Attenuation of the pupillary response to luminance and color changes during interocular suppression

Eiji Kimura

Department of Psychology, Faculty of Letters,
Chiba University, Chiba, Japan

Satoru Abe

Graduate School of Advanced Integration Science,
Chiba University, Chiba, Japan

Ken Goryo

Faculty of Human Development and Education,
Kyoto Women's University, Kyoto, Japan

The present study investigated the effects of interocular suppression on the pupillary constriction to luminance and color changes. Stable interocular suppression was produced by presenting a flickering high-contrast grating to one eye and a spatially homogeneous field to the other eye. The results showed that the pupillary responses to luminance as well as color changes were clearly attenuated during interocular suppression; the pupillary constriction to stimulus changes was delayed and reduced in amplitude when those changes occurred in the suppressed eye. The attenuation of the pupillary response was observed over a wide range of test contrast extending to well above the threshold level. Moreover, the properties of the suppressive effect were very similar to those assessed psychophysically using both detection thresholds for weak stimuli and reaction times for suprathreshold stimuli. Overall, the present study provided converging evidence that the pupillary response can be a useful objective probe of interocular suppression in humans. The results are discussed in view of possible differential involvements of subcortical and cortical visual processing in driving the pupillary response as well as in interocular suppression.

Introduction

Simultaneously presenting different stimuli to the corresponding retinal regions in each eye produces a perceptual conflict called binocular rivalry. During binocular rivalry, observers often perceive only one of the two images exclusively due to interocular suppression. Thus, interocular suppression can phenomenally suppress strong suprathreshold stimuli. Previous studies asked how far this interocular suppression extends beyond visual perception and investigated the effects of binocular rivalry on the oculomotor reflex such as the pupillary response (e.g., Barany & Hallden, 1948). One of the main interests of the previous researchers lay in the question of whether binocular rivalry can adversely affect subcortical visual processing mediating the pupillary light reflex. However, the results of the previous studies were not consistent. Some studies provided positive results showing that the pupillary light reflex to a luminance flash was reduced when the flash was presented to the suppressed eye (Barany & Hallden, 1948; Lorber, Zuber, & Stark, 1965; Richards, 1966; Brenner, Charles, & Flynn, 1969). However, other studies provided negative results (Lowe & Ogle, 1966; Bradshaw, 1969). Based on this diversity of the results, some researchers argued that "the pupil response cannot be reliably employed as an objective indicator of suppression" (Fox, 1991, p. 102). However, the diversity may be attributable to methodological issues (e.g., unstable or weak suppression during the pupil measurement; response variability in single-trial recording that was adopted in many previous studies). This study reinvestigates the effects of interocular suppression on the pupillary response in light of new findings in pupillometric research.

Recently, some new developments have been made in the field of pupillometric research that suggest that the pupillary response can be a useful objective measure for studying visual processing in humans. First, it has been established that pupillary constriction is driven by rich visual inputs. In addition to changes in ambient light intensity, the pupil constricts in response to other stimulus changes in chromaticity, spatial pattern, and

motion (Kohn & Clynes, 1969; Saini & Cohen, 1979; Slooter & van Norren, 1980; Young & Alpern, 1980; Ukai, 1985; Barbur & Forsyth, 1986; Barbur, Harlow, & Sahraie, 1992; Young, Han, & Wu, 1993; Young & Kennish, 1993; Young, Kimura, & DeLucia, 1995). Recent studies also showed that the pupil can respond to even more complex stimuli such as human faces (e.g., Conway, Jones, DeBruine, Little, & Sahraie, 2008).

Second, it is now clear that several afferent visual processes contribute to the pupillary response. Recent studies have established that the human pupillary light reflex (i.e., changes in the pupil diameter in response to changes in light intensity) is driven by a light-sensitive pigment called melanopsin as well as by rod and cone photopigments (Gamlin et al., 2007; Kawasaki & Kardon, 2007; Young & Kimura, 2008; McDougal & Gamlin, 2010). More importantly in the context of the present study, there is now good evidence for cortical contribution to the pupillary constriction to color, spatial pattern, and motion (Barbur & Forsyth, 1986; Barbur, Keenleyside, & Thomson, 1989; Heywood, Nicholas, LeMare, & Cowey, 1998; Weiskrantz, Cowey, & Le Mare, 1998; Wilhelm, Wilhelm, Moro, & Barbur, 2002; Barbur, 2004). When tested with hemianopic patients with occipital cortical lesions (postgeniculate lesions), pupillary color and pattern responses were either absent or much reduced to the stimuli presented to the blind hemifield, although the pupillary light reflex (i.e., pupillary response to intensity changes) was well preserved, particularly when the stimulus was of high contrast. Additionally, a lesion study with monkeys showed that the pupillary color response was abolished by removing the anterior inferotemporal cortex, while the pupillary light reflex was unaffected (Heywood et al., 1998). Moreover, there is also evidence for selective loss of the pupillary light reflex. Wilhelm et al. (2002) reported in patients with Parinaud's syndrome, which is caused by damage to the pretectal region in the dorsal midbrain, that the pupillary light reflex was almost abolished, while the pupillary color and pattern responses were little affected. In addition, Barbur, Wolf, and Lennie (1998) argued that the level of visual processing at which different stimulus attributes are analyzed can be reflected in the latency of the pupillary response (i.e., the time measured from the stimulus onset to the response onset). Thus, the findings that the pupillary color response was 40 to 50 ms slower than the pupillary light reflex were considered to reflect processing delays arising in the cortex (see also Young & Alpern, 1980; Gamlin, Zhang, Harlow, & Barbur, 1998). These findings suggest a possibility of investigating subcortical and cortical contributions to the pupillary responses using the pupillary light and color responses, respectively.

Third, recent studies provided converging evidence that the pupillary response exhibits response properties similar to those of perceptual responses (Slooter & van Norren, 1980; Krastel, Alexandridis, & Gertz, 1985; Barbur & Thomson, 1987; Cocker & Moseley, 1992; Kimura & Young, 1995; Young et al., 1995; Kimura & Young, 1996). For example, Kimura and Young (1996) showed that the pupillary constriction exhibits chromatic cancellation similar to hue cancellation in the percept. Specifically, the pupillary constriction evoked by a red flash can be cancelled by superimposing a green to the red flash and adjusting the intensity of the green flash. Moreover, cone opponency underlying the pupillary color response was very similar to that found psychophysically (see also Tsujimura, Wolffsohn, & Gilmartin, 2006; Kimura & Young, 2010). These findings suggest that the pupillary response is at least partially mediated by visual mechanisms similar to those underlying visual perception (e.g., Young et al., 1993; Kimura, 1997).

In addition to these new developments, important progress has been made in the studies investigating the relation of the pupillary response to cognitive mechanisms such as attention and visual awareness [for review, see Loewenfeld (1999); Laeng, Sirois, & Gredebäck (2012)]. Among others, Einhäuser, Stout, Koch, and Carter (2008) reported that the pupillary response reflects perceptual selection of rivalrous percepts; the pupil diameter increased just before perceptual switch when observers viewed various ambiguous stimuli, including binocularly rivalrous stimuli. This finding increased interest in the pupillometric study on binocular rivalry and triggered a new line of research (Hupé, Lamirel, & Lorenceau, 2009; Fahle, Stemmler, & Spang, 2011; Naber, Frässle, & Einhäuser, 2011). However, the question of whether interocular suppression attenuates the stimulus-driven pupillary constriction remains unanswered.

The main objective of this study was to both pursue the investigation of the effects of interocular suppression on the pupillary response and extend the investigation into new directions. One extension is to investigate the effects of interocular suppression on the pupillary color response as well as on the pupillary light reflex. Because of differential subcortical and cortical contributions to the pupillary light and color responses, the effects of interocular suppression may be different. Another extension is to investigate whether the possible effects of interocular suppression on the pupillary response are similar to those on the perceptual responses. This investigation is critical not only for establishing the usefulness of pupillometry as an objective, noninvasive method for studying interocular suppression but also for understanding the nature of the interocular suppression reflected in the pupillary response. Taking advantage of objective physiological

measures, the present study also compared the magnitude of possible suppression between when the test stimulus was near threshold and when the presentation of the test stimulus reversed perceptual dominance and thus the stimulus was clearly visible.

Instead of binocular rivalry, the present study used a paradigm similar to permanent suppression (Fox & Check, 1966) and continuous flash suppression (Tsuchiya & Koch, 2005) to produce steady interocular suppression in a temporally predictable fashion. By presenting a strong monocular stimulus, exclusive dominance of the monocular image was first established, and then a test stimulus was presented to the other eye to investigate the suppressive effects. This paradigm allowed us to measure the pupillary response in a time-locked fashion so that the responses obtained on many trials can be averaged to reduce the signal-to-noise ratio (SNR).

Method

Observers

Four observers participated in this study. All observers were naïve regarding the purpose of the experiment. They had normal or corrected-to-normal visual acuity, good stereopsis, and normal color vision as assessed with Ishihara pseudoisochromatic plates. All observers provided written informed consent after thorough explanation of the procedures before the experiment in accordance with the Declaration of Helsinki.

Apparatus

The apparatus for stimulus presentation has been described in detail in our previous paper [see Figure 1 in Abe, Kimura, & Goryo (2011)]. In brief, we used a custom-made haploscope that consisted of three 17-in. color monitors. The images on the left and right monitors (Flex Scan T566, Eizo Nanao Corporation, Ishikawa, Japan) were superimposed over the one on the front monitor (Press View 17SR, Radius, Tokyo, Japan), respectively, at the two beam splitters just in front of each eye of the observer. All monitors were placed at an optical distance of 57 cm from the eyes. The position of the equipment was aligned for each observer before each daily session.

The stimulus for the left eye and the right eye was presented on the left monitor and right monitor, respectively. The two monitors were controlled with two VSG 2/5 graphic cards (Cambridge Research Systems, Kent, UK) with 15-bit color resolution, a pixel resolution of 1024 × 768, and a frame rate of 100 Hz. The front monitor was controlled with a Radius board and had a pixel resolution of 1024 × 768 and a frame rate of 75 Hz. The Psychophysics toolbox extensions for Matlab were used in phosphor calibrations and colorimetric calculations (Brainard, 1997; Pelli, 1997).

To accurately measure minute pupillary responses, the observer's head was stabilized on a chin and forehead rest. An infrared light was used to illuminate the observer's pupil. A Pulnix video camera magnified and recorded the pupil image continuously over time. The signals from the camera were fed into a pupil tracking system (RK-716, ISCAN, Burlington, MA) where the pupil diameters were digitized with nine-bit resolution and sampled at 60 Hz. Digital output from the tracking system was calibrated with artificial pupils of diameters ranging from 2 to 9 mm placed in the plane of the observer's pupil. The digital resolution of the system was about 29 μm. The positions of both the infrared light and the video camera were adjusted to optimize the contrast of the pupil image before every measurement.

Stimuli

The suppressing stimulus was a circular square-wave grating of 2 c/deg and the size was 6° in diameter. Its Michaelson contrast was 0.5 and the mean luminance was 4 cd/m^2. The suppressing stimulus was presented to the right eye and flickered at 5 Hz in a counterphase fashion.

The test stimulus was spatially homogeneous and the size was 5.5° in diameter. It comprised either a luminance or a chromatic change that was defined in the DKL color space (Derrington, Krauskopf, & Lennie, 1984). The +Lum stimulus represented a luminance increment along the Lum axis. The +LM stimulus consisted of an isoluminant reddish change along the L-M axis, while the +S stimulus consisted of an isoluminant bluish change along the S axis. The contrast of the test stimulus was defined as vector length in the cone-contrast space (Brainard, 1996) and varied from the levels below the psychophysical detection threshold to the highest contrast available at a step of 0.3 log units. The highest contrast used was +0.1, −0.7, and +0.3 in log units for the +Lum, +LM, and +S stimuli, respectively. The highest luminance contrast to the background for the +Lum stimulus was 1.73 (6.9 cd/m^2). To eliminate sharp transients at the onset of the test stimulus, the contrast of the test stimulus was ramped up to its maximum value over 100 ms, kept at that value for 100 ms, and then ramped down in contrast over 100 ms. Both suppressing and test stimuli were presented at the center of a white

background field (x = 0.313, y = 0.329) subtending 12°
× 12°. Its luminance was 4 cd/m². The background field
was always presented to each eye during the experi-
ment.

The fixation pattern presented on all three monitors
comprised four white crosses. Each cross subtended
1.5° × 1.5° and was located at 4.5° away from the center
of the background field in the left, right, upper, and
lower directions.

Procedure and conditions

At the beginning of each daily session, each observer
dark adapted for at least 5 min and then preadapted to
the white background field for 2 min. Observers were
instructed to look at the center of the fixation pattern
during the measurement.

To investigate the effects of the suppressing stimulus,
two pairs of the suppression and control conditions
were tested: the dichoptic versus D-control (dichoptic-
control) conditions to investigate interocular suppres-
sive effects, and the monocular versus M-control
(monocular-control) conditions to investigate monoc-
ular suppressive effects. In the dichoptic condition, the
counterphase-flickering suppressing stimulus was pre-
sented to the right eye. During continuous dominance
of the suppressing stimulus, a test stimulus was
presented to the left eye (Figure 1A, left). In the D-
control condition, only the test stimulus was presented
to the left eye (Figure 1A, right). In the monocular
condition, the suppressing stimulus was the same as in
the dichoptic condition, but a test stimulus was
monocularly superimposed on the suppressing stimulus
in the right eye (i.e., either a luminance or a chromatic
change was added to the grating stimulus, depending
on the type of the test stimulus) (Figure 1C, left). In the
M-control condition, only the test stimulus was
presented to the right eye (Figure 1C, right).

On each trial within a session, the observer's key
press initiated the presentation of the suppressing
stimulus at the center of the fixation pattern and 2 s
later a test stimulus was presented. The timing of the
stimulus changes was the same in the control condi-
tions, although the suppressing stimulus was not
presented. We used a relatively long pretarget duration
of 2 s to allow the pupil to recover from the constriction
evoked by the onset of the suppressing stimulus. The
pupillary response was recorded from the left eye. Each
stimulus condition was repeated at least 30 times. The
pupillary responses to each stimulus condition were
averaged off-line.

In addition to the pupillometric measurement, both
the psychophysical detection threshold of the test
stimulus and the reaction time for detecting the test
stimulus were measured under the comparable stimulus

conditions to investigate interocular suppression at
near-threshold and suprathreshold contrast levels,
respectively. In the pupillometric experiment, observers
were also asked to report whether they could detect the
test stimulus on each trial. Based on the observer's
report, the frequency of seeing was calculated for
different test contrasts. Then, the detection threshold
was determined for each stimulus condition by fitting
the psychometric function using the psignifit toolbox
for Matlab, which implements the maximum-likelihood
method described by Wichmann and Hill (2001).

In separate experimental sessions, reaction times for
detection of the test stimulus were also measured for
each observer to investigate the effects of the sup-
pressing stimulus. The stimulus sequence was the same
as in the pupillometric experiment except that the
pretarget duration, during which the suppressing
stimulus was presented alone, was randomly varied
from 1.6 to 2.4 s to prevent observers from predicting
the onset of the test stimulus. Each stimulus condition
was repeated 18 or 24 times for different observers.

Results

Figure 1 shows the pupillary response waveforms
obtained in the dichoptic condition (Figure 1B) and in
the monocular condition (Figure 1D). The pupillary
responses to luminance increments (+Lum stimuli;
Figure 1B, D, left) and to chromatic changes (+S
stimuli; Figure 1B, D, right) were characterized by a
transient constriction (i.e., a decrease in the pupil
diameter). The pupillary constrictions in the dichoptic
condition (Figure 1B, red lines) were reduced compared
with those in the D-control condition (black lines).
Response attenuation was observed in the response to
color (right) as well as luminance changes (left) and
over a wide range of test contrast from near-threshold
to suprathreshold levels. In contrast, in the monocular
condition (Figure 1D), attenuation was not obvious in
the response to color changes (right), although it
appears large in the response to luminance changes
(left). The +LM stimuli produced similar results to the
+S stimuli, and thus the response waveforms were not
shown for brevity. Similar results were found for
different observers.

To quantify the response attenuation observed in the
dichoptic and monocular conditions, the peak con-
striction amplitude was measured and the contrast-
amplitude function was obtained in different stimulus
conditions (Figure 2). In general, the pupillary con-
striction monotonically increased as a function of test
contrast. The response gain for the +LM stimulus was
slightly smaller than that for the +Lum and +S stimuli.
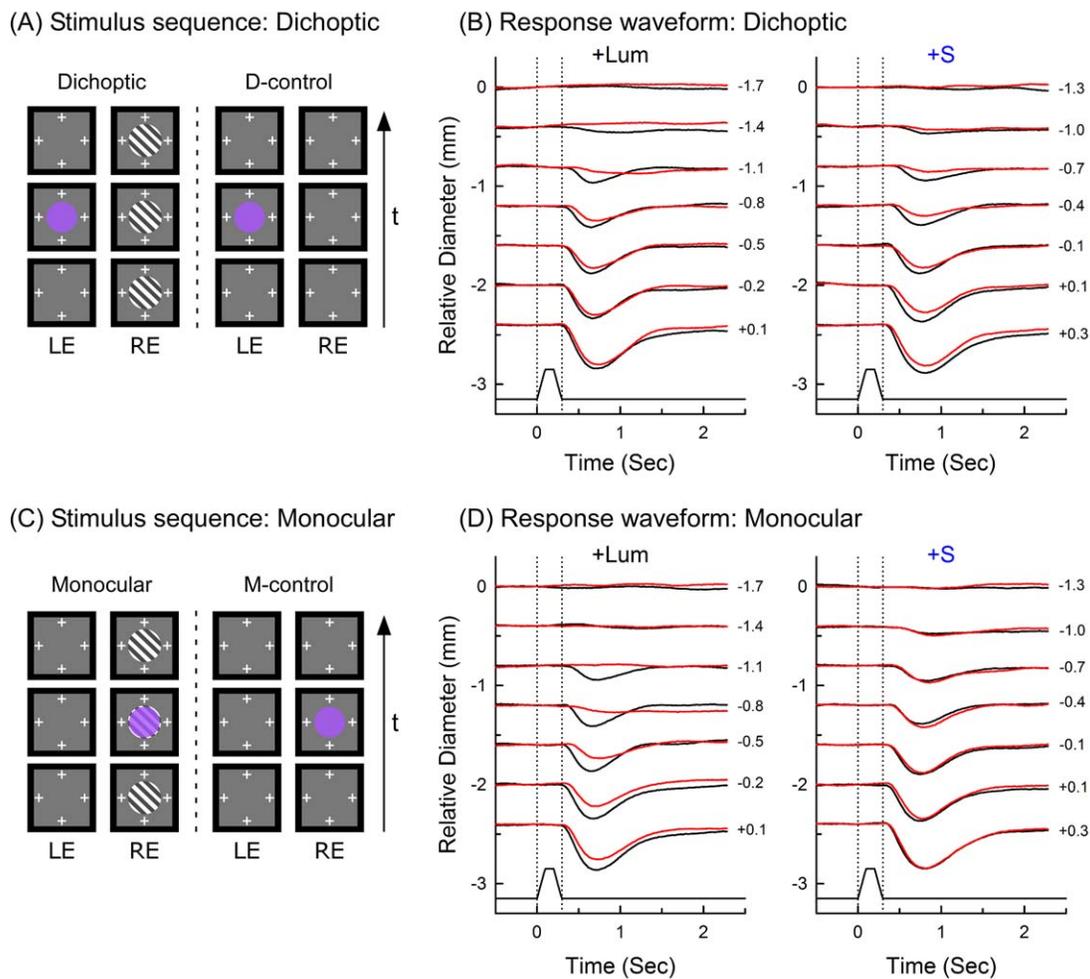A Naka-Rushton function (Naka & Rushton, 1966;

Figure 1. Pupillary response waveforms averaged across different observers. The top row shows stimuli and results in the dichoptic and D-control conditions, whereas the bottom row shows those in the monocular and M-control conditions. Parts A and C illustrate the stimulus sequence. LE = left eye; RE = right eye. See text for details. Parts B and D illustrate typical changes in the pupil diameter caused by the stimulus change. The temporal profile of a stimulus change is illustrated by a line at the bottom. The onset of the test stimulus occurred at time zero and the offset at 0.3 s. The results on the left side show the responses evoked by the +Lum stimuli (i.e., luminance increments), while those on the right side show the responses evoked by the +S stimuli (i.e., isoluminant bluish changes). Black lines in each graph show the responses measured in the control condition, while red lines show those in the suppression condition. The pupillary response is characterized by a transient constriction (downward deflection) following the stimulus change. The responses evoked by different log test contrasts, which are indicated by the number shown to the right of each response waveform, were displaced downward in successive 0.4-mm steps for clarity.

Boynton, Demb, Glover, & Heeger, 1999) was fitted to each set of data:

$$A(C) = g \cdot C/(C + k),$$

where A is constriction amplitude, C is test contrast, g is a gain parameter, and k is a half-saturation constant. In curve fitting, the gain parameter was kept identical for different sets of data in each test stimulus condition and only the half-saturation constant, which controls the horizontal position of the contrast-amplitude function, was varied as a free parameter. As shown in Figure 2, the contrast-amplitude functions could be described reasonably well by Naka-Rushton functions

(dashed, dotted, and solid lines for the control, monocular, and dichoptic conditions, respectively). Thus, sensitivity reduction due to suppression can be quantified as a difference in the half-saturation constant between the suppression and control conditions.

To summarize the sensitivity reduction, the curve fitting was conducted for each observer's contrast-amplitude functions and the differences in the half-saturation constant were averaged across different observers (Figure 3, left). In the dichoptic condition, sensitivity reduction was found for both luminance and chromatic changes (Figure 3A, left). In contrast, in the
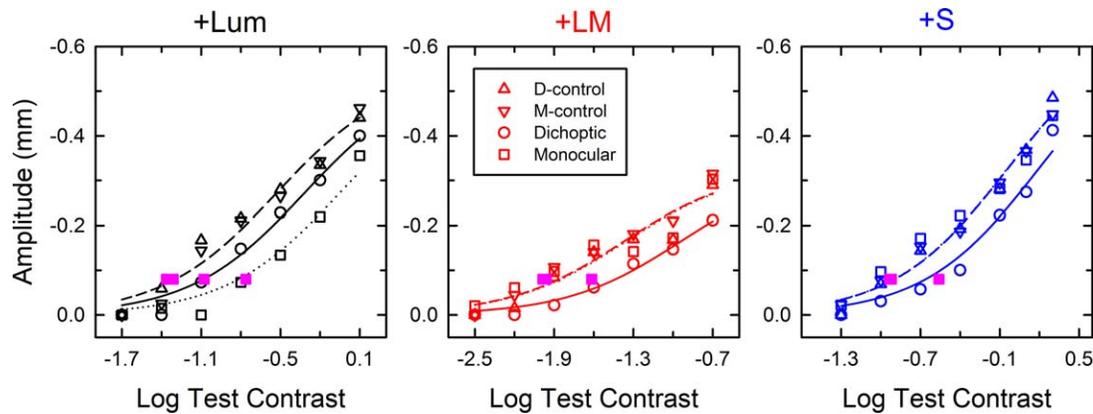
Figure 2. Contrast-amplitude functions for the +Lum (left), +LM (middle), and +S (right) stimuli. In this and following figures, negative millimeters of amplitudes represent pupillary constrictions. Peak constriction amplitudes were measured in the response waveforms averaged across different observers and plotted as a function of test contrast. Different symbols designate the results in the different stimulus conditions as shown in the legend. The observation that the data set in the suppression condition shifts to the right relative to the one in the control condition indicates attenuation of the pupillary response due to suppression. Different lines are Naka-Rushton functions (Naka & Rushton, 1966; Boynton et al., 1999) fitted to each set of the data. As two control conditions, in which only the test stimulus was monocularly presented to one eye, provided nearly identical results (upright and inverted triangles), a single function was fitted to those data (dashed line). It should be noted that for the +LM and +S stimuli, the functions fitted to the results in the monocular condition (dotted lines) and those in the control conditions (dashed lines) were almost identical and difficult to distinguish from one another. Solid purple square symbols in each panel indicate the psychophysical detection thresholds. They were arbitrarily placed at the amplitude of 0.08 mm.

monocular condition, it was much larger for luminance than for chromatic changes. The results were analyzed with a two-way repeated-measures ANOVA (analysis of variance), with stimulus condition (dichoptic vs. monocular) and test stimulus type (+Lum, +LM, or +S stimulus) serving as the within-subject variables. The main effect of the stimulus condition was not statistically significant [$F(1,3) = 2.37$, $p = 0.221$], but that of the test stimulus type was significant [$F(2,6) = 9.38$, $p = 0.014$]. The interaction between the stimulus condition and the test stimulus type was also statistically significant [$F(2,6) = 20.46$, $p = 0.002$]. The post hoc analysis of the interaction showed that the simple main effect of the test stimulus type was statistically significant in the monocular condition [$F(2,12) = 25.09$, $p < 0.0001$], while it was not in the dichoptic condition [$F(2,12) = 2.51$, $p = 0.123$]. The multiple comparison tests using Ryan's method ($\alpha = 0.05$) showed that sensitivity reduction for the +Lum stimulus was larger than that for the +LM and +S stimuli in the monocular condition. In short, the pattern of sensitivity reduction in the dichoptic condition was different from that in the monocular condition, which suggests that the sensitivity reduction in the dichoptic condition was actually caused by interocular suppression. The different patterns of suppression found with luminance and chromatic changes in the dichoptic and monocular conditions suggest that different visual processes contribute to the pupillary responses to luminance and color responses. Moreover, the pattern of the results in

the monocular condition makes unlikely the possibility that rods mediate the processing of the +S stimuli. The scotopic luminance contrast was similar between the +Lum and +S stimuli (the contrast of the most intense stimulus was 1.73 and 1.67, respectively). If rods contributed substantially to the pupillary (or psychophysical) responses, the larger sensitivity reduction would be observed for the +S stimuli as well.

The effects of the suppressing grating stimulus were also investigated using psychophysical detection thresholds. To illustrate the similarity between the pupillometric and psychophysical results, the psychophysical detection threshold in each condition is indicated by solid purple square symbols in Figure 2. The symbols arbitrarily placed at the amplitude of 0.08 mm are nearly on the Naka-Rushton functions fitted to the pupil amplitude data. This means that the psychophysical detection threshold was similar to the pupillometric threshold with a criterion amplitude of about 0.08 mm. Sensitivity reduction due to interocular suppression was also quantified as a threshold elevation for the test stimulus in the suppression condition relative to that in the control condition. The sensitivity changes derived psychophysically (Figure 3, right) exhibited patterns that were very similar to those found pupillometrically (Figure 3, left). The results of ANOVA were also similar (see Supplementary Results A). Thus, the effects of interocular suppression evaluated with the pupillary constriction were very similar to those found with the psychophysical

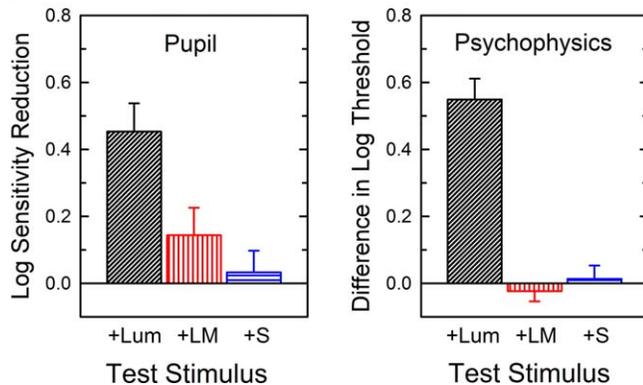## (A) Dichoptic
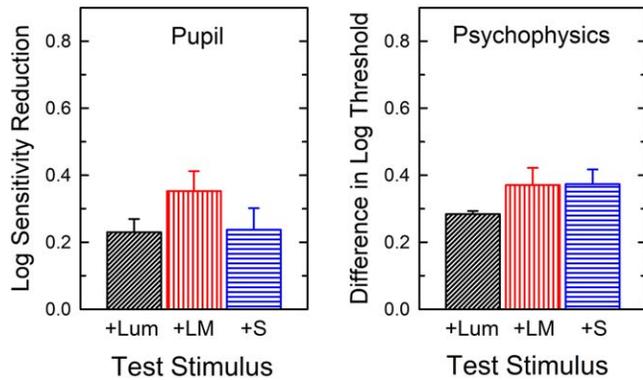
(B) Monocular

Figure 3. Sensitivity reduction measured with the pupillary constriction amplitudes (left) and with the psychophysical detection thresholds (right). Results in (A) the dichoptic condition and (B) the monocular condition. Error bars represent +1 (or −1) SEM across different observers.

threshold, although the suppressive effect was observed over a wide range of test contrast in the pupillary response.

The psychophysical investigation using reaction times for simple detection of the test stimulus revealed that the effect of the suppressing stimulus on perception was not limited at near-threshold contrast levels (Figure 4B). Even when the test contrast was well above the detection threshold, responding to the test stimulus was consistently delayed. Thus, reversing perceptual dominance takes some time, which confirms the previous findings (O'Shea, 1987). Moreover, the nature of suppression was qualitatively very similar to that found with the pupillary constriction and the psychophysical detection threshold. In the dichoptic condition, the reaction time was consistently larger than that in the D-control condition over a wide range of the test contrast for both luminance and chromatic changes (circles vs. upright triangles). In contrast, in the monocular condition, the increase in reaction time was large for luminance changes, while it was very small, if present, for chromatic changes

(squares vs. inverted triangles). Similar analysis was also carried out on the pupillary response latency. As a result, we found very similar patterns of suppressive effects on the response latency over a wider range of test contrast (Figure 4A). Here, the latency was measured from the time of the stimulus onset to the time at which the pupil began to constrict in response to a stimulus change.

To summarize the sensitivity change in time domain caused by the suppressing stimulus (Figure 4) in a way comparable with that found with the pupillary constriction and the psychophysical threshold (Figure 3), the test contrast that was required to achieve a criterion latency was derived using the negatively decelerating exponential functions fitted to the contrast-latency functions measured for each observer. The criterion latency was arbitrarily set to around 400 ms and fixed for all stimulus conditions and test stimulus types. Then, how much test contrast was increased in the suppression condition relative to that in the control condition was calculated. The results are shown in Figure 5. The patterns of suppression in both dichoptic and monocular conditions were qualitatively similar to those shown in Figure 3. The results of ANOVA were also similar (see Supplementary Results B and C).

Similar patterns of the suppressive effect for the reaction time and the pupillary response latency (Figure 4) raised a question of how well their absolute values are correlated. Figure 6 shows the results of the correlation analysis. In general, the pupillary response latency was similar in absolute value to the manual reaction time. However, the pupillary response to luminance changes (Figure 6, left) occurred earlier than the manual reaction, particularly when the test contrast was near threshold (i.e., when the latency was larger). Thus, the slope of the regression lines was smaller than unity (0.57 in the control condition and 0.75 in the suppression condition). Moreover, the pupillary response to +LM changes was differentially delayed in the suppression condition (Figure 6B, center) relative to that in the control condition. This differential suppression was not obvious for the +Lum and +S stimuli.

We further investigated the question of whether a difference in response latency can be found between the pupillary responses to luminance and color changes by analyzing the responses in the control condition. The results showed that the pupillary responses to chromatic changes were consistently delayed by about 40 to 60 ms relative to those to luminance changes, although the response latency varied with constriction amplitude (Figure 7). The amount of the delay was similar to that found in the previous studies (Young & Alpern, 1980; Barbur et al., 1998).
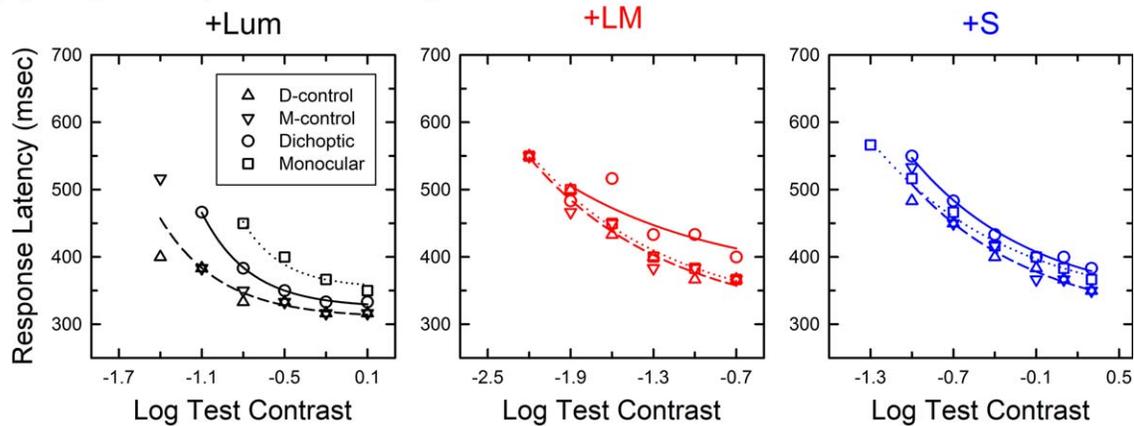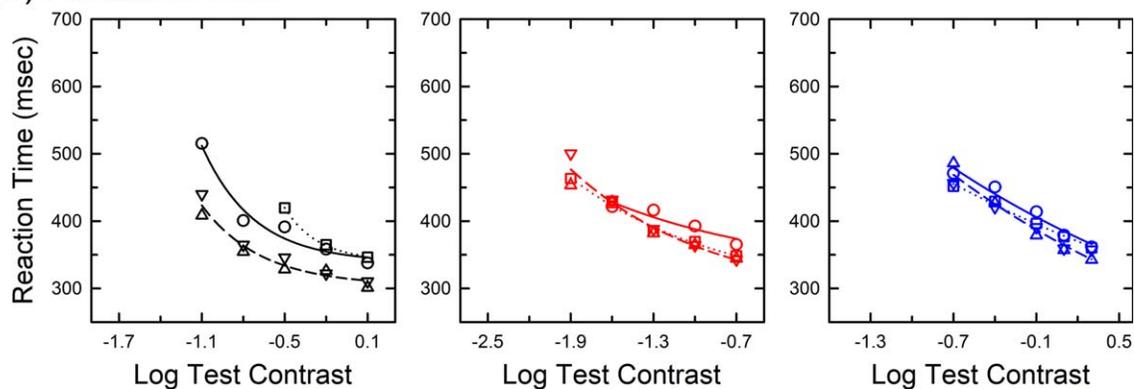
Figure 4. Contrast-latency functions for the +Lum (left), +LM (middle), and +S (right) stimuli. (A) Response latency for the pupillary constriction; (B) reaction time for detection of the test stimulus. Different symbols designate the results in the different stimulus conditions as shown in the legend. Different lines are negatively decelerating exponential functions fitted to each set of the data: dashed lines for the results in the D- and M-control conditions, dotted lines for those in the monocular condition, and solid lines for those in the dichoptic condition.

Discussion

The present study investigated the effects of inter-ocular suppression on the pupillary response and found that the pupillary constrictions to both luminance and color changes (i.e., both pupillary light and color responses) were clearly attenuated by a dichoptically presented suppressing stimulus. This non-stimulus-specific sensitivity loss alone may not be convincing evidence for interocular suppression because the results can be accounted for by more general causes, such as a decrease in pupil responsivity due to continuous strong stimulation by a flickering suppressing stimulus. However, when the test flashes were monocularly superimposed on the suppressing stimulus, differen-tially strong suppressive effects were found in the pupillary light reflex. The pupillary color response was affected little, if any, in the monocular condition. These findings support the interpretation that the nonspecific

suppressive effects in the dichoptic condition actually reflect interocular suppression. The suppressive effect can be characterized as a constant sensitivity reduction over a wide range of test contrast; it was observed at contrast levels from near threshold to the highest contrast tested in this study. In view of previous pupillometric studies, it is worth mentioning the importance of high SNR in the measurement. In some cases, the response attenuation is not large, and thus high SNR is critical for evaluating the suppressive effects.

The present study also showed that the patterns of sensitivity reduction caused by interocular suppression were very similar between the pupillary response and the psychophysical measures such as detection thresh-olds and reaction times. With all response measures regarding both response magnitude (pupillary con-striction amplitude and detection threshold) and response latency (pupillary response latency and reaction time), the magnitude of the suppressive effects
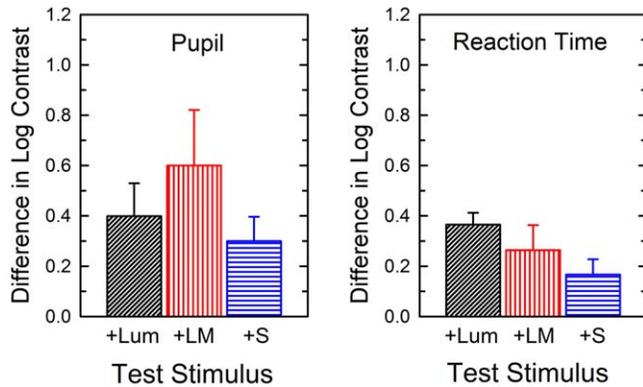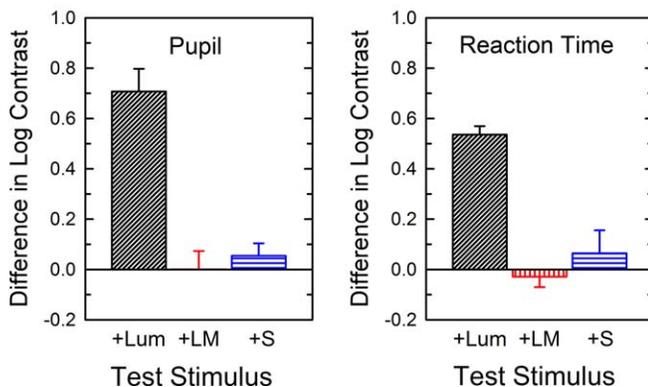
Figure 5. Sensitivity reduction measured with the pupillary response latency (left) and with the reaction time (right). Results in (A) the dichoptic condition and (B) the monocular condition. Error bars represent +1 (or −1) SEM across different observers.

was similar for both luminance and chromatic stimuli in the dichoptic condition, whereas the effects were much larger for luminance stimuli in the monocular condition. Moreover, the magnitudes of suppression were also similar among different response measures. Overall, the close similarities between the pupillometric and psychophysical results suggest that different response measures reflect the activities of similar visual processes. Thus, it is not likely that the present pupillometric results are accounted for by the pupil-specific binocular interactions such as subcortical binocular convergence in the pupillary pathway that produces similar binocular responses even with monocular simulation (Loewenfeld, 1999; Gamlin, 2006).

Because differential contributions of different visual pathways to the psychophysical as well as pupillary responses have been hypothesized, the present findings can be discussed in several different frameworks. One way to understand the present findings is in view of different components of the pupillary constriction. Previous studies provided evidence that the pupillary

light reflex comprises transient and sustained components (e.g., Young et al., 1993; Barbur, 2004). Moreover, these previous studies showed that the two components exhibit different response properties in addition to differences in temporal property. For example, the transient component exhibits higher contrast gain and saturates at relatively low contrast, whereas the sustained component has lower contrast gain and its amplitude increases monotonically with luminance contrast. Although discussion on the pupillary visual pathway underlying the different components remains speculative due to limited anatomical and neurophysiological evidence, it is worth mentioning a model of the pupillary visual pathway proposed by Barbur (2004) that can account well for various experimental findings. In this model, it is assumed that the response properties of the two components of the pupillary light reflex are mainly determined by transient and sustained retinal inputs to the olivary pretectal nucleus (OPN) in the midbrain (i.e., the visual center in the subcortical pupillary pathway). It is further assumed that the sustained component is mostly driven by retinal inputs, whereas the transient component requires an excitatory cortical projection to the OPN to be effective. This arrangement is hypothesized because in hemianopic patients the transient response component was attenuated while the sustained component was intact in blind hemifields; nonetheless, both components were nearly abolished with damages to the pretectal region in the midbrain. Also based on the findings with brain damage patients, the pupillary color response is assumed to be directly driven by cortical projection to the midbrain, although the cortical projections are assumed to be distinct for the pupillary color response and for the transient component of the pupillary light reflex. Differences in subcortical and cortical inputs assumed in the model to mediate the pupillary light and color responses are consistent with converging evidence that the pupillary color response is significantly delayed relative to the pupillary light reflex (Young & Alpern, 1980; Barbur et al., 1998; Figure 7 in this study).

In view of this model, the differential effects of the monocular and interocular suppressing stimuli are accounted for by subcortical and cortical contributions, respectively. The large amplitude reduction found with the pupillary light reflex in the monocular condition is likely to reflect a masking effect of the dynamic suppressing stimulus on the transient component. Barbur (2004) reported similar results produced by dynamic luminance noise. The moderate amplitude reduction found with the pupillary light reflex in the dichoptic condition can be accounted for, if interocular suppression attenuates cortical projection contributing to the transient component and thus makes the transient component less effective. Similar weakening
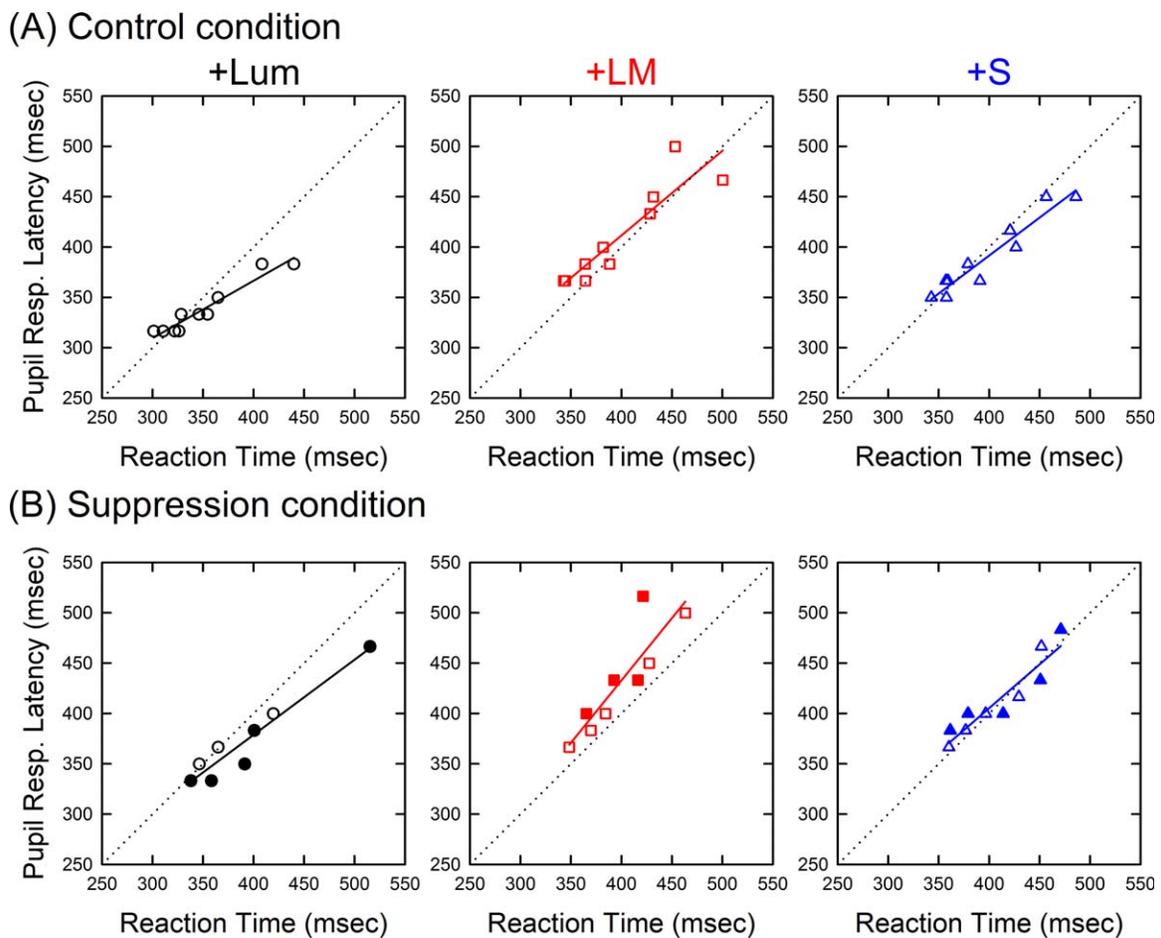
Figure 6. Scatter plots between reaction time and pupillary response latency measured in the same stimulus conditions for the +Lum (left), +LM (center), and +S (right) test stimuli. Results in (A) the control condition and (B) the suppression condition. The analysis was carried out using the average data across different observers. In each graph, the dotted line shows a line with unity slope and the solid line shows a regression line fitted to each data set. In the results in the suppression condition, solid symbols denote the data in the dichoptic condition, while open symbols show those in the monocular condition.
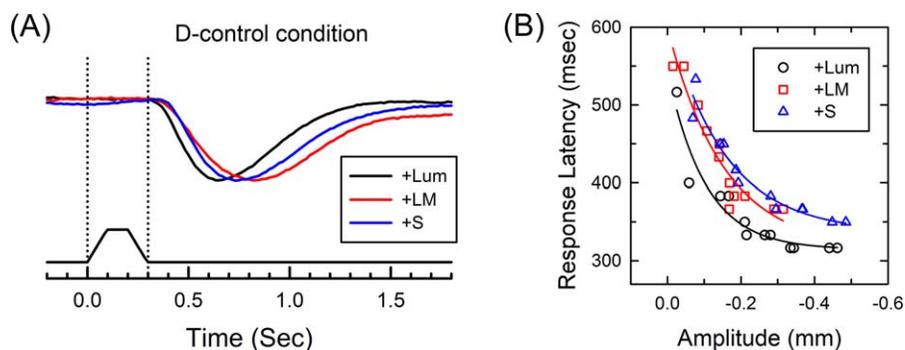

Figure 7. Comparisons in response latency across the pupillary responses evoked by different test stimuli. (A) Comparisons in the response waveform. The waveforms of similar amplitudes were selected for different test stimuli in the D-control condition and normalized to have the identical amplitude for comparison. The pupillary constrictions to chromatic changes (red and blue lines) were delayed relative to those to a luminance increment (black line). (B) Response latency as a function of constriction amplitude. Different symbols designate the results for different test stimuli as shown in the legend. Different lines are negatively decelerating exponential functions fitted to each set of data.

of another cortical projection can also account for the moderate sensitivity reduction in the pupillary color response. However, the model may need to be slightly extended to account for the amplitude reduction found with intense luminance stimuli in the dichoptic condition. Because the transient component saturates at lower luminance contrast, the finding of amplitude reduction extending to a higher contrast range implies that the sustained component was also inhibited by the dichoptic suppressing stimulus. Thus, the possibility may need to be considered that interocular suppression also adversely affects subcortical visual processing mediating the sustained component or perhaps the pupillary light reflex at large.

The present findings can also be discussed in view of previous psychophysical studies on the effects of stable interocular suppression caused by strong monocular stimulation. Some earlier studies used a paradigm called permanent suppression, which refers to a stable suppression produced by presenting a much stronger stimulus such as a stationary high-contrast achromatic grating to one eye and a spatially homogeneous field to the other eye (Fox & Check, 1966; Ridder, Smith, Manny, Harwerth, & Kato, 1992; Ooi & Loop, 1994). One of the important questions addressed by the previous studies was whether interocular suppression can selectively suppress color or luminance sensitivities. Ridder et al. (1992) investigated the effects of permanent suppression on increment-threshold spectral sensitivity function and found a general reduction in sensitivity for all test wavelengths, although a selective loss in color sensitivity had been found with conventional binocular rivalry (Smith, Levi, Harwerth, & White, 1982). Subsequently, Ooi and Loop (1994) investigated the effects of permanent suppression on detection thresholds and found somewhat different results. They found suppression of both color and luminance sensitivities, but the effect was larger on color sensitivity. More recently, a stronger form of stable interocular suppression, called continuous flash suppression (CFS), has been developed (Tsuchiya & Koch, 2005). The CFS can be produced by presenting a series of different spatial patterns to one eye at a rate of about 10 Hz and may be regarded as a dynamic version of permanent suppression. Using the CFS with achromatic Mondrian patterns, previous studies also showed that the detection of both chromatic and achromatic stimuli was suppressed (e.g., Tsuchiya & Koch, 2005; Hong & Blake, 2009) and that the suppression differentially affected different visual features of a target; that is, the identification of target orientation was much worse than that of target color (Hong & Blake, 2009). Moreover, Hong and Blake (2009) showed that the CFS with a chromatic Mondrian pattern more effectively suppressed chromatic processing. Collectively, the interocular suppres-

sion is nonselective in that sensitivity reduction is not restricted to visual features similar to those of the suppressing stimulus. However, at the same time, the suppression can differentially attenuate the processing of some visual features, depending on stimulus properties of the suppressing stimulus and similarities between the suppressing and test stimuli. The present results are consistent with nonselective suppression, but the pattern of the results can be different if we use a chromatic suppressing grating.

The previous psychophysical findings have been discussed in the context of the contributions of the parvocellular (PC) and magnocellular (MC) pathways (e.g., Ooi & Loop, 1994; He, Carlson, & Chen, 2005; Hong & Blake, 2009) because these pathways exhibit distinctly different chromatic properties as well as different spatial and temporal properties (e.g., Livingstone & Hubel, 1988; Lee, 1996; Kaplan, 2004). Particularly, the PC pathway is considered the primary pathway in color vision. Some previous studies proposed that, based on the larger suppressive effect on color sensitivity, interocular suppression adversely affects the PC pathway more than the MC pathway (Ooi & Loop, 1994). With more collective evidence, He et al. (2005) argued that the PC pathway is more involved in binocular rivalry in general than the MC pathway. Hong and Blake (2009) took a more neutral stand and proposed that either the PC or MC pathways can be differentially affected by appropriately selecting the suppressing and test stimuli.

The present finding can also be understood in this PC–MC framework. Flickering a high-contrast achromatic grating as in the present study creates a steady train of transients and would produce a strong suppressive effect on the MC neurons, particularly in the same eye, which can account for a differentially large suppression of luminance sensitivity in the monocular condition. This large suppression of luminance sensitivity would be specific to the monocular pathway and occur before binocular convergence. Otherwise, the magnitude of suppression with luminance stimuli in the dichoptic condition would be equal to or larger than that in the monocular condition, not in the reverse order. The results in the dichoptic condition are consistent with strong involvement of the PC pathway in interocular suppression because the decrease in color sensitivity was larger in the dichoptic condition compared with that in the monocular condition.

Interestingly, several studies (Ooi & Loop, 1994; Hong & Blake, 2009) discussed the possibility that neural events underlying interocular suppression can be found at early stages, such as lateral geniculate nucleus (LGN), where the PC and MC pathways remain anatomically segregated. Consistent findings that neural activity in the LGN can be modulated during

binocular rivalry have been reported in brain imaging studies (Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2005). However, it should also be pointed out that some investigators argue that differential PC–MC contributions to interocular suppression themselves do not require that the suppression be exerted in the LGN (He et al., 2005; Denison & Silver, 2011). The subcortical involvement in interocular suppression is interesting in view of the model of the pupillary visual pathway (Barbur, 2004). The transient and sustained components exhibit at least partially similar response properties to the MC and PC pathways, respectively. Moreover, previous pupillometric studies proposed that different aspects of the pupillary response to various visual stimuli are associated with the activities in the PC and MC pathways, although the relationship between the transient or sustained components and the MC or PC pathways may not be simple (Young et al., 1993; Young & Kennish, 1993; Kimura & Young, 1995, 1999; Tsujimura, Wolffsohn, & Gilmartin, 2003; Tsujimura et al., 2006; Kimura & Young, 2010). Further studies are definitely needed to investigate possible interactions between subcortical and cortical processing underlying interocular suppression and to relate different components of the perceptual pathway to those of the pupillary visual pathway.

Finally, it is important to note that the pupillary response investigated in this study was constriction, in contrast to the pupillary dilation associated with perceptual switch during binocular rivalry in the previous studies (Einhäuser et al., 2008). In fact, the pupillary response evoked by changes in visual stimulus is almost always constriction (e.g., Barbur, 2004). Although the pupillary dilation to luminance decrements is well known, the pupillary constriction can be evoked if the color or pattern of the stimulus is changed simultaneously with luminance decrement. Furthermore, the pupillary constriction and dilation are mainly controlled by the sphincter and dilator muscles of the iris, respectively, and these muscles are in turn driven by different components of the autonomic nervous system (McDougal & Gamlin, 2008). Thus, we believe that the previous and present findings reflect different aspects of the neural processing underlying the pupillary response. Presumably, the previous findings with the pupillary dilation are more closely related to increased cognitive activity or cognitive load (Laeng et al., 2012).

In conclusion, although the pupillary constriction driven by light intensity changes is generally believed to be a primitive reflex, the present study showed that it can also be modulated by interocular suppression. Furthermore, striking similarities between psychophysical and pupillometric measures were found in the effects of interocular suppression. These present findings support the idea that the pupillary response can be a useful objective probe of binocular interaction. With the pupillary response, interocular suppression can be evaluated over a wide contrast level and in terms of both response magnitude and response latency.

Acknowledgments

References

Abe, S., Kimura, E., & Goryo, K. (2011). Eye- and feature-based modulation of onset rivalry caused by the preceding stimulus. *Journal of Vision*, *11*(13): 6, 1–18, http://www.journalofvision.org/content/11/13/6, doi:10.1167/11.13.6. [PubMed] [Article]

Barany, E. H., & Hallden, V. (1948). Phasic inhibition of the light reflex of the pupil during retinal rivalry. *Journal of Neurophysiology, 11,* 25–30.

Barbur, J. L. (2004). Learning from the pupil: Studies of basic mechanisms and clinical applications. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (Vol. 2, pp. 641–656). Cambridge, MA: MIT Press.

Barbur, J. L., & Forsyth, P. M. (1986). Can the pupil response be used as a measure of the visual input associated with the geniculo-striate pathway? *Clinical Vision Science, 1,* 107–111.

Barbur, J. L., Harlow, A. J., & Sahraie, A. (1992). Pupillary responses to stimulus structure, colour and movement. *Ophthalmic and Physiological Optics, 12,* 137–141.

Barbur, J. L., Keenleyside, M. S., & Thomson, W. D. (1989). Investigation of central visual processing by means of pupillometry. In J. J. Kulikowski, C. M. Dickinson, & I. J. Murray (Eds.), *Seeing contour and colour* (Vision and Visual Health Care Vol. 3, pp. 431–451). Oxford, UK: Pergamon Press.

Barbur, J. L., & Thomson, W. D. (1987). Pupil responses as an objective measure of visual acuity. *Ophthalmic and Physiological Optics, 7,* 425–429.

Barbur, J. L., Wolf, J., & Lennie, P. (1998). Visual processing levels revealed by response latencies to changes in different visual attributes. *Proceedings of the Royal Society of London B, 265,* 2321–2325.

Boynton, G. M., Demb, J. B., Glover, G. H., & Heeger, D. J. (1999). Neuronal basis of contrast discrimination. *Vision Research, 39,* 257–269.

Bradshaw, J. L. (1969). Brightness of the dominant field, and pupillary reflexes in retinal rivalry. *The British Journal of Psychology, 60,* 351–356.

Brainard, D. H. (1996). Cone contrast and opponent modulation color spaces. In P. K. Kaiser & R. M. Boynton (Eds.), *Human color vision* (2nd ed., pp. 563–579). Washington, DC: Optical Society of America.

Brainard, D. H., (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436.

Brenner, R. L., Charles, S. T., & Flynn, J. T. (1969). Pupillary responses in rivalry and amblyopia. *Archives of Ophthalmology, 82,* 23–29.

Cocker, K. D., & Moseley, M. J. (1992). Visual acuity and the pupil grating response. *Clinical Vision Science, 7,* 143–146.

Conway, C. A., Jones, B. C., DeBruine, L. M., Little, A. C., & Sahraie, A. (2008). Transient pupil constrictions to faces are sensitive to orientation and species. *Journal of Vision,* 8(3):17, 1–11, http://journalofvision.org/content/8/3/17/, doi:10.1167/8.3.17. [PubMed] [Article]

Denison, R. N., & Silver, M. A. (2011). Distinct contributions of the magnocellular and parvocellular visual streams to perceptual selection. *Journal of Cognitive Neuroscience, 24,* 246–259, doi:10.1162/jocn_a_00121.

Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology, 357,* 241–265.

Einhäuser, W., Stout, J., Koch, C., & Carter, O. (2008). Pupil dilation reflects perceptual selection and predicts subsequent stability in perceptual rivalry. *Proceedings of the National Academy of Sciences, USA, 105,* 1704–1709, doi:10.1073/pnas.0707727105.

Fahle, M. W., Stemmler, T., & Spang, K. M. (2011). How much of the "unconscious" is just pre-threshold? *Frontiers in Human Neuroscience,* 5(120):1–6, http://www.frontiersin.org/Journal/10.3389/fnhum.2011.00120/full, doi:10.3389/fnhum.2011.00120.

Fox, R. (1991). Binocular rivalry. In D. Regan (Ed.), *Vision and visual dysfunction* (Vol. 9, pp. 93–110). Basingstoke, UK: Macmillan.

Fox, R., & Check, R. (1966). Binocular fusion: A test of the suppression theory. *Perception and Psychophysics, 1,* 331–334.

Gamlin, P. D. R. (2006). The pretectum: Connections and oculomotor-related roles. *Progress in Brain Research, 151,* 379–405.

Gamlin, P. D. R., McDougal, D. H., Pokorny, J., Smith, V. C., Yau, K.-W., & Dacey, D. M. (2007). Human and macaque pupil responses driven by melanopsin-containing retinal ganglion cells. *Vision Research, 47,* 946–954.

Gamlin, P. D. R., Zhang, H., Harlow, A., & Barbur, J. L. (1998). Pupil responses to stimulus color, structure and light flux increments in the rhesus monkey. *Vision Research, 38,* 3353–3358.

Haynes, J. D., Deichmann, R., & Rees, G. (2005). Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature, 438,* 496–499.

He, S., Carlson, T., & Chen, X. (2005). Parallel pathways and temporal dynamics in binocular rivalry. In D. Alais & R. Blake (Eds.), *Binocular rivalry* (pp. 81–100). Cambridge, MA: MIT Press.

Heywood, C. A., Nicholas, J. J., LeMare, C., & Cowey, A. (1998). The effect of lesions to cortical areas V4 or AIT on pupillary responses to chromatic and achromatic stimuli in monkeys. *Experimental Brain Research, 122,* 475–480.

Hong, S. W., & Blake, R. (2009). Interocular suppression differentially affects achromatic and chromatic mechanisms. *Attention, Perception, and Psychophysics, 71,* 403–411, doi:10.3758/APP.71.2.403.

Hupé, J.-M., Lamirel, C., & Lorenceau, J. (2009). Pupil dynamics during bistable motion perception. *Journal of Vision,* 9(7):10, 1–19, http://journalofvision.org/content/9/7/10/, doi:10.1167/9.7.10. [PubMed] [Article]

Kaplan, E. (2004). The M, P, and K pathways of the primate visual system. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (pp. 481–493). Cambridge, MA: MIT Press.

Kawasaki, A., & Kardon, R. H. (2007). Intrinsically photosensitive retinal ganglion cells. *Journal of Neuro-Ophthalmology, 27,* 195–204.

Kimura, E. (1997). Nature and origin of visual signals mediating chromatic pupillary responses. In D. Yager (Ed.), *OSA trends in optics and photonics* (Vol. 11, pp. 185–190). Washington, DC: Optical Society of America.

Kimura, E., & Young, R. S. L. (1995). Nature of the

pupillary responses evoked by chromatic flashes on a white background. *Vision Research, 35,* 897–906.

Kimura, E., & Young, R. S. L. (1996). A chromatic-cancellation property of human pupillary responses. *Vision Research, 36,* 1543–1550.

Kimura, E., & Young, R. S. L. (1999). S-cone contribution to pupillary responses evoked by chromatic flash offset. *Vision Research, 39,* 1189–1197.

Kimura, E., & Young, R. S. L. (2010). Sustained pupillary constrictions mediated by an L- and M-cone opponent process. *Vision Research, 50,* 489–496, doi:10.1016/j.visres.2010.01.001.

Kohn, M., & Clynes, M. (1969). Color dynamics of the pupil. *Annals of the New York Academy of Sciences, 156,* 931–950.

Krastel, H., Alexandridis, E., & Gertz, J. (1985). Pupil increment thresholds are influenced by color opponent mechanisms. *Ophthalmologica, 191,* 35–38.

Laeng, B., Sirois, S., & Gredebäck, G. (2012). Pupillometry: A window to the preconscious? *Perspectives on Psychological Science, 7,* 18–27, doi:10.1177/1745691611427305.

Lee, B. B. (1996). Receptive field structure in the primate retina. *Vision Research, 36,* 631–644.

Livingstone, M. S., & Hubel, D. H. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science, 240,* 740–749.

Loewenfeld, I. E. (1999). *The pupil: Anatomy, physiology, and clinical applications.* Boston, MA: Butterworth-Heinemann.

Lorber, M., Zuber, B. L., & Stark, L. (1965). Suppression of the pupillary light reflex in binocular rivalry and saccadic suppression. *Nature, 208,* 558–560, doi:10.1038/208558a0.

Lowe, S. W., & Ogle, K. N. (1966). Dynamics of the pupil during binocular rivalry. *Archives of Ophthalmology, 75,* 395–403.

McDougal, D. H., & Gamlin, P. D. (2010). The influence of intrinsically-photosensitive retinal ganglion cells on the spectral sensitivity and response dynamics of the human pupillary light reflex. *Vision Research, 50,* 72–87, doi:10.1016/j.visres.2009.10.012.

McDougal, D. H., & Gamlin, P. D. R. (2008). Pupillary control pathways. In I. B. Allan, A. Kaneko, M. S. Gordon, & W. Gerald (Eds.), *The senses: A comprehensive reference* (Vol. 1, pp. 521–536). New York: Academic Press.

Naber, M., Frässle, S., & Einhäuser, W. (2011). Perceptual rivalry: Reflexes reveal the gradual nature of visual awareness. *PLoS ONE, 6*(6), e20910, 1–12, doi:10.1371/journal.pone.0020910.

Naka, K. I., & Rushton, W. A. H. (1966). S-potential from colour units in the retina of fish (Cyprinidae). *Journal of Physiology, 185,* 536–555.

O'Shea, R. P. (1987). Chronometric analysis supports fusion rather than suppression theory of binocular vision. *Vision Research, 27,* 781–791.

Ooi, T. L., & Loop, M. S. (1994). Visual suppression and its effect upon color and luminance sensitivity. *Vision Research, 34,* 2997–3003.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision, 10,* 437–442.

Richards, W. (1966). Attenuation of the pupil response during binocular rivalry. *Vision Research, 6,* 239–240.

Ridder, W. H., III, Smith, E. L., III, Manny, R. E., Harwerth, R. S., & Kato, K. (1992). Effects of interocular suppression on spectral sensitivity. *Optometry and Vision Science, 69,* 227–235.

Saini, V. D., & Cohen, G. H. (1979). Using color substitution pupil response to expose chromatic mechanisms. *Journal of the Optical Society of America, 69,* 1029–1035.

Slooter, J., & van Norren, D. (1980). Visual acuity measured with pupil responses to checkerboard stimuli. *Investigative Ophthalmology and Visual Science, 19,* 105–108, http://www.iovs.org/content/19/1/105. [PubMed] [Article]

Smith, E. L. I., Levi, D. M., Harwerth, R. S., & White, J. M. (1982). Color vision is altered during the suppression phase of binocular rivalry. *Science, 218,* 802–804.

Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience, 8,* 1096–1101, doi:10.1038/nn1500.

Tsujimura, S., Wolffsohn, J. S., & Gilmartin, B. (2003). Pupil responses associated with coloured afterimages are mediated by the magno-cellular pathway. *Vision Research, 43,* 1423–1432.

Tsujimura, S., Wolffsohn, J. S., & Gilmartin, B. (2006). Pupil response to color signals in cone-contrast space. *Current Eye Research, 31,* 401–408.

Ukai, K. (1985). Spatial pattern as a stimulus to the pupillary system. *Journal of the Optical Society of America A, 2,* 1094–1100.

Weiskrantz, L., Cowey, A., & Le Mare, C. (1998). Learning from the pupil: A spatial visual channel in the absence of V1 in monkey and human. *Brain, 121,* 1065–1072.

Wichmann, F. A., & Hill, N. J. (2001). The psycho-

metric function I: Fitting, sampling and goodness-of-fit. *Perception and Psychophysics, 63,* 1293–1313.

Wilhelm, B. J., Wilhelm, H., Moro, S., & Barbur, J. L. (2002). Pupil response components: Studies in patients with Parinaud's syndrome. *Brain, 125,* 2296–2307.

Wunderlich, K., Schneider, K. A., & Kastner, S. (2005). Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nature Neuroscience, 8,* 1595–1602.

Young, R. S. L., & Alpern, M. (1980). Pupil responses to foveal exchange of monochromatic lights. *Journal of the Optical Society of America, 70,* 697–706.

Young, R. S. L., Han, B.-C., & Wu, P.-Y. (1993). Transient and sustained components of the pupillary responses evoked by luminance and color. *Vision Research, 33,* 437–446.

Young, R. S. L., & Kennish, J. (1993). Transient and sustained components of the pupil response evoked by achromatic spatial patterns. *Vision Research, 33,* 2239–2252.

Young, R. S. L., & Kimura, E. (2008). Pupillary correlates of light-evoked melanopsin activity in humans. *Vision Research, 48,* 862–871.

Young, R. S. L., Kimura, E., & DeLucia, P. R. (1995). A pupillometric correlate of scotopic visual acuity. *Vision Research, 35,* 2235–2241.