0, p < 0.01$), as well as an interaction between the two ($F(14,70) = 4.67, p < 0.01$)¹.

Additional analysis on the duration of constriction and likelihood in a given trial of a significant constriction showed the same trends as those for amplitude for both experiments. Duration increased with increasing size of constriction, as did the likelihood of a significant constriction

¹ Worth noting is the presence of relatively large constrictions at the end of flicker periods; this likely represent transients corresponding to the luminance increment at the end of flicker periods, but may also represent a potential OFF transient to the response (Kimura and Young, 1995)¹ Further analysis is necessary to determine if this is the case.

(defined as the pupil diameter during the flicker period being significantly smaller than during the preceding control period by a one-tailed t-test ($\alpha = 0.05$)) on a given trial (Data not shown).

Discussion

This study has found a pupillary constriction in response to chromatic flickering stimuli. This response exists whether the components of the flicker are perceptually equiluminant, or of an equal physical luminance, and the response persists even when the flicker is of a lower luminance than a preceding solid color. The amplitude of pupillary response depends on both color and frequency parameters. For the color dependence, hue-modulated (color-color) flicker, particularly Red-Blue and Blue-Green flicker, consistently produced stronger constrictions than luminance-modulated (color-black) flicker. For frequency dependence, lower frequency flicker generally produced more powerful constrictions, although the color-dependence of flicker was most visible between 6 and 13 Hz.

These results are significant in at least two respects. First, the pupillary constriction appears to be due specifically to the dynamic change in chromaticity of the display, rather than the luminance.

The color-dependence strongly suggests an interaction between color and temporal dynamics in producing a response, supporting the notion of more complex control of pupillary responses.

Second, the results may have some implication to the condition of photosensitivity, due to overlap

between parameters which cause stronger constrictions in normal observers and those which preferentially induce photoparoxysmal response in photosensitive patients.

Interaction between color and temporal dynamics

In regards to the first point mentioned above, luminance does not seem to be an active factor in the constriction responses reported here, for several reasons. In the first experiment, when the stimulus was always at the same physical luminance throughout, luminance can also be excluded as a cause of constriction, since it never varied for hue-modulated flicker and the mean temporal luminance does not change for luminance-modulated flickers. Further it can be argued that small perceptual differences between physically equiluminant colors are also not responsible for this constriction. Consider that if small differences in the perceived brightness of the color components of flicker caused a response like the one seen, then Color-Black flicker, which has much larger alternations in perceived brightness during flicker than Color-Color flicker, would be expected to be a much more powerful stimulus. Instead, Color-Black flicker produced constrictions of a significantly smaller amplitude than Color-Color flicker.

Moreover, pupil constrictions were found in the second experiment, when the luminance of the flickering stimulus was always less than that of the nonflickering stimulus. If luminance was governing this response, dilation would be expected, and in fact dilation was found for some conditions at 13Hz. However, for some trials in all conditions, and especially at lower temporal frequencies, constrictions and not dilations were found.

It is interesting to note, however, that the responses to both Color-Black and Color-Color flickers were much reduced in the second experiment, most likely resulting from an additional luminance-driven response tending towards dilation. This suggests that both of these flickers are at least partially mediated by the same mechanism, and suggests that the dynamic nature of the display is a critical factor. However, the temporal modulation is not the only critical factor to constriction, since Color-Color flickers produce such stronger responses than Color-Black flickers. The interaction between changes in chromaticity and temporal modulation that seems to be necessary for the strongest responses.

It is this unique interaction which is not suggested by previous investigation on the pupillary response. The pupillary response to single changes in chromaticity of a stimulus has been well-documented by Barbur and others (1992, 1998), and the pupillary response to single flashes has been examined as a function of wavelength (Kimura and Young, 1995). It might be expected that the mechanisms responsible for these constrictions could cause transient constrictions for single changes (essentially very low frequencies) while producing sustained responses at higher frequencies. Indeed, the inverse relationship between a flicker's temporal frequency and its power in producing constrictions may be consistent with this. However, this would not account for the fact that juxtaposed colors can produce stronger responses than color-black flickers of the same time-averaged luminance.

Relation to photosensitivity

The unusual color-dependence of the responses reported here suggests a possible link between these responses and the condition of photosensitivity. Photosensitivity is defined as the occurrence (on an EEG) of spikes or spikes and waves in response to intermittent light stimulation (Doose and

Waltz, 1993). In most photosensitive subjects, both frequency and color play an important role in the likelihood of seizures. Takahashi and Tsukahara (1976) found that Red-Black flicker between 10-20 Hz, particularly at 15 Hz, has been found to be the most common color-frequency combination to which photosensitive patients are sensitive, other colors having much weaker effects. Others have reported that frequencies up to 25, 50 even 84 Hz are effective for some subjects (Wilkins *et al.*, 1978; Jeavons *et al.*, 1975).

Until recently, however, hue-modulated flicker has not been intensively investigated as a seizure-inducing stimulus. This is partially because the equipment used in clinical settings to generate intermittent photic stimulation of patients can not easily be made to generate color-color flicker. Yet the most notorious case of photosensitivity in recent memory was generated by red-blue flicker, when in 1997 over 700 children in Japan were hospitalized after experiencing seizures while viewing an episode of the cartoon *Pocket Monsters* (Ishida *et al.*, 1998). The stimulus which provoked this incident was a red-blue flicker of about 15 Hz with a jittering pattern, and was generally viewed on televisions which had a further interlaced pattern and a 60Hz refresh rate.

It has been known for some time that flickering stimuli can induce rhythmic activity in the brain (Ranger and Singer, 1998; Walter and Walter, 1949). The differential pupillary response to different color and frequency flickers may reflect differential ability at inducing rhythmic activity for these stimuli. If this is the case, then the pupil response may reflect the action of a cortical gain control mechanism. Recently, Porciatti *et al.* (2000) examined visual evoked potential (VEP) responses to temporally-modulated luminance gratings in photosensitive and non-photosensitive subjects. The responses showed a number of differences between groups, including an apparent

absence of amplitude saturation with increasing contrast and overall higher VEP contrast in photosensitive subjects. This evidence strongly indicates a contrast gain control mechanism in non-photosensitive subjects, the lack of which may underlie photosensitivity. Although differences in VEP response to chromatic red-green gratings were not found to be significant, the study did not examine flickers including blue and another color, which may be more important since it was red-blue and blue-green flickers that were found to be most powerful at producing constrictions, and the former having been the causal stimulus in the 1997 incident.

The pupillary response to a dynamic stimulus such as flicker may be a defensive response. Since we know these stimuli can generate rhythmic activity in the brain to the point of seizure generation, there is a known risk to this stimulus; the pupil's constriction may reduce exposure to that risky stimulus in non-photosensitive observers. It has been shown that brighter flickers have a greater power at inducing seizures (Takahashi and Tsukahara, 1976, 1998), and presumably greater retinal illuminance from a flicker only serves to make the stimulus more dangerous. Constrictions reported here can range up to 50% of the pupil diameter, which reduces the overall illuminance to 1/4 of its original value; this may well be enough to keep a stimulus out of the range where it is strong enough to induce seizure, and it may be some abnormality of this mechanism in the patients that feeds forward to seizure generation.

Our results also have a more practical implication. In some studies the pupils of photosensitive patients were pharmacologically dilated before EEG recordings were made during a visual stimuli. If the pupillary mechanism is involved in this condition, findings that are made with the pupil dilation procedure may not be applicable to seizures occurring in a non-laboratory setting, such as

ordinary viewing of a television. Further examination of the pupillary response, as well as other measures of activity (EEG, MEG, fMRI) in photosensitive subjects could reveal the exact mechanism and relation between flicker-induced pupillary constriction and photosensitive seizures.

Acknowledgments

We thank Christian Scheier, Bhavin Sheth, and Johanna Weber for technical assistance and advice. Part of this research has been presented at the 2000 annual meeting of Association for Research in Vision and Ophthalmology (Sayres *et al.*, 2000). This work was support by NTT Communication Science labs and NHK, Japan.

References

- Anstis, S. M. and Cavanagh, P. (1983) A minimum motion technique for judging equiluminance. In Mollons, J. D. and Sharpe, L. T. (Eds.), *Color vision: physiology and psychophysics*, 155-166, London: Academic Press.
- Barbur, J. L., Harlow, A. J., and Sahraie, A. (1992) Pupillary responses to stimulus structure, colour and movement. *Ophthalm Physiol Optics* 12, 137-141.
- Barbur, J.L., Wolf, J., and Lennie, P. (1998) Visual processing levels revealed by response latencies to changes in different visual attributes. *Proc R Soc Lond B* 1412, 2321-5.
- Brainard, D. H. (1997) The Psychophysics Toolbox, *Spat Vis* , 10, 443-446.
- Doose, H. and Waltz, S. (1993) Photosensitivity - genetics and clinical-significance. *Neuropediatrics* 24, 249-255.
- Hess, E. H., and Polt, J. M. (1960) Pupil size in relation to the interest value of visual stimuli. *Science* 132, 349-350.
- Hess, E. H., and Polt, J. M. (1964) Pupil size in relation to mental activity during simple problem solving. *Science* 143, 1190-1192.
- Ishida, S., Yamashita, Y., Matsuishi, T., Ohshima, M., Ohshima, T., Kato, H. and Maeda, H. (1998) Photosensitive seizures provoked while viewing "Pocket Monsters", a made-for-television animation program in Japan. *Epilepsia* 39, 1340-1344
- Jeavons, P.M. and Harding, G. F. A. (1975) *Photosensitive Epilepsy*. William Heinemann, London.
- Kimura, E. and Young, R. S. L. (1995) Nature of the pupillary responses evoked by chromatic flashes on a white background. *Vis Res*, 35, 897-906.
- Kimura, E. and Young, R. S. L. (1996) A chromatic-cancellation property of human pupillary responses. *Vis Res*, 36, 1543-1550.
- Kimura, E. and Young, R. S. L. (1999) S-cone contribution to pupillary responses evoked by chromatic flash offset. *Vis Res*, 39, 1189-1197.
- Kohn, M. and Clynes, M. (1969) Color dynamics of the pupil. *Annals New York Acad Sci*, 156, 931-950.
- Lowenfeld, I. E. (1993) *The Pupil: Anatomy, physiology, and clinical applications (Vol. I)*. Ames: Iowa State University Press.

- Niedenthal, P. M. and Cantor, N. (1986) Affective responses as guides to category-based influences. *Motivation and Emotion*, 10, 217-231.
- Pelli, D. G. (1997) The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spat Vis*, 10, 437-442.
- Porciatti, V., Bonanni, P., and Guerrini, R. (2000) Lack of cortical contrast gain control in human photosensitive epilepsy. *Nat Neurosci* 3(3):259-263.
- Ranger, G., and Singer, W. (1998) The response of cat visual cortex to flicker stimuli of variable frequency. *Eur J Neurosci* 10:1856-1877.
- Sayres, R., Drew, P., Watanabe, K., and Shimojo, S. (2000) Pupillary responses to chromatic flicker *Invest Ophthalmol and Vis Sci* 41(4):S809. Abstract nr. 4296.
- Takahashi, T. and Tsukahara, Y. (1976) Influence of color on the photoconvulsive response. *Electroencephalogr Clin Neurophysiol*, 41, 124-136.
- Takahashi, T., Tsukahara, Y. (1998) Photoparoxysmal response elicited by flickering dot pattern stimulation and its optimal spatial frequency of provocation. *Electroencephalogr Clin Neurophysiol*, 106, 40-43.
- Troelstra, A. (1968) Detection of time-varying light signals as measured by the pupillary response. *J Opt Soc Am* 20, 364-78.
- Walter, V. J. and Walter, W. G. (1949) Central effects of rhythmic sensory stimulation. *Electroencephalogr Clin Neurophysiol*, 2, 57-86.
- Wilkins, A. J., Darby, C. E., Binnie, C. D., Stefansson, S. B., Jeavons, P.M., and Harding, G. F. A. (1978) Television epilepsy - the role of pattern. *Electroencephalogr Clin Neurophysiol*, 47, 163-171.
- Young, R. S. L. and Alpern, M. (1980) Pupil responses to foveal exchange of monochromatic lights. *J Opt Soc Am*, 70, 697-706.

Figure Captions

Figure 1. Pupillary responses for Experiment 1. *a)*, Schematic of Experiment 1. *b)* and *c)*, Average waveforms of pupil diameter for different color and frequency flickers in Experiment 1, expressed as mean percent change (from control-period baseline) in diameter. Solid line: response at 3Hz; dashed line: 6Hz, dotted line: 13Hz. Gray bar at bottom indicates flicker stimulus. *b)* shows responses to luminance-modulated (color-black) flicker, *c)* shows responses to hue-modulated (color-color) flicker. *d)*, Representative waveforms from different observers for 3Hz flicker. The example waveforms for responses to Red-Black and White-Black flicker have been displaced 2 mm successively downwards for clarity.

Figure 2. Dependence of constriction size (expressed as percent change from control-period baseline) on color and frequency parameters for Experiment 1. *a)*, luminance-modulated flicker, *b)*, hue-modulated flicker. Error bars represent standard error of the mean.

Figure 3. Pupillary responses for Experiment 2. *a)*, Schematic of Experiment 2. *b)* and *c)*, Average waveforms of pupil diameter for different color and frequency flickers in Experiment 2, expressed as mean percent change (from control-period baseline) in diameter. Solid line: response at 3Hz; dashed line: 6Hz, dotted line: 13Hz. Gray bar at bottom indicates flicker stimulus. *B)* shows responses to luminance-modulated (color-black) flicker, *c)* shows responses to hue-modulated (color-color) flicker. *d)*, Representative waveforms from different observers for 3Hz flicker. The example waveforms for responses to Red-Black and White-Black flicker have been displaced 2 mm successively downwards for clarity.

Figure 4. Dependence of constriction size (expressed as percent change from control-period baseline) on color and frequency parameters for Experiment 2. *a*), luminance-modulated flicker, *b*), hue-modulated flicker. Error bars represent standard error of the mean.

Figure 1.

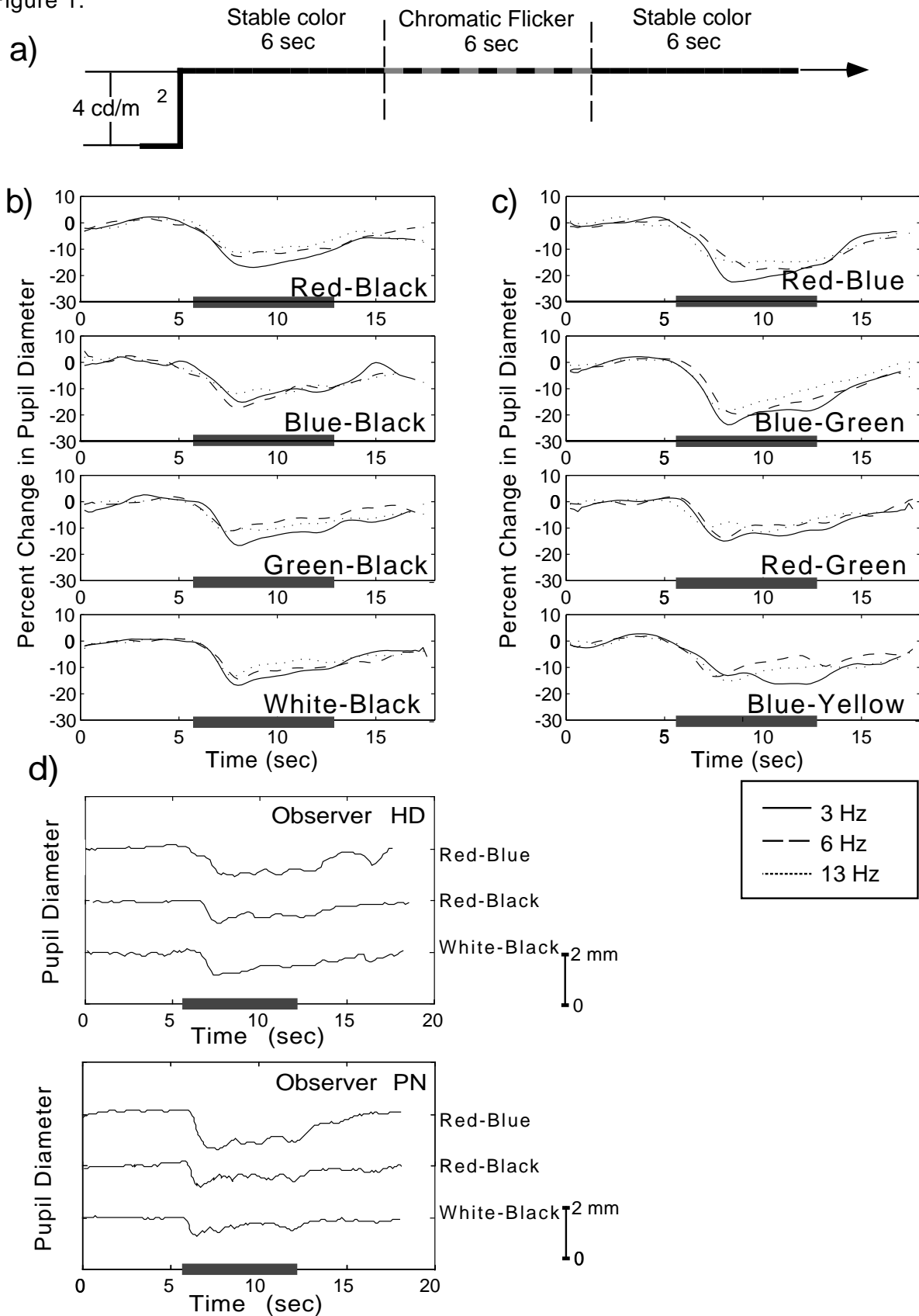
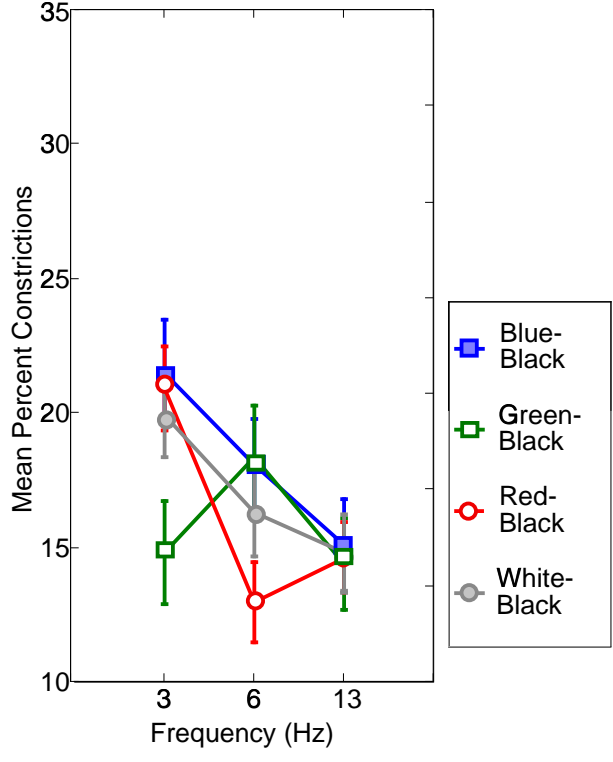


Figure 2.

a) Luminance-Modulated Flicker



b) Hue-Modulated Flicker

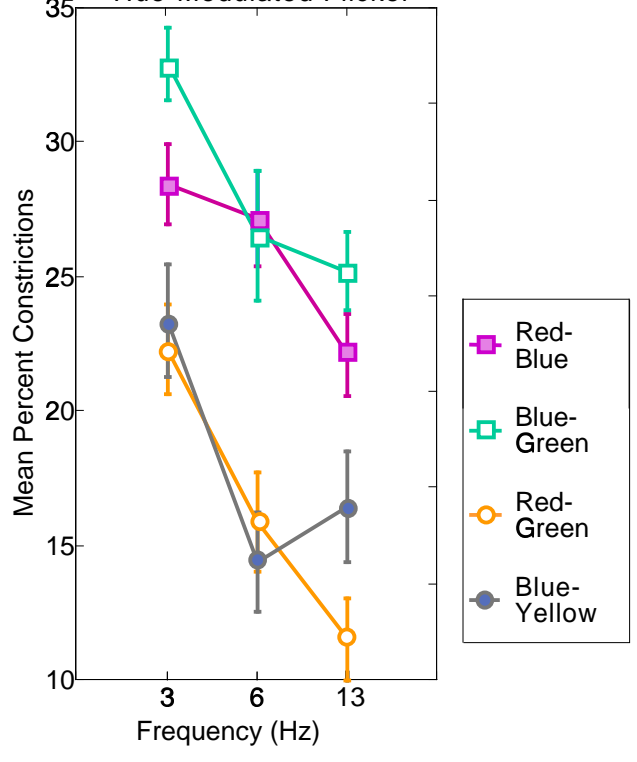


Figure 3.

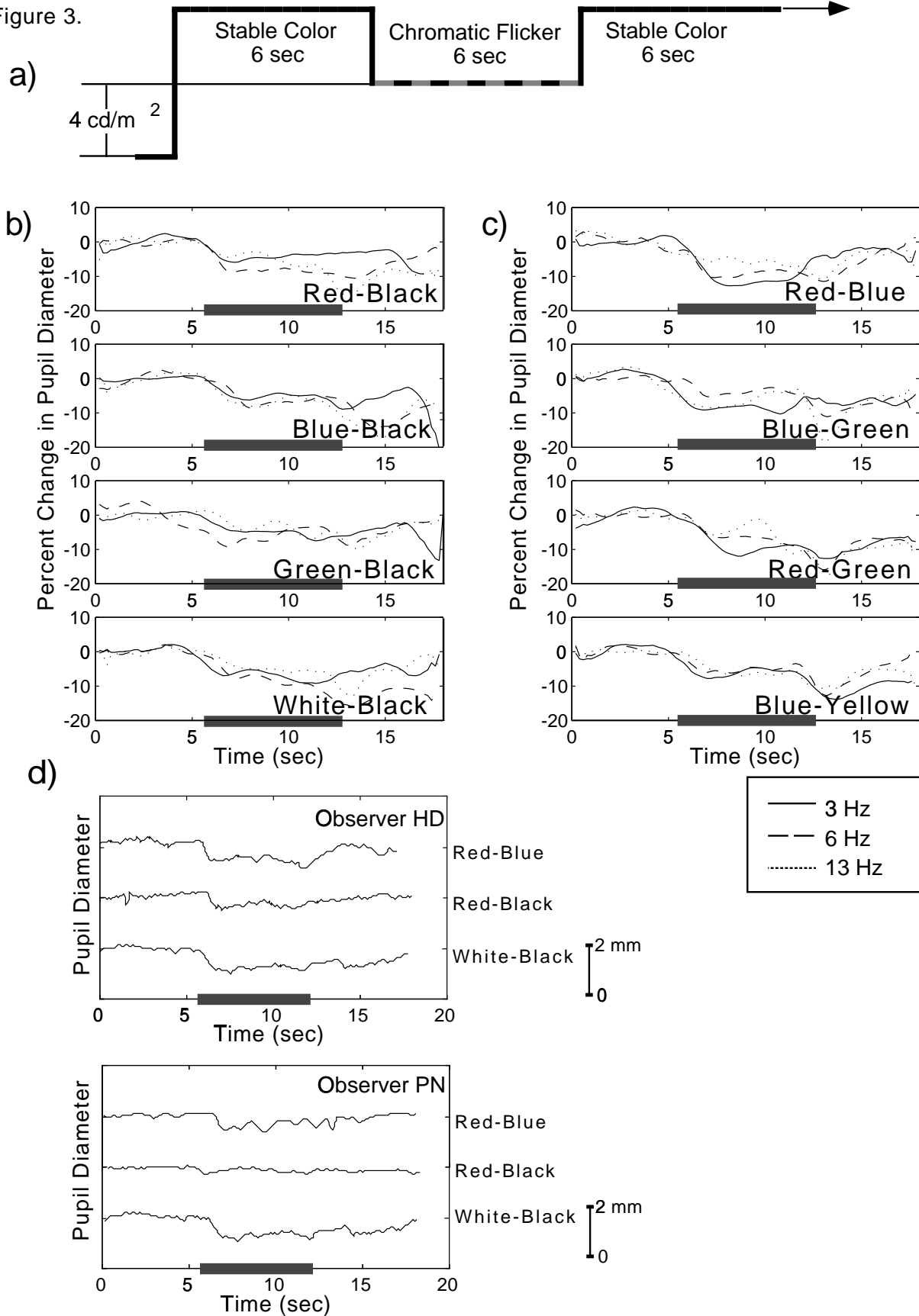
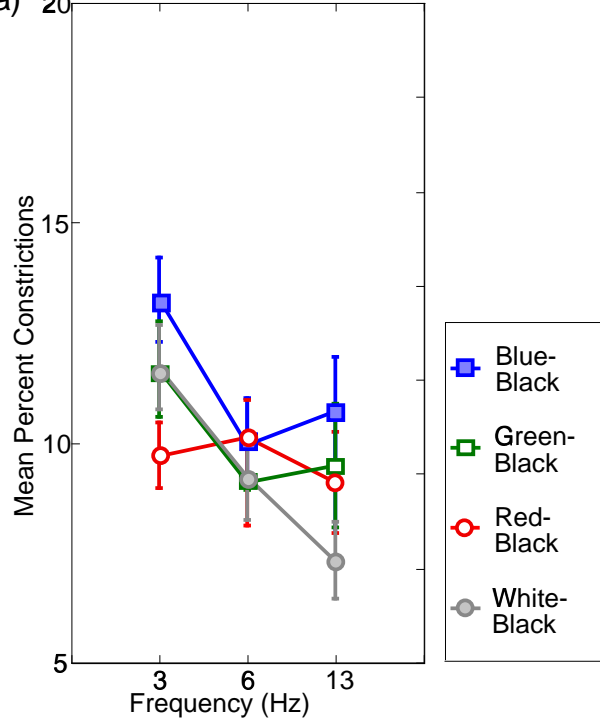


Figure 4.

a) Luminance-Modulated Flicker



b) Hue-Modulated Flicker

