Monocular and binocular mechanisms mediating flicker adaptation

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ABSTRACT

Flicker adaptation reduces subsequent temporal contrast sensitivity. Recent studies show that this adaptation likely results from neural changes in the magnocellular visual pathway, but whether this adaptation occurs at a monocular or a binocular level, or both, is unclear. Here, two experiments address this question. The first experiment exploits the observation that flicker adaptation is stronger at higher than lower temporal frequencies. Observers' two eyes adapted to 3 Hz flicker with an incremental pulse at 1/4 duty cycle, either in-phase or out-of-phase in the two eyes. At the binocular level, the flicker rate was 6 Hz in the out-of-phase condition if the two eyes' pulse trains sum. Similar sensitivity reduction was found in both phase conditions, as expected for independent monocular adapting mechanisms. The second experiment tested for interocular transfer of adaptation between eyes. Results showed that (1) flicker adaptation was strongest with adapting and test fields in only the same eye, (2) adaptation can be partially transferred interocularly with adaptation in only the opposite eye, and (3) adaptation was weakened when both eyes were adapted simultaneously at different contrasts, compared to test-eye adaptation alone. Taken together, the findings are consistent with mechanisms of flicker adaptation at both the monocular and binocular level.

1. Introduction

Prolonged viewing of temporal luminance-modulated flicker (flicker adaptation) reduces subsequent contrast sensitivity (e.g. sensitivity to subsequent flicker; Pantle, 1970; Smith, 1971). The sensitivity reduction can be generalized to flicker at non-adapted temporal frequencies (Nilsson, Richmond, & Nelson, 1975; Shady, MacLeod, & Fisher, 2004), and the magnitude of adaptation depends on the spatial correspondence between the test and adapting fields (Robinson & de Sa, 2012). Sensitivity is reduced most when the test flicker is the same size and presented at the same location as the adapting flicker.

Although this flicker adaptation has been well documented in psychophysical studies for decades, the underlying neural mechanism is not fully understood. The primate visual system has parallel visual pathways that convey signals from the retina to the cortex, among which two are most studied: the magnocellular

(MC) and parvocellular (PC) pathways (Hubel & Wiesel, 1972; Leventhal, Rodieck, & Dreher, 1981; Livingstone & Hubel, 1988). Although these pathways have distinguishing neural characteristics and play different roles in various perceptual functions (Callaway, 2005; Kaplan, 2004; Lee, Pokorny, Smith, Martin, & Valberg, 1990; Livingstone & Hubel, 1987, 1988), they both process achromatic contrast information (Kaplan & Shapley, 1986). Studies suggest, however, that flicker adaptation may result from adaptation in the MC pathway but not the PC pathway. A physiological study demonstrates that responses of MC cells but not PC cells are suppressed after prolonged adaptation to a high-contrast temporally-modulated grating (Solomon, Peirce, Dhruv, & Lennie, 2004). Parallel to this physiological finding, recent psychophysical work demonstrates that flicker adaptation occurs in the inferred MC but not PC pathway of human observers (Zhuang, Pokorny, & Cao, 2015). In that study, the steady-pedestal and pulsed-pedestal paradigms were used (Pokorny, 2011; Pokorny & Smith, 1997) to measure contrast sensitivity in the inferred MC and PC pathways. Results show that MC but not PC contrast sensitivity decreases significantly after adapting to flicker of 20% or higher contrast (following experiments here show that 10% contrast also is sufficient to reduce contrast sensitivity). Further, the reduction

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of contrast sensitivity is stronger with higher (10 Hz) than lower (2 Hz) temporal-frequency adapting flicker. Thus, both physiological and psychophysical results find flicker adaptation is due to neural response changes in the MC pathway but not the PC pathway.

A remaining question is whether flicker adaptation occurs at a monocular and/or binocular locus in the MC pathway. At the monocular level, the MC and PC pathways are separated from retina to V1 (Callaway, 2005; Kaplan, 2004; Merigan & Maunsell, 1993; Schiller & Logothetis, 1990). At the binocular level starting from V1, the MC and PC pathways converge, but each pathway still provides predominant input to separate parts of the brain and for different visual functions (Schiller & Logothetis, 1990). For instance, the MC pathway dominates input to the dorsal visual stream, which plays primary roles in spatial and motion processing; whereas the PC pathway dominates input to the ventral visual stream, which plays primary roles in form and object processing (Haxby et al., 1991; Nassi & Callaway, 2006; Ungerleider & Haxby, 1994). The current study focuses on determining whether the mechanism(s) of flicker adaptation are at a monocular and/or binocular locus in the MC pathway.

Earlier studies investigating the monocular versus binocular locus have mixed results (Moulden, Renshaw, & Mather, 1984; Schieting & Spillmann, 1987; Smith, 1971; Thabet, Wilkinson, Wilson, & Karanovic, 2013). Some studies support a monocular adapting mechanism (Smith, 1971), while others report a binocular component (Schieting & Spillmann, 1987; Thabet et al., 2013). Different experimental stimuli and paradigms were used in these studies, which may partially explain the inconsistent findings. None of the paradigms in these previous studies assessed contrast sensitivity specifically within the MC pathway.

In the present study, two psychophysical experiments used the steady-pedestal paradigm (Pokorny, 2011; Pokorny & Smith, 1997) to determine whether flicker adaptation occurs at a monocular and/or binocular level in the MC pathway. The first experiment examined whether a phase difference between the adapting flicker presented to the two eyes affected binocular contrast sensitivity. This was examined by exploiting the observation, cited above, that flicker adaptation is stronger at higher than lower temporal frequencies. A pilot experiment for the current study showed 6 Hz flicker leads to a significantly larger contrast sensitivity reduction than 3 Hz flicker. Subsequently, observers adapted to 3 Hz flicker, either in-phase in the two eyes or 180-degree out-of-phase. The flicker in each eye had an incremental pulse at 1/4 duty cycle (83 ms pulse in each 333 ms cycle). At the binocular level, the flicker rate was 6 Hz in the out-of-phase condition if the pulse trains in the two eyes sum. Therefore, if adaptation occurs at the binocular level, the adaptation should be stronger in the out-of-phase than in-phase condition.

The second experiment investigated whether flicker adaptation can be transferred interocularly. In the primate visual system, visual information from each eye is processed separately until at least the lateral geniculate nucleus (LGN) (Blasdel & Fitzpatrick, 1984; Hubel & Wiesel, 1972; Parker, 2007). Binocular neurons, which combine signals from the two eyes, have been found in V1 and in extrastriate cortex (Parker, 2007). Using dichoptic stimulation, in which different visual stimuli are presented simultaneously to the two eyes, psychophysical studies can determine whether a process occurs prior to or after the level of binocular combination (D'Antona, Christiansen, & Shevell, 2014; D'Antona, Kremers, & Shevell, 2011; Teixeira et al., 2014). In this experiment, observers adapted to different stimuli in the two eyes and then monocular contrast sensitivity was measured under various adapting conditions. Critically, if adaptation is purely monocular, then flicker adaptation in one eye alone should not alter contrast sensitivity in the contralateral non-adapted eye.

2. Experiment I – phase effect on binocular contrast sensitivity

2.1. Methods

2.1.1. Observers

Three observers participated in Experiment I (1 male, 22 years, and 2 females 25 and 33 years). One observer was author X.Z. and two observers were naïve. All had normal or corrected-to-normal visual acuity. Participants provided informed consent and the study was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.1.2. Apparatus

A Sony 19″ CRT color monitor controlled by an iMac computer was used to display the visual stimuli. The monitor had a refresh rate of 75 Hz and was calibrated for the spectral outputs of the red, green, and blue guns using a Photo Research PR-650 spectroradiometer. Linearity of the light output from each gun was established using an International Light radiometer/photometer (IL-1700). An eight-mirror haploscope was used to project different stimuli to the two eyes. Positions of two of the mirrors were adjustable to accommodate observers' interocular distances for optimal binocular fusion.

2.1.3. Visual stimuli and procedure

A pedestal array of four $1 \times 1°$ squares was presented at the center of the monitor screen. The pedestal was surrounded by a homogeneous achromatic $18.4° \times 13.8°$ rectangular field at 12.0 cd/m². A gap of 0.09° separated the four squares from each other. Observers viewed the stimuli from a distance of 49.4 in., and were instructed to fixate throughout the experiment on a cross $(0.09 \times 0.09°)$ centered within the pedestal array. All stimuli were achromatic (MacLeod–Boynton chromaticity coordinates $L/(L + M)$ = 0.665 and $S/(L + M) = 1$, where the unit of $S/(L + M)$ was normalized to 1.0 for the chromaticity metameric to equal-energy-spectrum 'white').

Each experimental block started with 10 s initial adaptation, followed by a staircase procedure with repeated trials. There were three phases in each staircase trial: a 1-s pre-test adaptation phase, a test phase of 26.7 ms, and a post-test adaptation phase that lasted until a response was made by the observer (Fig. 1). During the initial adaptation, as well as during the two adaptation phases of each staircase trial, the pedestal was shown either steadily at a given fixed luminance level (the average pedestal luminance) or flickering with temporal square-wave luminance modulation around the average pedestal luminance. Observers adapted to either the steady or the flickering pedestal. During the test phase, one of the four squares, randomly chosen, increased or decreased its luminance (this is the test square) while the other three squares remained at the average pedestal luminance. There was a 200 ms interval with the four squares at the average pedestal luminance between phases. The observers' task was to identify the test square in a 4AFC task. In a given experimental block, the average pedestal luminance was fixed and a 2-yes/1-no randomized double-staircase procedure was used to determine the threshold luminance for discrimination. Each staircase started with an easily discriminable luminance change (a step size of 20% luminance from the average pedestal luminance) and then, whenever a reversal occurred, the luminance change was halved until a minimum step size of 0.3125% was reached. The staircase stopped after the tenth reversal at the minimum step size. The average value of the last six reversals was taken as the discrimination threshold for that pedestal luminance. In each experimental session, thresholds for seven average pedestal luminances were measured in seven randomly ordered blocks: 6.0 cd/m², 7.6 cd/m², 9.5 cd/m², 12.0 cd/m²,