Flicker Adaptation Desensitizes the Magnocellular but Not the Parvocellular Pathway

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Purpose. Anatomical and physiological studies show that in primates, visual information is conveyed through two parallel pathways, including the magnocellular (MC-) and parvocellular (PC-) pathways. However, the functional separation between the two pathways remains controversial and challenging. To resolve this, we show a psychophysical approach to desensitize the inferred MC-pathway of human observers independently of the inferred PC-pathway.

Methods. The steady-pedestal and pulsed-pedestal paradigms that allow detection and discrimination to be mediated by only the inferred MC- or PC-pathway were used. Three observers (one male, aged 43 years, and two females, aged 33 and 62 years) adapted to either a steadily presented pedestal or a 2- or 10-Hz 50% contrast square-wave modulated luminance flicker. Contrast discrimination thresholds were measured following the flicker adaptation.

Results. Flicker adaptation reduces contrast detection and discrimination of the MC-pathway but not the PC-pathway, with larger MC losses from 10-Hz (~0.28 log unit loss, $P < 0.05$ for all observers) than 2-Hz flicker (~0.13 log unit loss, $P < 0.05$ for one or two observers depending on stimulus size). Further, our results show that the PC-pathway does not mediate the contrast detection threshold at the background luminance following MC-pathway desensitization.

Conclusions. This study demonstrates the feasibility of independently manipulating sensitivity of the MC-pathway in human observers. Our paradigms provide powerful tools to independently investigate the perceptual functions in the MC- and PC-pathways. This could lead to a better understanding of the perceptual functions of these pathways.

Keywords: flicker adaptation, psychophysics, magnocellular/parvocellular, contrast sensitivity

Convergent evidence from physiological and anatomical studies shows that there are two prominent parallel visual pathways that convey visual information from the retina to the cortex in the primate visual system; that is, the magnocellular (MC-) and parvocellular (PC-) pathways.[1–3] Neurons in these two pathways (i.e., parasol and midget ganglion cells or M and P cells in the lateral geniculate nucleus [LGN], respectively) differ in number, morphology, and physiological response characteristics.[4–6] Furthermore, the two pathways are correlated with different aspects of human perception[7,8]; that is, the MC-pathway is related to the processing of luminance, motion,[7] and high-frequency temporal modulation,[9] and the PC-pathway is related to the processing of color, acuity, and form.[7] Studies have also suggested that processing in both the MC-[10–13] and the PC-[12–14] pathways has influence in attentional guidance and eye movement. Impairments of neurons in these two pathways are associated with some diseases, such as glaucoma and optic neuritis.[15–19] It is therefore important scientifically and clinically to understand the neuronal and perceptual functions of these pathways. However, despite the advance in technology and our great understanding of these pathways, there remains a gap between human perceptual observations and primate anatomical and physiological results. One of the challenges to better link perceptual functions with neuronal response properties comes from the difficulty in examining the processing in these visual pathways separately at a perceptual level. In the current study, we demonstrate a psychophysical approach to independently manipulate the contrast detection and discrimination sensitivities of the inferred MC- and PC-pathways of human observers.

Primate physiological studies show that prolonged exposure to high-contrast stimulation strongly suppresses contrast responses of the ganglion cells and LGN cells in the MC- but not PC-pathways.[20] This effect is not specific to orientation, motion direction, spatial frequency, or temporal frequency, and may arise from the bipolar cells in the retina.[21] At the perceptual level, many human psychophysical studies have shown that temporal contrast adaptation reduces temporal contrast sensitivity.[22–24] However, it has not been considered whether this adaptation effect at the perceptual level results from neuronal response changes within the MC- or PC-pathway, or both, in part due to lack of a methodology allowing independent investigation of contrast processing in these pathways at the perceptual level.

To approach this question, we adapted observers with a square-wave luminance modulated flicker, followed by an examination of the contrast sensitivity in the inferred MC- and PC- pathways using the steady- and pulsed-pedestal

paradigms.[25,26] These paradigms were developed based on physiological findings that MC and PC ganglion cells respond differently to achromatic contrast.[27] Magnocellular ganglion cells show fast increase of response with increasing contrast (high contrast gain) and response saturation at relatively low contrasts. On the other hand, PC ganglion cells show shallower linear increase of response with increasing contrast across a wide range of contrast. Psychophysical studies show that thresholds measured with the steady-pedestal and pulsed-pedestal paradigms resemble the physiological contrast response function of the MC and PC ganglion cells, respectively,[25] from which it can be inferred that these paradigms can separately measure psychophysical contrast sensitivity of the inferred MC- and PC-pathways on human observers.[25,26]

The present study aimed to test whether flicker adaptation alters contrast sensitivity of the inferred MC- and/or PC-pathway using the steady-pedestal and pulsed-pedestal paradigms. Based on previous physiological studies,[20] we hypothesized that flicker adaptation would lead to a reduction of MC-mediated contrast sensitivity (measured with the steady-pedestal paradigm) but not PC-mediated sensitivity (measured with the pulsed-pedestal paradigm). As previous physiological studies found that high temporal frequency contrast modulation suppresses MC cell responses in the LGN more strongly than low temporal frequency adaptation,[20] we expected that flicker adaptation in the steady-pedestal paradigm would be stronger with a higher temporal frequency. Additionally, LGN cells in the MC- and PC-pathways have different receptive field sizes, leading to different spatial-frequency tuning.[28] The MC cells in the LGN are more sensitive to low than high spatial frequencies, while the PC cells in the LGN are more sensitive to high than low spatial frequencies. An earlier study shows that pulsed- and steady-pedestal contrast discrimination sensitivities vary with stimulus spatial parameters[29]; therefore, we determined whether the flicker adaptation effects depended on the spatial characteristics of the stimuli.

Methods

Observers

Three observers participated in the experiment (one male, aged 43 years, and two females, aged 33 and 62 years; two authors and one naïve observer). All had normal or corrected-to-normal visual acuity. Participants provided consent, and the study protocols were approved by the Institutional Review Board at the University of Illinois at Chicago and were in compliance with the Declaration of Helsinki.

Apparatus

An NEC (Tokyo, Japan) 19-inch CRT color monitor controlled by an iMac (Cupertino, CA, USA) computer displayed the visual stimuli. The spectral outputs of the red, green, and blue guns were calibrated using a PR-670 Spectrophotometer (Photo Research, Inc., Chatsworth, CA, USA). The luminance of each phosphor was measured for 1024 levels of input integer value with an International Light IL-1700 current meter with a silicon detector (SDE033/U; International Light Technologies, Peabody, MA, USA). Look-up tables were constructed to represent relations between voltage integer values and phosphor luminances.

Visual Stimuli and Procedure

The visual stimulus was a pedestal, consisting of an array of four equal-sized squares with each subtending $1^\circ \times 1^\circ$ or $0.57^\circ \times 0.57^\circ$, surrounded by a homogeneous achromatic $37^\circ \times 27^\circ$ rectangular field of 12.0 cd/m^2. Separation between squares was 0.088° in visual angle from a viewing distance of 57 cm. A cross of $0.088^\circ \times 0.088^\circ$ that served as a fixation aid and was present at the center of the array throughout the experiment.

In both steady-pedestal and pulsed-pedestal paradigms, the measurement started with a 10-second preadaptation phase, followed by a staircase procedure for contrast discrimination threshold determination. Each staircase trial consisted of three phases, including a 1-second pretest adaptation phase, a 26.7-ms test phase, and a posttest adaptation phase waiting for the observer's response (Fig. 1). The stimulus parameters, including presentation duration (26.7 ms) and square sizes (1° and 0.57°), were chosen to achieve a large separation between MC and PC functions based on previous findings using the pedestal paradigms.[25,26,29] During the pretest and posttest adaptation phases in the steady-pedestal paradigm, the pedestal with a predefined luminance level (i.e., pedestal luminance) was shown together with the background. Observers adapted to both the background and the pedestal luminances. By contrast, during both adaptation phases in the pulsed-pedestal paradigm, only the background was shown, not the pedestal. In other words, observers adapted to only the background luminance, not the pedestal luminance. While the adaptation phases differ in the steady- versus pulsed-pedestal paradigms, the test phases were identical in both paradigms, during which the pedestal was presented with three of the four squares having the predefined pedestal luminance and one of them (i.e., the test square) having an incremental or decremental luminance from the predefined pedestal luminance. Observers were instructed to identify the test square in a four-alternative-forced-choice (4AFC) task; that is, observers reported which square in the array differed in luminance from remaining squares. While the predefined pedestal luminance was fixed in a given block, the luminance of the test square varied according to a 2-yes-1-no double-random staircase procedure that allowed estimation of the contrast discrimination threshold from the predefined pedestal luminance. The staircase started with an easily discriminable test square luminance increment or decrement, with an initial step size of 20% contrast (i.e., test square luminance 20% higher or lower than the pedestal luminance). Whenever a reversal occurred, that is, the moving direction of the staircase changed, the step size was halved until a minimum step size of 0.3125% was reached. The staircase procedure continued until 10 reversals at the minimum step size occurred. The average value of the last six reversals was taken as the discrimination threshold for that pedestal luminance. Full details of the pedestal paradigms and the staircase procedure can be found in the original paper.[25] Thresholds for eight predefined pedestal luminances were estimated in both the steady- and pulsed-pedestal paradigms: 8.5, 9.5, 10.7, 12.0, 13.4, 15.1, 16.9, and 19.0 cd/m^2. Increment pedestals (luminance brighter than the background) and decrement pedestals (luminance darker than the background) were included to measure discrimination thresholds in the ON- and OFF-pathways, respectively.[26] For either pedestal polarity (decrement or inclement pedestals), incremental and decremental discrimination thresholds were similar[26]; therefore, to be time efficient, we chose to measure the discrimination thresholds in the same polarity as the pedestals (i.e., the test square always had a luminance increment for the increment pedestals or had a luminance decrement for the decrement pedestals). The order of the eight pedestal luminance blocks was randomized in each paradigm.

For both paradigms, observers were tested following one of two adaptation conditions: (1) a nonflickering adaptation condition, in which the adapting background and pedestal were steadily presented during the adaptation phases; and (2) a flickering adaptation condition, in which a 2- or 10-Hz 50%

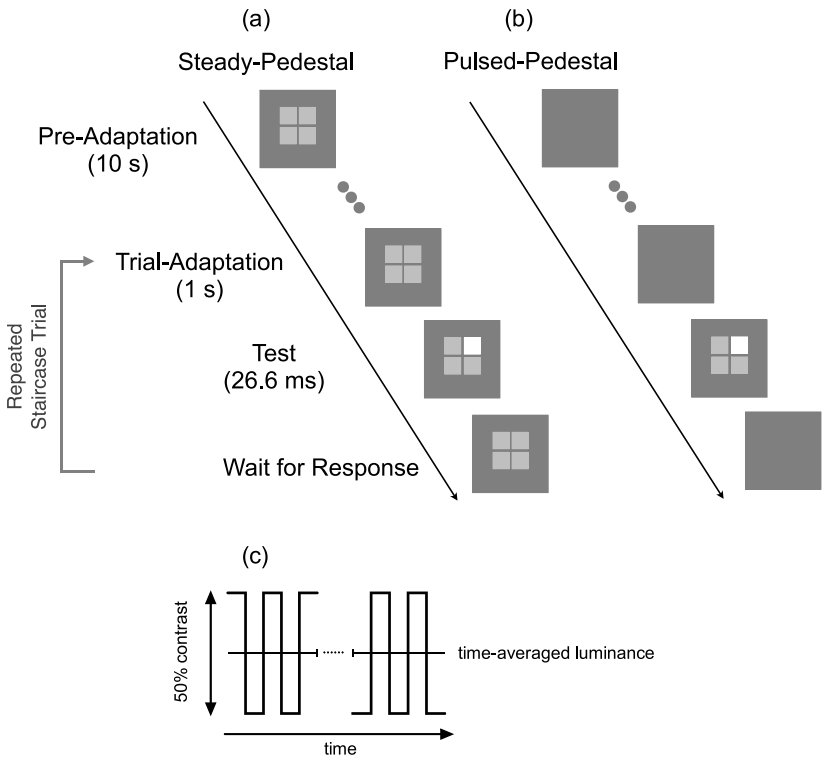

Figure 1. Experimental procedures in the (**a**) steady-pedestal paradigm and (**b**) pulsed-pedestal paradigms. In both paradigms, there was a 10-second preadaptation phase before a staircase procedure started. Each staircase trial started with a 1-second readaptation that was followed by a 26.7-ms test and a postadaptation phase waiting for the observer's response. The observer was instructed to identify the location of the test square that had a different luminance than other squares in the pedestal. The next staircase trial automatically initiated after the response. (**c**) Luminance modulation during the 10-second preadaptation and 1-second readaptation phases at the pedestal location. The luminance modulation was 50% from the time-averaged luminance, which was equal to various predefined pedestal luminances in different blocks in the steady-pedestal paradigm, but was always equal to the surround luminance in the pulsed-pedestal paradigm. The modulation frequencies were at 2 or 10 Hz.

contrast square-wave modulated luminance flicker was presented at the pedestal location along with a steady surround. In the steady-pedestal paradigm, the time-averaged adapting luminance of the flicker was equal to the predefined pedestal luminance, whereas in the pulsed-pedestal paradigm, the time-averaged luminance of the flicker was the same as the luminance of the surrounding background that was steadily presented.

We performed two follow-up control experiments with the steady-pedestal paradigm. The first experiment evaluated whether adaptation contrast was a critical parameter by testing three different adaptation contrasts (20%, 50%, and 100%). The second experiment assessed whether flicker at the borders of the test field were critical to adaptation. We temporally modulated both the surrounding background and the pedestal during adaptation in one condition (flickering pedestal and background), and compared it to the condition (flickering pedestal, steady background) in which only the pedestal was modulated. The temporal frequency in both control experiments was 10 Hz. Two observers (two females, aged 33 and 62 years; one author and one naïve observer) who participated in the main experiment also participated in the control experiments.

Data Analysis and Modeling

Data from the two paradigms were analyzed separately for each observer. Thresholds for each pedestal luminance level in each paradigm were estimated three times on separate days for each observer. The average thresholds across the three repetitions were then taken as the threshold estimates.

Two primate physiology-based models (Equations 1 and 2) were used to describe the threshold data from the pedestal paradigms. Detailed rationale and theories underlying these models can be found in previous papers.[25,26,30] A Threshold Versus Radiance (TVR) function with slope of 1 was used to describe the thresholds from the steady-pedestal paradigm:

$$\log(\Delta I) = K_s + \log(I), \quad (1)$$

where K_s is the free parameter and $-K_s$ represents the absolute contrast sensitivity (in log units) mediated by the inferred MC-pathway. Thresholds from the pulsed-pedestal paradigm can be modeled using the following equation:

$$\log(\Delta I) = K_p + \log\left[(C + C_{sat})^2\right] - log(C_{sat}), \quad (2)$$

where C is the Weber contrast of the pedestal luminance with respect to the background luminance [i.e., $C = |I - I_{bg}|/I_{bg}$], K_p and C_{sat} are free parameters; $-K_p$ represents the absolute contrast sensitivity (in log units) and C_{sat} is related to contrast gains for the inferred PC-pathways. A nonlinear regression procedure by least squares in Stata 13.0 (StataCorp LP, College Station, TX, USA) was used to estimate the parameters for the models specified in Equations 1 and 2 and generate associated 95% confidence intervals.

Note that the models described in Equations 1 and 2 did not treat the incremental contrast sensitivity (in the ON-pathway) separately from the decremental contrast sensitivity (in the OFF-pathway). Some studies have suggested a contrast gain asymmetry between the ON- and OFF-pathways,[31–35] potentially due to an asymmetrical neural wiring in the cortex between the ON- and OFF-pathways (e.g., more neurons in the

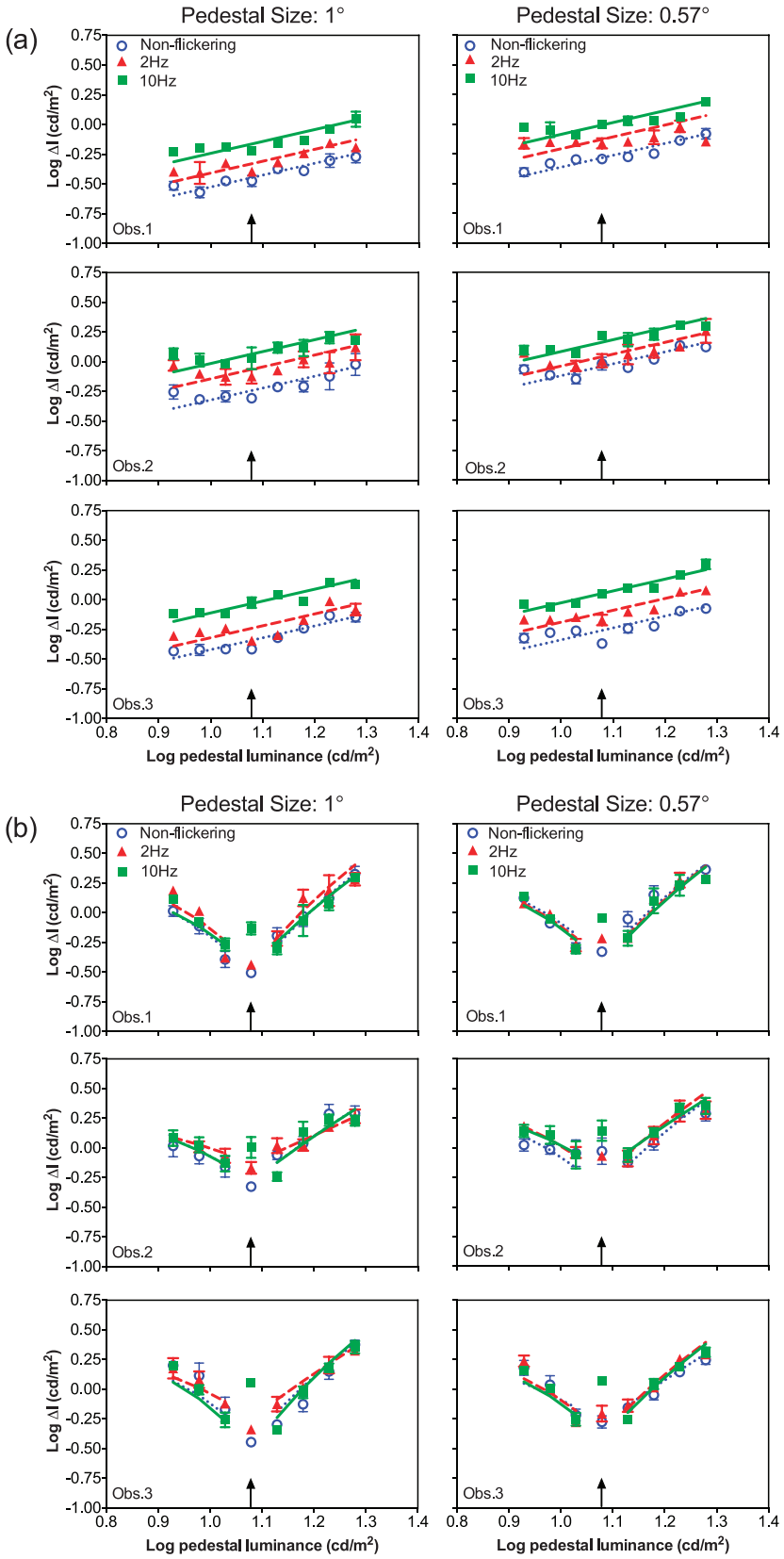

Figure 2. Thresholds and model fits in the (**a**) steady-pedestal paradigm and (**b**) pulsed-pedestal paradigm, with the two stimulus sizes: 1° (*left*) and 0.57° (*right*) for the three observers. Three adaptation conditions are nonflickering (*blue circles*), 2-Hz flicker (*red triangles*), and 10-Hz (*green squares*) flicker. The *black arrow* shows the luminance of the background.

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Table. Estimates of Contrast Sensitivity and Confidence Interval (CI)

	Observer 1		Observer 2		Observer 3	
	$-K_s$	CI	$-K_s$	CI	$-K_s$	CI
Steady pedestal ($-K_s$)						
1°						
Nonflickering	1.53	1.49, 1.56	1.32	1.27, 1.38	1.43	1.39, 1.47
2 Hz	1.42	1.36, 1.48*	1.17	1.09, 1.25*	1.33	1.25, 1.40
10 Hz	1.24	1.20, 1.29*	1.01	0.95, 1.08*	1.12	1.07, 1.17*
0.57°						
Nonflickering	1.37	1.33, 1.42	1.13	1.08, 1.19	1.35	1.28, 1.41
2 Hz	1.25	1.16, 1.34	1.05	0.97, 1.13	1.20	1.15, 1.25*
10 Hz	1.10	1.04, 1.16*	0.93	0.89, 0.97*	1.04	1.01, 1.06*
Pulsed pedestal ($-K_p$)						
1°						
Nonflickering	0.07	0.01, 0.13	0.04	−0.08, 0.16	0.02	−0.12, 0.17
2 Hz	0.00	−0.11, 0.12	0.16	0.06, 0.26	0.08	−0.03, 0.18
10 Hz	0.08	−0.01, 0.16	0.04	−0.12, 0.20	0.13	−0.27, 0.53
0.57°						
Nonflickering	−0.02	−0.13, 0.10	0.01	−0.15, 0.12	0.07	−0.09, 0.23
2 Hz	0.00	−0.09, 0.09	0.09	−0.17, 0.00	0.04	−0.08, 0.16
10 Hz	0.01	−0.08, 0.10	0.04	−0.13, 0.05	0.01	−0.07, 0.09

* $P < 0.05$ when comparing the CI of flicker conditions with the nonflickering condition.

OFF-pathway than in the ON-pathway in V1[32,33]). However, the physiological evidence is equivocal, as other researchers did not observe the asymmetry.[9,36–39] Psychophysical data from the pedestal paradigms for incremental and decremental contrast discrimination in the original paper,[25] as well as in the current study, also showed some small ON and OFF asymmetry. The probable cause of this asymmetry is spread light from the surround into the test fields for two reasons. (1) Decremental discrimination thresholds deviate from the model predictions at higher decremental pedestal contrasts, and the deviations are greater for smaller square sizes. (2) Computational modeling indicated that spread light could account for such deviations.[29] To simplify our analysis, we did not consider any potential ON and OFF asymmetry in the modeling, and the models were able to describe the data satisfactorily.

Results

Main Experiment

Results were consistent across the three observers. The measured thresholds for the steady and pulsed paradigms are shown in Figure 2. Flicker adaptation reduced sensitivity (shown as elevated thresholds in Fig. 2a) measured with the steady-pedestal paradigm, but not with the pulsed-pedestal paradigm (Fig. 2b). In the steady-pedestal paradigm, thresholds following flicker adaptation (2 or 10 Hz) were higher than for the nonflickering adaptation condition (Fig. 2a), with thresholds from 10-Hz adaptation higher than those from the 2-Hz adaptation condition. In contrast, the pulsed-pedestal paradigm yielded similar thresholds for all adapting conditions (Fig. 2b).

An interesting finding in the pulsed-pedestal data is that, following flicker adaptation, the observed thresholds formed a W-shaped pattern, with the threshold at the background adapting luminance higher than the predicted thresholds from the pulsed-pedestal model, which were the intersection points of the two arms of the V-shaped functions.

The estimated MC and PC contrast sensitivity from the models in Equations 1 and 2, as well as the confidence intervals (CI), is shown in the Table. Compared to the nonflickering condition, flicker adaptation reduced MC sensitivity ($-K_s$) from the steady-pedestal paradigm (Table). The mean desensitization effect was approximately 0.28 and 0.13 log units for the 10-Hz and 2-Hz flicker, respectively. Consistent with earlier findings,[29] sensitivities were lower for small-size than large-size stimuli (Table). The two stimulus sizes showed similar flicker adaptation effects for both of the paradigms. By contrast, the PC sensitivity ($-K_p$) from the pulsed-pedestal paradigm showed much smaller differences among different adapting conditions (Fig. 2b; Table).

Control Experiments

For both observers, thresholds for the three adaptation contrast levels tested in control experiment I were similar (Fig. 3). In other words, the flicker adaptation effect was similar for the three adaptation contrast levels tested at 10 Hz. Meanwhile, in control experiment II, thresholds from the flickering background condition were comparable to those from the steady background condition (Fig. 4). That is, the flicker adaptation effect in the MC-pathway was similar when both the background and the pedestal were flickered compared to when the pedestal alone was flickered.

Discussion

While psychophysical studies have shown that flicker adaptation reduces contrast sensitivity, the differential flicker adaptation in the MC- and PC-pathways has not been investigated. In the present study, using the steady- and pulsed-pedestal paradigms, we found that flicker adaptation comes from desensitization of the inferred MC-pathway but not the PC-pathway. Meanwhile, as expected, high temporal frequency flicker is more effective in desensitizing the MC-pathway since the MC-pathway is more sensitive to high than low temporal frequencies.[9,28] The desensitization effect was similar for different sizes of the stimuli, suggesting that this effect is not specific to the spatial extent of the stimuli.

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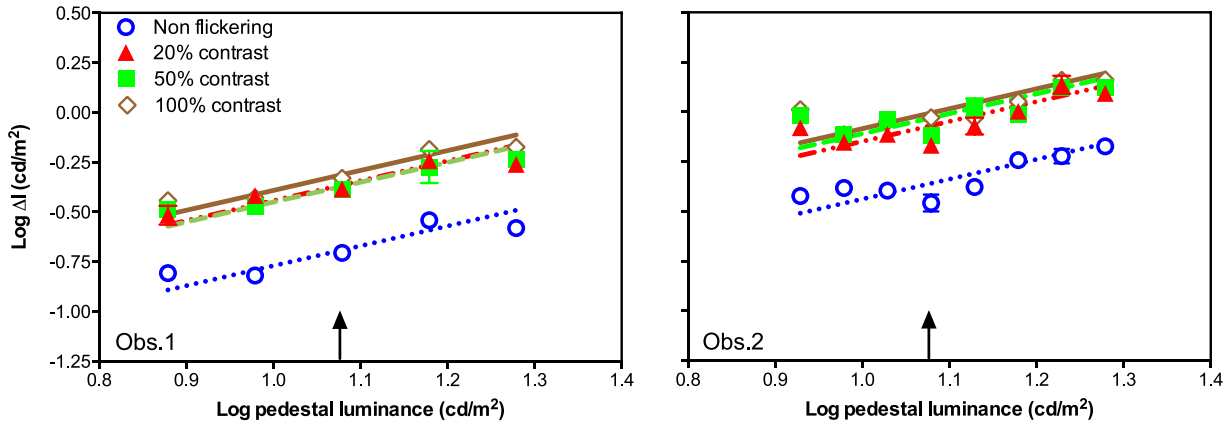

FIGURE 3. Thresholds and model fits in the steady-pedestal paradigm for different adaptation contrasts (20%, *red triangles*; 50%, *green squares*; and 100%, *brown diamonds*), as compared to thresholds in the nonflickering adaptation condition (*blue circles*).

These results provide a psychophysical parallel to the primate physiological findings,[20] showing that temporal contrast adaptation suppresses contrast responses of cells in the MC-pathway but not those in the PC-pathway. The response suppression observed in MC cells is possibly due to a contrast adaptation, which likely originates principally in bipolar cells in the retina.[40] The current findings showed no evidence of PC-pathway sensitivity change from flicker adaptation at either retinal or postretinal levels. Compared with MC cells, PC cells are more sensitive to lower temporal frequencies[9,28]; however, adapting to a low temporal frequency flicker of 2 Hz does not alter the sensitivity of the PC-pathway. These findings suggest that adaptation to pattern, such as motion direction[41] or orientation,[42] observed in psychophysics and potentially mediated by cortical mechanisms, may be related to adaptation in the MC-pathway rather than in the PC-pathway.

A notable feature of the pulsed-pedestal data is the W-shaped pattern of the thresholds following flicker adaptation. That is, the threshold at the background adapting luminance is higher than the predicted value from the pulsed-pedestal model. Rather, the threshold at this point follows the prediction from the steady-pedestal model. This suggests that even though the PC-pathway is predicted to be more sensitive than the MC-pathway at the background adapting luminance following MC-pathway desensitization, the contrast detection threshold at this luminance is not determined by the PC-pathway. This observation is seen not only following flicker adaptation (Fig. 2b) but also in previously published pulsed-pedestal data obtained using small, briefly presented stimuli.[29] The pulsed- and steady-pedestal paradigms show different spatial summation functions, with thresholds for small field sizes estimated to be lower for the pulsed- than for the steady-pedestal paradigms. Here, as following flicker adaptation, the data showed an insensitivity of the PC-pathway to contrast in a homogeneous luminance field. Our interpretation is that under the pulsed-pedestal stimulus conditions, low-contrast PC-mediated discrimination requires MC system stimulus edge information, with the MC system providing outlines of the four possible stimulus positions between which PC-mediated discrimination occurs. Both psychophysical[43] and physiological studies[44–47] support this interpretation, showing that position information is poorly coded for equiluminous borders. In a homogeneous luminance field, the locations of the four squares are equiluminant with the surrounding adaptation field (identical in luminance and chromaticity). Thus, under conditions in which the MC system sensitivity is below that of the PC system, PC system-mediated thresholds are elevated, interpreted here as due to uncertainty as to the positions of the four fields that need be discriminated. Taken together, these results are consistent with the idea that after steady adaptation to a homogeneous luminance field, contrast detection is mainly governed by the MC-pathway for stimulus conditions where the MC threshold is higher than that for the PC-pathway. Other

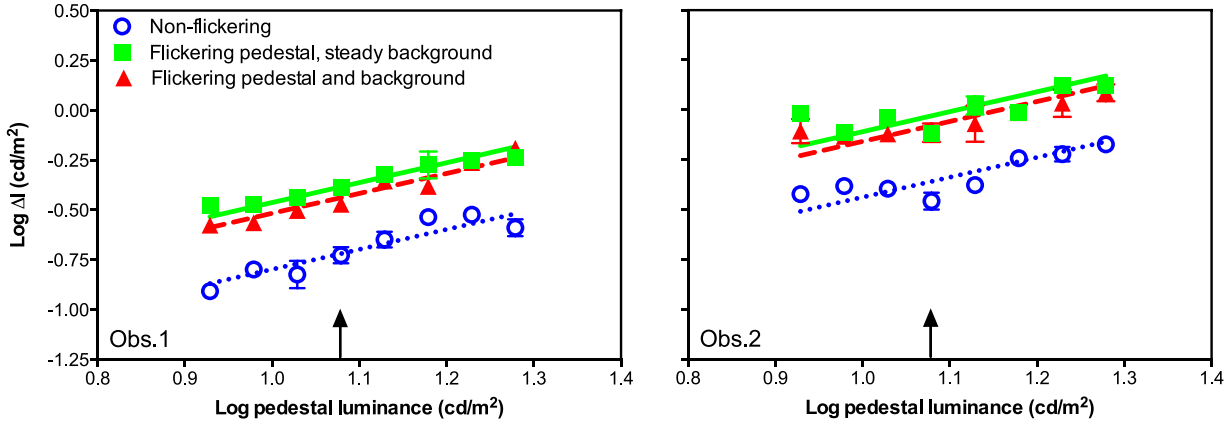

FIGURE 4. Thresholds and model fits in the steady-pedestal paradigm for the conditions in which only the pedestal was flickered during adaptation (steady background, *green squares*), and in which both the surrounding background and the pedestal were flickered during adaptation (flickering background, *red triangles*), and when both the background and the pedestal were not flickered (nonflickering, *blue circles*).

psychophysical studies reveal an interaction between parvocellular-mediated chromatic sensitivity and magnocellular luminance positional information.[48,49] A possible physiological substrate may lie in a population of cortical V1 cells that exhibit combined responses to color and luminance.[50,51]

An earlier psychophysical study found that flicker adaptation to the same size and same location of the test field resulted in a larger reduction of sensitivity than adaptation to a larger flickering field that included the test field.[24] A plausible explanation is that neurons detecting the edge between the test field and the surrounding background play important roles in flicker detection and contrast discrimination. When flickering only the test field, neurons at the edge may respond more vigorously to reversal in edge contrast, leading to more suppression in activity afterward, than they do to conjoint luminance modulation of both sides of the edge when flickering an adaptation field larger than the test field. By contrast, here, we found that the observed desensitization effect was comparable although slightly larger when flickering the entire stimulus field, including the pedestal and surround, compared with flickering only the pedestal, suggesting the important contribution of local flicker adaptation. This difference from previous psychophysical study[24] is likely due to a difference in experimental conditions.

The MC- and PC-pathways have different roles in various visual functions,[7] including motion and color or form perception, and diseases affect them differently.[15] To study their specific roles in each perceptual function and their interaction with diseases, it is important to have tools to independently psychophysically examine the perceptual function in these pathways. The present paradigms offer feasible tools to do so. For example, one could examine the perceptual influence of desensitizing the MC-pathway on motion perception. This could lead to a better understanding of the functions in these pathways. Further, the steady- and pedestal-paradigms have been applied in various studies to examine the contrast processing of the inferred MC- and PC-pathways under various experimental conditions. Studies using these paradigms showed that the contrast processing in the inferred MC- and PC-pathways is affected differently in patients with eye diseases[17,52] or other neural disorders[53,54] or after alcohol intoxication.[30] The present study offers an additional tool that could be applied in clinical research to examine possible alterations in adaptation in the two pathways in patients with ophthalmic or systemic disease.

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