PERGAMON

Vision Research 41 (2001) 1119–1131

Vision Research

www.elsevier.com/locate/visres

Comparing increment and decrement probes in the probed-sinewave paradigm

S. Sabina Wolfson *, Norma Graham

Department of Psychology, Columbia University, Mail Code 5501, New York, NY 10027, USA

Received 4 July 2000; received in revised form 21 December 2000

Abstract

Using the probed-sinewave paradigm, we explore the differences between increment and decrement probes across a range of frequencies (approx. 1–19 Hz). In this paradigm, detection threshold is measured for a small test probe presented on a large sinusoidally flickering background (at eight different phases). Probe thresholds are very similar for increment and decrement probes, but there is a very small (and systematic) difference: increment thresholds are usually slightly higher relative to decrement thresholds during the part of the cycle when the background's intensity is increasing. Although Wilson's (1997, *Vis. Neuro*., 14, 403–423) model substantially underestimates the size of this difference, it predicts some phase dependency. However, the existence of On- and Off-pathways in Wilson's model is *not* important for these predictions. A recent model by Snippe, Poot, and van Hateren (2000, *Vis. Neuro*., 17, 449–462) may be able to predict this result by using explicit contrast-gain control rather than separate On- and Off-pathways. Auxiliary experiments measuring the perceived polarity of the probe provide a further argument suggesting that separate On- and Off-pathways are not useful in explaining increment and decrement probe thresholds.

Keywords: Light adaptation; Temporal frequency; Flicker; Computational model; Probed-sinewave paradigm; Increment; Decrement; Dynamics

1. Introduction

Humans are able to adapt to a range of ambient light levels which varies by a factor of at least 10^8. In this paper we continue our examination of adaptation to moderate fluctuations in light level (Hood & Graham, 1998; Wolfson & Graham, 2000). Specifically, we examine the differences between increment and decrement probes in the probed-sinewave paradigm.

In the probed-sinewave paradigm, threshold is measured for detecting a small, brief probe superimposed on a background which modulates sinusoidally over time. In our experiments this flickering background is much larger than the probe. We vary the frequency of the flickering background from 1.2 to 18.8 Hz and measure detection thresholds for both increment and decrement probes. The probes are present at eight different phases with respect to the flickering background. Exemplar increment and decrement probe stimuli are shown in Fig. 1a,b, respectively.

The concept of measuring detection threshold for a probe presented at different times with respect to a modulated background began with work by Boynton, Sturr, and Ikeda (1961) who measured increment probe thresholds on a squarewave modulated background. Subsequent early work by Shickman (1970) and Maruyama and Takahashi (1977) measured increment probe thresholds on a sinewave modulated background.

The probed-sinewave paradigm combines pieces from two different traditions of studying light adaptation. The *periodic tradition*, in which temporal contrast sensitivity for a flickering light is measured (e.g. de Lange, 1958; Kelly, 1961), and the *aperiodic tradition*, in which, for example, threshold is measured for a small, brief probe presented on a large, longer flash (e.g. Crawford, 1947; Geisler, 1978; Hood, 1978; Adelson, 1982). For excellent reviews of the light adaptation literature see Shapley and Enroth-Cugell (1984), Hood and Finkelstein (1986), and Hood (1998). Graham and Hood (1992) found that models from the periodic tradition

* Corresponding author. Tel.: + 1-212-8543006; fax: + 1-212-8543609.

E-mail address: sabina@psych.columbia.edu (S.S. Wolfson).

0042-6989/01/$ - see front matter
PII: S0042-6989(01)00009-8

could account for phenomena from that tradition, but not from the aperiodic tradition (and vice versa). However, by combining components from these models Hood and Graham (1992; von Wiegand, Hood, & Graham, 1995) could construct 'merged' models which could account for both tradition's phenomenon. But, when the merged models were compared to probed-sinewave results they failed to account for important characteristics of those results (Hood, Graham, von Wiegand, & Chase, 1997).

Hood et al. (1997) found the probed-sinewave paradigm to be a strong test of light adaptation models. Since all the models considered by Hood et al. (1997) failed to adequately account for the probed-sinewave results they were tested on, Hood and Graham (1998) considered a new model of light adaptation from Wilson (1997). Hood and Graham (1998) found that Wilson's (1997) model could account for many aspects of probed-sinewave results at both low and high frequencies of the flickering background. Wolfson and Graham (2000) further tested Wilson's (1997) model against results from experiments which targeted various aspects of probed-sinewave timing. Wolfson and Graham (2000) found that Wilson's (1997) model did *not* account for some aspects of the results but generally *did* account for the timing results. In this paper, we will continue our exploration of Wilson's (1997) model. We will also briefly consider the five models from Hood et al. (1997) as well as a new model from Snippe, Poot, and van Hateren (2000). Snippe et al.'s (2000) model accounts quite well for their probed-sinewave data and we hope that the model will be explored further in the future.

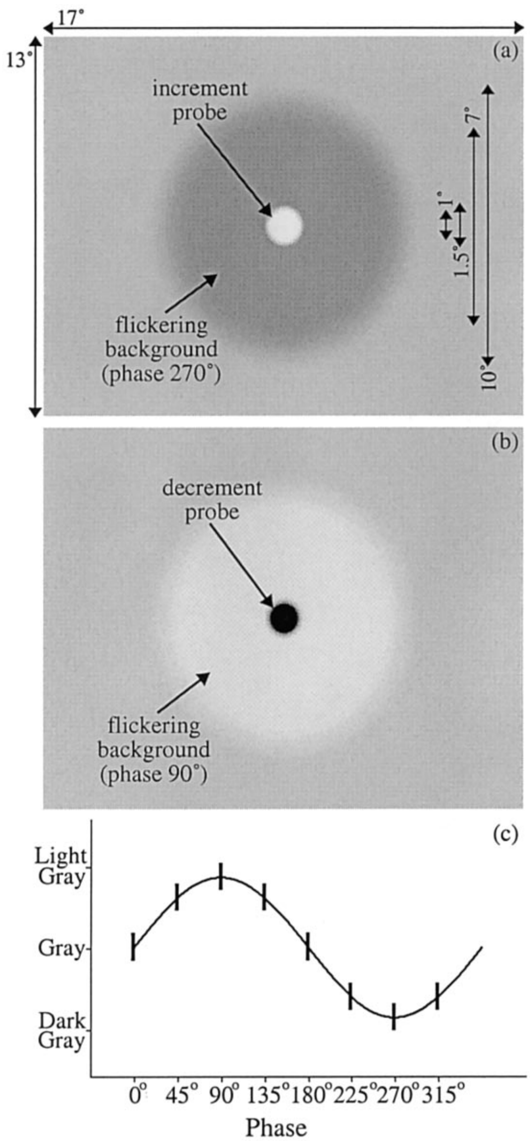

Fig. 1. The spatial stimulus characteristics of: (a) an increment probe presented on a flickering background at a phase of 270°, and (b) a decrement probe presented at a phase of 90°. (c) Temporal profile of the flickering background showing the eight different phases at which the probe is presented.

Numerous studies of light adaptation have employed increment and decrement probes of various types (e.g. Krauskopf, 1980). However, previous work in the probed-sinewave paradigm has only used increment probes, except for one paper (DeMarco, Hughes, & Purkiss, 2000) and one abstract (Snippe, Poot, & van Hateren, 1998) which used both increments and decrements. These other researchers' experiments overlap with a subset of ours, but their methods and stimuli differ greatly from ours. We will compare their results to ours below (in Section 3.2).

The study of increments and decrements is often tied to the idea that increments may be detected by the On-pathway and decrements by the Off-pathway. Wilson's (1997) model of retinal light adaptation contains both On- and Off-pathways, allowing us to explore this idea. To further consider this idea, we measured the subject's perception of the probe's polarity in a subset of the experiments reported here; that is, we asked the subject to report whether the probe looked like an increment or a decrement.

Another reason for studying increments and decrements is that they might push the operating point of the visual system in different directions on some saturating (compressive) nonlinear function. Increments might be likely to push in the direction that is saturating and therefore raise threshold more than decrements. Thus, increments and decrements might have different effects that would reveal the characteristics of the saturating nonlinearity. The differences might reveal both the degree of compression and the timing relative to the background.

The results reported in this paper show that increment and decrement probe thresholds are quite similar. However, there is a small and systematic difference between increment and decrement probe thresholds: when the flickering background is increasing in intensity, increment probe thresholds are generally higher relative to decrement probe thresholds.

2. Methods

2.1. Subjects

The five subjects in this study were Columbia University undergraduates, or recent graduates, and were paid for their time. Subjects were naive as to the purpose of the experiments, but JC, MR, and HH had run in other probed-sinewave experiments before participating in the experiments reported here. All subjects had a corrected visual acuity of 20/20 or better.

2.2. Apparatus

Stimuli were presented on an AppleVision 1710 monitor (75 Hz refresh rate) controlled by an Apple Macintosh 9500. The mean luminance of the stimuli was approximately 52 cd/m^2; this is the same luminance used by Wolfson and Graham (2000) and similar to the 250 Trolands (Td) used by Hood and Graham (1998). Stimuli were generated and presented using MathWorks' MATLAB with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Lookup-table values were set so that the relationship between pixel value and display luminance was linear. Subjects ran in a dimly lit room with free viewing.

2.3. Stimuli

2.3.1. General description

The spatial configuration of the stimulus is shown in Fig. 1a,b. It is the same as used in Wolfson and Graham (2000). The probe is centered within the flickering background, and the flickering background is centered within the monitor's screen. The viewing distance was 1 m. The probe subtended 1.5° while the background subtended 10° of visual angle. The probe and the flickering background had gradual edges of width 0.5° and 3°, respectively. Four sticks were attached to the edges of the monitor, so that subjects could maintain fixation; the sticks extended approximately 3° into the monitor, pointing towards the center of the screen. The area of the screen beyond the flickering background was held steady at the mean luminance of the flicker.

The background flickered at either 1.2, 2.3, 4.7, 9.4, or 18.8 Hz (these particular frequencies are due to the CRT's refresh rate). The modulation of the flickering background was either 57% (as was used in Hood et al., 1997; Wolfson & Graham, 2000) or 28.5%.

The probe was either an increment or a decrement in intensity with respect to the flickering background. The probe was presented for one frame (approx. 13 ms) at one of eight phases (0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°) as shown in Fig. 1c.

2.3.2. CRT display

The general description of the stimuli (Section 2.3.1) considers the spatial and temporal characteristics separately. This is a simplification since these stimuli were presented on a CRT. There is a complicated spatiotemporal structure in these stimuli because: (i) each frame is drawn raster line by raster line, from one edge of the screen to the other; and (ii) each point decays within a small fraction of the frame duration. Thus each point in a stimulus is fully 'on' for a short part of the 13 ms frame duration and is then decaying or 'off' for the rest of the frame duration; further, different points in a stimulus are 'on' at different moments. The time-averaged luminance of each point on the display was 52 cd/m^2.

The probe in the experiments reported here was presented for one frame, occupying 1/75th of a second or approximately 13 ms. The mean intensity during the 13 ms frame duration is what is reported as the probe's intensity.

For most of this paper, the usual convention of ignoring the fine spatiotemporal structure of the stimuli is followed. However, it is returned to briefly in footnote 3 (Section 4.1) where, in the context of Wilson's (1997) model, the possible implications of this fine temporal structure are mentioned.

2.3.3. Time sampling of the stimulus

There were S samples (frames) per cycle of the flickering background, where S was 64, 32, 16, 8, and 4 for frequencies (f) of 1.2, 2.3, 4.7, 9.4, and 18.8 Hz, respectively.

For all but the highest frequency, these samples were described as follows:

$$M(x) = \sin(xf2\pi \div 64), \quad x = 0, 1, \ldots S-1$$

The probes were added to the samples having phases 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°. For example, for $f = 1.2$ Hz, the probes were added to the samples for which $x = 0$, 8, 16, 24, 32, 40, 48, and 56.

At the highest frequency (18.8 Hz) there were only four samples, S, per cycle. Thus, in order to investigate all eight phases, we used two versions of this flickering background. The first version is described by the above equation with $S = 4$. These four samples can also be seen as coming from a sawtooth wave. Probes were added to the samples having phases 0°, 90°, 180°, and 270°. The second version is generated by the below equation with $S = 4$:

$$M(x) = \sin(xf2\pi \div 64), \quad x = 0.5, 1.5, \ldots S-0.5$$

These four samples can be seen as coming from a square wave. Probes were added to the samples having phases 45°, 135°, 225°, and 315°.

2.4. Procedure

Throughout the experiments the background either flickered or was steady gray, always at the same mean luminance. During each trial

- the background flickered for 2.56 s,
- then the background flickered for one cycle in which a probe was presented,
- then the background flickered for 0.85 s more,
- then the screen turned gray for 1 s,
- then a beep sounded, indicating that the subject could respond.

The intensity of the probe on each trial was determined by a QUEST (Watson & Pelli, 1983) staircase (60% detection threshold). Multiple staircases were intermixed as described below.

In some of the experiments (which are called *Threshold Experiments*), the subject indicated whether they saw or did not see the probe by pressing the ‘y’ or ‘n’ key on the keyboard. After the subject’s response, the next trial began.

Other experiments (which we will call *Perceived Polarity Experiments*) examined *both* probe threshold and the subject’s perception of the probe polarity. In these experiments, the subject pressed an additional response key (after pressing the ‘y’ or ‘n’) which was coded as: definitely increment, probably increment, unknown, probably decrement, or definitely decrement. The subject was not given feedback about the correctness of this response.

Each experimental session consisted of two blocks: (1) a block in which the background was flickering; and (2) a block in which the background was steady gray. The order of these two blocks was random. Each session was repeated at least twice.

In the Threshold Experiments, the block using a flickering background consisted of P staircases at a single frequency, where P is the number of phases. For frequencies from 1.2 to 9.4 Hz, P was 8. At the highest frequency (18.8 Hz) there were two different versions for each of which P was 4 (see Section 2.3.3). Trials of the P staircases were intermixed within a block. In the block using a steady background, there was one staircase. Trials of increment and decrement probes were *not* intermixed within a block. Each staircase was 30 trials long. In these experiments there were 12 different types of session: 2 probe polarities × 6 ‘frequencies’ (the four lower frequencies + two versions at the highest frequency).

In the Perceived Polarity Experiments, each block using a flickering background consisted of $P \times 2$ intermixed staircases since increment and decrement probes were intermixed. In the block using a steady background, there were two staircases (one with an increment probe and one with a decrement probe). Each staircase was reduced to 15 trials. In these experiments there were only six different types of session since the probe polarities were intermixed.

In general, the 12 (in the Threshold Experiments) or 6 (in the Perceived Polarity Experiments) different types of sessions were run in a random order. There was a minor exception for the data shown in Fig. 2 on rows 7 and 8: the sessions at frequencies 1.2, 9.4, and 18.8 Hz were run first (randomly intermixed), followed by sessions at 2.3 and 4.7 Hz (randomly intermixed).

2.5. Other experiments

The findings reported below are robust. In other experiments run on four subjects (MR, JC, and two others) we measured probe thresholds but somewhat different stimulus parameters and somewhat different procedures. The stimuli consisted of a 17 ms, 1.25° (approx.) probe on an 18° (approx.) background. The background flickered continually during and between trials. The frequencies of flicker were 0.94, 1.88, 3.75, 7.50, and 15.00 Hz (due to the CRT’s refresh rate of 60 Hz). In these experiments, trials of different phases, polarities and frequencies were *not* intermixed. The thresholds results are nearly identical to the Threshold Experiments’ results shown below and so are not reported here.

An auxiliary set of Threshold Experiments was run to check false alarm rates on two subjects (HH and JC). In these experiments, blank trials (trials without a probe) were randomly intermixed among the probe trials. The proportion of blank trials was 1/9th. For both subjects, the false alarm rates were very low (less than 1%) and did not differ across frequency or probe polarity. The threshold results from these auxiliary experiments did not differ from the results of the Threshold Experiments shown below and so are not reported here.

3. Experimental results

The data are summarized in Figs. 2 and 3. The error bars show ± 2 standard errors (S.E.) of the mean.

Fig. 2 shows the measured probe thresholds plotted as a function of the probe phase; we refer to the resulting curves as *probe-threshold-versus-phase curves*. Thresholds for increment probes are shows as open symbols; thresholds for decrement probes are shown as filled symbols. Increment and decrement probe thresholds on the flickering background are plotted relative to those on a steady gray background. The threshold levels on the steady background are listed in Table 1. Fig. 3 shows the difference between the increment and decrement curves of Fig. 2 on an enlarged scale. In both figures, the upper 3 rows (circle symbols) show data obtained with a flickering background at

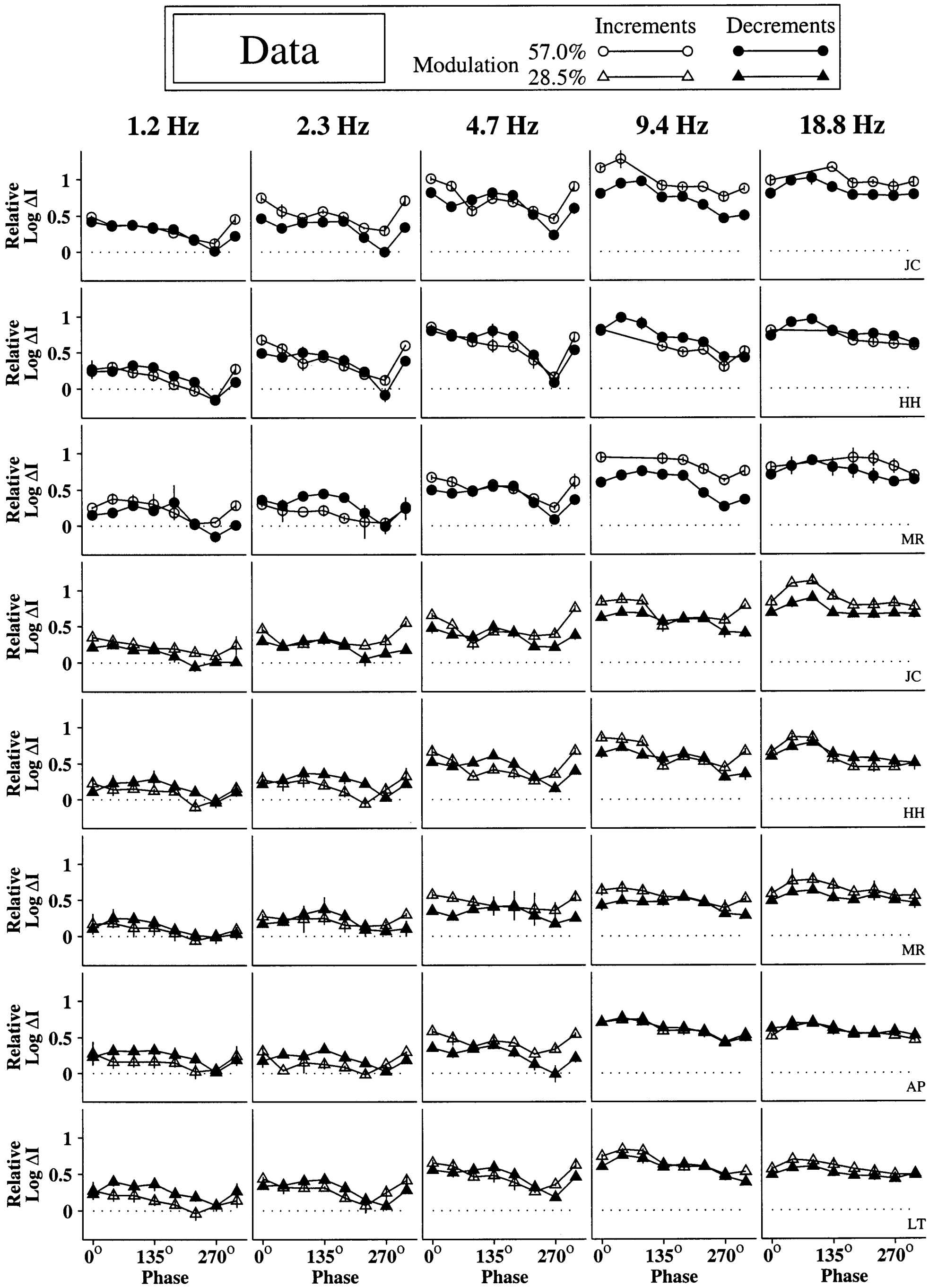

Fig. 2. Probe-threshold-versus-phase curves for increment probes (open symbols) and decrement probes (filled symbols). Error bars show $\pm$ 2 S.E. of the mean. Each column contains data obtained with a different frequency of the flickering background. Each row contains data from a particular subject with a particular flickering background modulation (57% circle symbols, 28.5% triangle symbols). The data in rows 1, 2, 4, and 6 are the threshold measurements from the Perceived Polarity Experiments (in which increment and decrement trials were intermixed). The other rows are from the Threshold Experiments (in which increment and decrement trials were in different blocks). Data points have been omitted when the probe at its maximum possible value was still below the subject's threshold (during one or more of the sessions). Increment and decrement probe thresholds on the flickering background are plotted relative to those on a steady gray background. The dotted horizontal line at 0 represents the probe threshold on a steady gray background (see Table 1 for steady state values). The number of repeated sessions per data point is listed in Footnote 1.

57% modulation, and the lower five rows (triangle symbols) show data obtained with a flickering background at 28.5% modulation. Each row shows data from one subject (at a particular flickering background modulation), and each column shows data from a particular frequency of the flickering background.

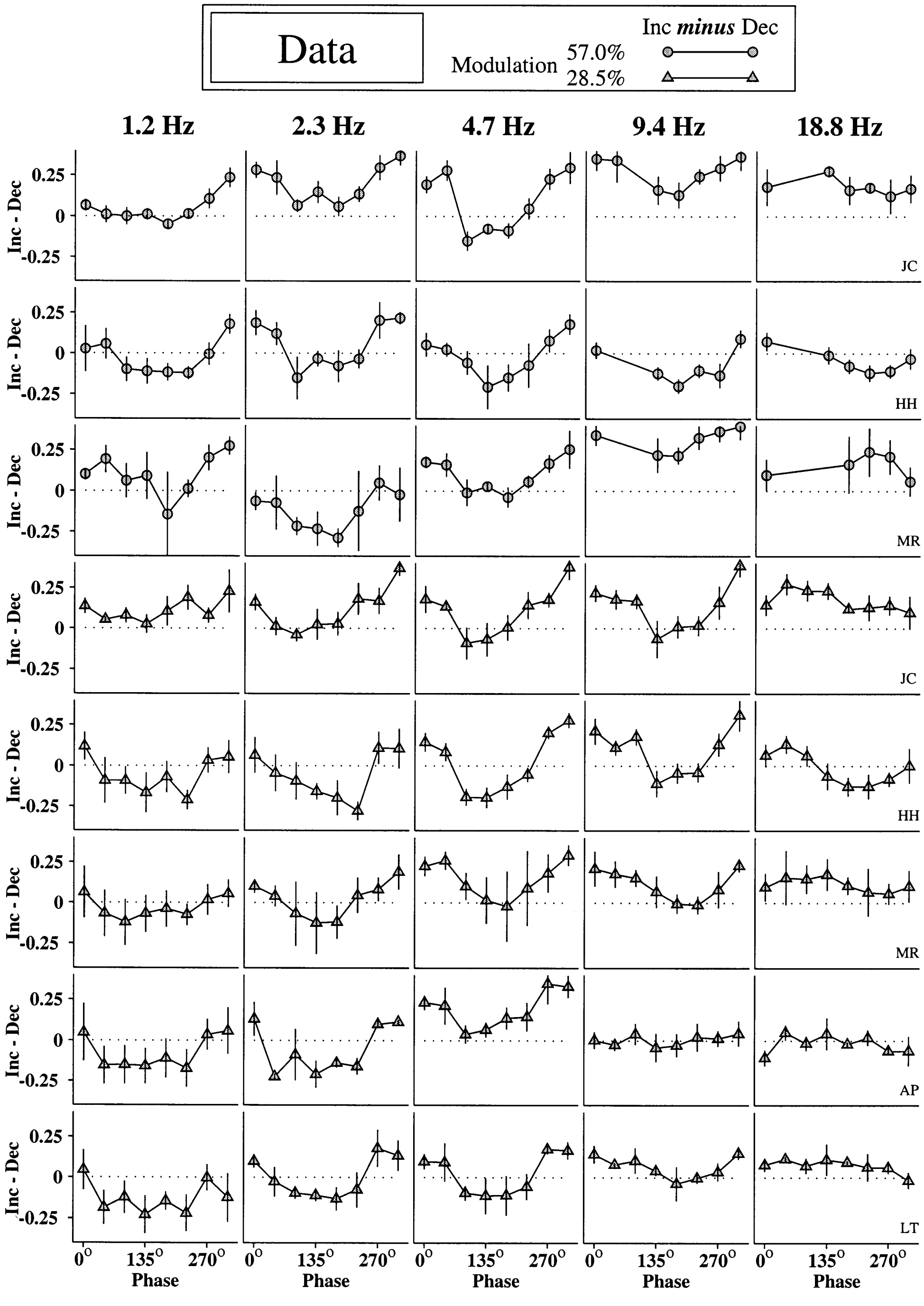

Fig. 3. Difference between increment and decrement probe-threshold-versus-phase curves shown in Fig. 2. Error bars show ±2 S.E. of the mean. Other conventions as in Fig. 2. For frequencies up to 9.4 Hz, the difference curves are generally U-shaped; that is, the thresholds for increments are relatively higher than those for decrements when the intensity of the background is increasing (at phases between 270° and 90°).

Each data point is the average from at least two sessions.[1]

[1] The number of repeated sessions per point in Fig. 2 is listed below. In rows 7 and 8 each point is the average of two sessions (except row 8 at 18.8 Hz increment 'sawtooth' phases which have three sessions). In rows 1, 2, 4, and 6 each point is the average of three sessions. In row 5 each point is the average of four sessions. In row 3, the number of sessions per point varied from 2 to 5 non-systematically due to some scheduling confusion.

These results are discussed in the next several subsections.

3.1. Probe-threshold-versus-phase curve shape

As has been found many times before (Boynton et al., 1961; Shickman, 1970; Maruyama & Takahashi 1977; Hood et al., 1997; Wu, Burns, Elsner, Eskew, & He, 1997; DeMarco et al., 2000; Shady, 1999; Snippe et al., 2000; Wolfson & Graham, 2000), probe threshold varies as a function of phase, as shown in Fig. 2. In our results, probe threshold is generally lowest at approximately 270° and highest between 315° and 45°. The exact shape of the probe-threshold-versus-phase curves varies a great deal in the literature, though at low (e.g. 1 Hz) and high (e.g. 30 Hz) frequencies there is more agreement.

3.2. Increments versus decrements

The probe-threshold-versus-phase curves in Fig. 2 are very similar for increment (open symbols) and decrement (filled symbols) probes. However, there is a small and systematic difference between increment and decrement probe thresholds at all but the highest frequency. This difference is approximately a U-shaped function of phase when plotted as in Fig. 3. In general, increment probe thresholds are *relatively* higher than decrement probe thresholds when the flickering background is increasing in intensity (phases between 270° and 90°, i.e. the ends of the curves).

Our data are fairly consistent with other probed-sinewave increment and decrement data (DeMarco et al., 2000; Snippe et al., 1998). The data are compared in the following two subsections.

Table 1
Background frequency of paired blocks[a]

1.2 Hz	2.3 Hz	4.7 Hz	9.4 Hz	18.8 Hz	
0.018	0.016	0.015	0.015	0.017	JC
0.019	0.024	0.018	0.023	0.023	
0.027	0.022	0.026	0.033	0.027	HH
0.022	0.021	0.022	0.025	0.022	
0.034	0.055	0.034	0.027	0.037	MR
0.044	0.042	0.043	0.050	0.042	
0.014	0.015	0.018	0.016	0.015	JC
0.020	0.021	0.023	0.021	0.020	
0.027	0.033	0.026	0.026	0.032	HH
0.025	0.023	0.026	0.025	0.024	
0.047	0.035	0.032	0.035	0.043	MR
0.053	0.042	0.049	0.047	0.056	
0.026	0.041	0.033	0.031	0.031	AP
0.023	0.034	0.044	0.026	0.024	
0.033	0.031	0.031	0.032	0.033	LT
0.028	0.027	0.026	0.029	0.030	

[a] Steady state probe threshold levels (ΔI) measured on a steady gray background. The number at the top of each column gives the frequency of the flickering background in the blocks paired with the blocks in which the steady state threshold was measured. Each pair of rows corresponds to a panel in Fig. 2. Increment probe thresholds are in the upper row (for each subject); decrement probe thresholds are in the lower row. I is in the range from 0 to 1, where 1 is twice the mean luminance (and the mean luminance is approx. 52 cd/m^2). This is the same scale as was used in Wolfson and Graham (2000) Figs. 5 and 6. Note that all values in a given row of the table were collected under the same conditions but in different sessions; thus, the values in a given row show session to session variability.

3.2.1. DeMarco, Hughes, and Purkiss (2000)

DeMarco et al. (2000), in a subset of their experiments, examined increment and decrement probes on a 1 Hz sinusoidally flickering background (63% modulation, mean illuminance of 741 Td, 570 nm arc lamp source, 2° probe and background surrounded by dark, 12–100 ms probe duration, three subjects). Subtracting their decrement probe thresholds from their increment probe thresholds generally yields U-shaped functions (as does our data at 1.2 Hz in Fig. 3) though the magnitude of the difference (Log ΔI) is generally greater than in our results.

The biggest effect they show is a dramatically higher decrement threshold than increment threshold at 270° (which they call 90°) accompanied by an equal or higher increment threshold (than decrement threshold) at both neighboring phases (225° and 315°, which are their 45° and 135°). We do *not* find this effect; which of the differences between our and their experimental conditions produces this difference in results is unclear.

One major difference between the DeMarco et al. (2000) experiment and the experiments reported here is that of spatial configuration. Their probe was the same size and shape as the background and in the same location. Thus, an observer could not see the probe and background simultaneously so the observer had to compare the probe to the background across time. In experiments like ours — the probe is small and the background is large — the subject can compare the probe to the background at one instant in time. It has been shown in another experimental paradigm that some aspects of results from adaptation experiments are different when the background and test have coincident edges than when the background is much larger than the test (Battersby & Wagman, 1962).

Overall, the agreement between the data is substantial given the differences in the experimental situations: increment thresholds tend to be higher, relative to decrement thresholds, when the probe is presented as the background is increasing in intensity.

3.2.2. Snippe, Poot, and van Hateren (1998)

Snippe et al. (1998 and personal communication) examined increment and decrement probes on a sinusoidally flickering background between 1.56 and 50 Hz (50% modulation, mean illuminance of 7500 Td, yellow-green LEDs, 1° probe, 17° background, 7.5 ms probe duration, two subjects). They only used four

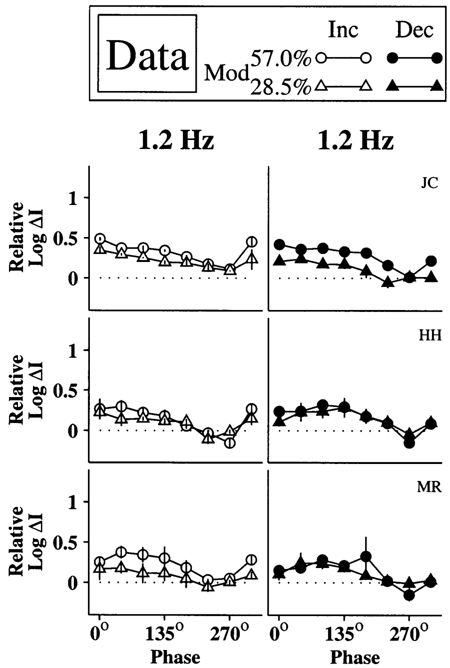

Fig. 4. Comparison of data obtained with 57% flickering background modulation (circle symbols) and 28.5% flickering background modulation (triangle symbols) at 1.2 Hz. Subset of data from Fig. 2. Error bars show ± 2 S.E. of the mean.

phases (0°, 90°, 180°, 270°), so the comparisons one can make are limited. They find differences between increments and decrements which are roughly the same as ours in magnitude (Log ΔI). At their middle frequencies (6.25 and 12.5 Hz), this difference is U-shaped (as in ours). At higher frequencies (25, 33, and 50 Hz) they generally do not find a U-shaped function, nor did we (at 18.8 Hz). The major discrepancy occurs in the low frequency range where the U-shaped function is not clear in their results (1.56 Hz) but is in our results (1.2 Hz).

3.3. dc-level

The average (across phase) of the probe-thresholds (the *dc-level*) increases as frequency increases up to at least 9.4 Hz and is still high at 18.8 Hz. This result can be seen by inspecting the average height of the probe-threshold-versus-phase curves in Fig. 2 from left to right. At the low frequencies, probe threshold sometimes dips below the steady state level (dotted horizontal line), but at the higher frequencies this never happens. In all the studies that have looked at a range of temporal frequencies (at photopic levels of illumination), dc-level has been found to increase over the range from about 0.5 Hz to 10 or 20 Hz and then decrease again at higher frequencies (Shickman, 1970; Maruyama & Takahashi, 1977; Hood et al., 1997; Wu et al., 1997; Snippe et al., 2000; Shady, 1999).

3.4. Reduced background modulation

Decreasing the modulation of the flickering background from 57% to 28.5% slightly reduces the dc-level and peak-trough distance of the probe-threshold-versus-phase curves (which is consistent with Wu et al., 1997). Fig. 4 shows these results for the 1.2 Hz modulating background (a subset of the data from Fig. 2). The error bars show ± 2 S.E. of the mean.

3.5. Perceived Polarity Experiments

Initially we did not intermix increment and decrement probe trials, but subjects reported sometimes perceiving an increment in a decrement block of trials. To document this observation, we ran intermixed increment and decrement trials and had subjects rate their perception of the probe's polarity (the Perceived Polarity Experiments). In Figs. 2 and 3, the threshold results from the Perceived Polarity Experiments are in the 1st, 2nd, 4th, and 6th rows; these results do not look systematically different from the Threshold Experiments (all other rows).

The results documenting the subjects' perception of polarity are shown in Fig. 5 (please ignore the light and dark gray backgrounds for the moment). Plotted on the y-axis is a measure of misperception (increment probe perceived as a decrement probe or vice versa) which is between 0 (no misperceptions) and 30 (maximal misperceptions).[2] As can be seen in Fig. 5 (top row), increment probes are rarely misperceived (open triangles are very near 0 at all phases for both subjects). This result also holds with a 28.5% modulation background (not shown). Decrement probes are occasionally misperceived: in Fig. 5 (bottom row), subject JC's data (filled leftward-pointing triangles) are above 0 at low frequencies at the middle phases. However, subject HH (filled rightward-pointing triangles) does not show many misperceptions. The results with 28.5% modulation (not shown) are similar. Two other subjects who ran less extensively show the same pattern of results as JC.

4. Discussion and summary

In this section we compare our experimental results to predictions from existing models of light adaptation.

[2] After each trial the subject rated their perception of the probe as *definitely decrement* (-2), *probably decrement* (-1), *unknown* (0), *probably increment* (1), *definitely increment* (2). In a block of trials there were 15 trials per phase per probe polarity. The ratings for the incorrectly perceived probes were summed (for a particular phase with a particular probe polarity) and the absolute value was taken, producing a value between 0 and 30. The plotted point is the average of these values across repeated sessions.

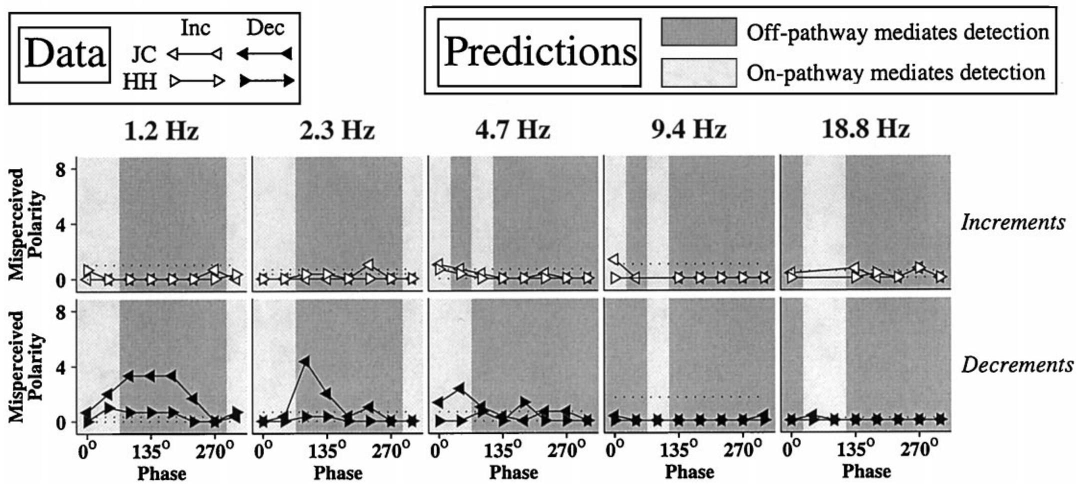

Fig. 5. Perceived Polarity Experiments results and predictions. Data are plotted with symbols; the *y*-axis is a measure of misperceived probe polarity (see text and Footnote 2). Predictions from Wilson's (1997) model are shown as light and dark gray backgrounds: dark gray indicates that the Off-pathway mediates detection in the predictions, and light gray indicates the On-pathway does. The perceived polarity results are not well predicted by which mechanism in Wilson's model mediated detection.

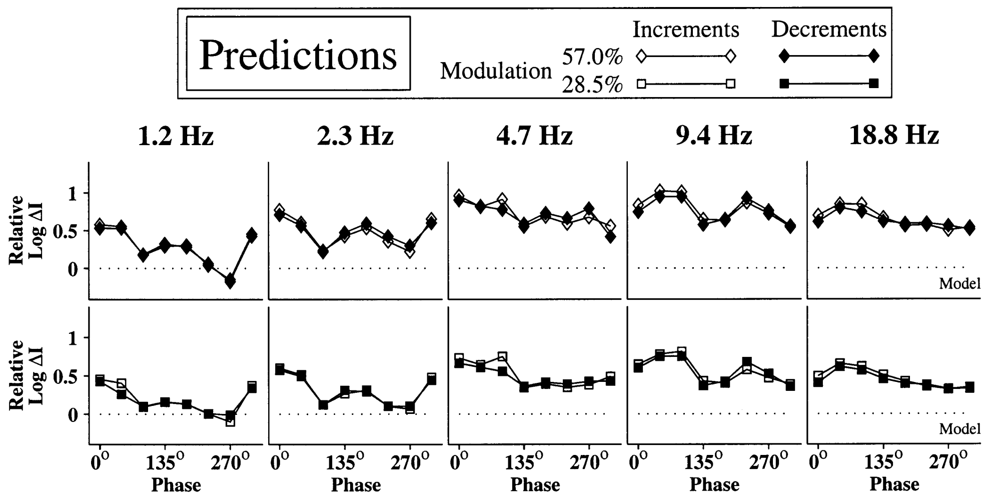

Fig. 6. Predictions from Wilson's (1997) model for increment and decrement probe-threshold-versus-phase curves (open and filled symbols, respectively). The predictions are plotted in the same manner as the data in Fig. 2.

We focus on Wilson's (1997) model which, at the time of this set of experiments, seemed the most promising. First, we present this model's predictions. Next, we discuss several other models, particularly the five models of Hood et al. (1997) and the new model of Snippe et al. (2000), followed by some general modeling implications. We conclude with a summary of the experimental and modeling results.

4.1. Predictions of Wilson's (1997) model

Wilson's (1997) model of light adaptation is a series of differential equations describing the various cells found in the retina. The model is described in Wilson (1997), Hood and Graham (1998), and Wolfson and Graham (2000). We use the exact same parameters as in Hood and Graham (1998), but the parameters describing the stimulus — i.e., the mean luminance (200 Td), probe duration (approx. 13 ms), and temporal profile of the stimulus — were changed to match those actually used in the experiments here.

The predictions shown here (and those shown in Wolfson & Graham, 2000) assumed the sinusoidal flicker was sampled very finely. In fact, however, on the CRT the stimulus is coarsely sampled due to its refresh rate, and has a complicated time-course within each sample. We have computed predictions using various approximations of the actual time-course of the stimuli

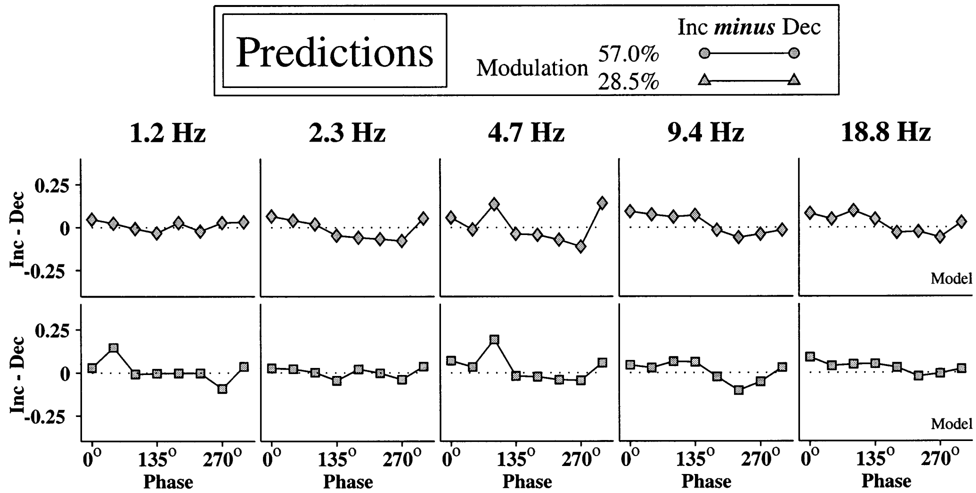

Fig. 7. Difference between predicted increment and decrement probe-threshold-versus-phase curves plotted in Fig. 6. These predictions are plotted in the same manner as the data in Fig. 3.

and these predictions do not differ meaningfully from the predictions presented here.[3]

Figs. 6 and 7 show the predictions from Wilson's (1997) model for the threshold results shown in Figs. 2 and 3, respectively. The model plots are formatted in the same manner as the data plots with the same axes. These predictions are discussed in the next several subsections.

[3] In the predictions shown in Figures 5–8, the time course (the sinusoidal flicker plus the probe increment and decrement) was sampled very finely (every ms). Further the predictions were computed as a function of time only. Implicitly, this is equivalent to integration across space while assuming that space and time are separable dimensions in the model and in the stimuli. However, as mentioned in Section 2.3.2, the CRT stimuli we used had a complicated fine structure. This fine structure might seem of particular relevance to the high-frequency flicker stimuli in which there were only four frames on the CRT per cycle: perhaps effects might occur in response to 'continuous-time' stimuli that would not occur with the time-sampled stimuli we used because they were attenuated by temporal integration. We wished to do some exploration of the possible consequences of this fine temporal structure in the stimuli, and the model provided an opportunity to do so which our equipment did not. Thus, in addition to the predictions shown here, we did two further sets of predictions for all five frequencies with 57% modulation. The first set of predictions is appropriate if adaptation processes are very local: then the input to the model should equal the luminance measured at the center of the probe stimulus as a function of time. For this set of predictions we approximated the time course of the phosphor rise and fall within each 13 ms frame duration by a single cycle of a triangle wave having a full-width at half-height of 3 ms. The second set of predictions is appropriate if adaptation processes are very global: then the input to the model should equal the integrated light over the whole CRT screen as a function of time. For this set of predictions, we approximated the time course of each frame as a rectangular pulse occupying the full duration of the 13-ms frame so the stimulus time course was a series of 13-ms steps. We have not burdened the reader with results from these other two sets of predictions because, although there are small differences between them and also between each of them and the predictions shown here, these differences are non-systematic and affect none of the conclusions here. Notice that the similarity among all three sets of predictions means that, even at the highest frequencies, the time-sampling done in the generation of the stimulus was not sufficient to affect the predictions, presumably because there is so much integration in the model (as in the human visual system).

4.1.1. Probe-threshold-versus-phase curve shape

Fig. 6 shows the model predictions for the probe-threshold-versus-phase curves across frequency and probe polarity. The model predicts quite well the probe-threshold-versus-phase curve at the low frequencies (compare Fig. 6 to Fig. 2 at 1.2 and 2.3 Hz; see also, Hood & Graham, 1998; Wolfson & Graham, 2000). The model also predicts the curve shape fairly well at the highest frequency (compare Fig. 6 to Fig. 2 at 18.8 Hz; see also Hood & Graham, 1998). However, the model generally predicts the wrong shape for the curves at the middle frequencies (e.g. compare Fig. 6 to Fig. 2 at 9.4 Hz). Note that at the middle frequencies there is substantial disagreement among published results.

4.1.2. Increments versus decrements

Wilson's (1997) model does predict that the probe-threshold-versus-phase curves for the increment and decrements probes are very similar (compare Fig. 6 open symbols to filled symbols). The difference between the increment and decrement curves is shown in Fig. 7. These differences show some similarity to the data (Fig. 3): the difference curves (gray symbols) show a small difference between increment and decrement probe thresholds and the shape of the difference curve is generally U-shaped. However, the model predicts a much smaller difference than is generally found and a less consistent U-shape (in particular the model sometimes shows a large difference around 45°–90° which is not seen in the data).

Why does Wilson's (1997) model generally predict a U-shape? In particular, is the existence of two kinds of

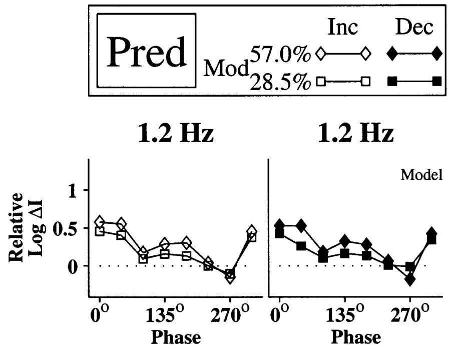

Fig. 8. Predictions from Wilson's (1997) model for probe threshold with 57% flickering background modulation (diamond symbols) and 28.5% flickering background modulation (square symbols) at 1.2 Hz. These predictions are plotted in the same manner as the data in Fig. 4.

pathways (On- versus Off-) crucial? It is not. The U-shape occurs in both the On- and Off-pathway predictions, individually, for the difference curves. The effect in the predicted difference curve for the psychophysical thresholds (Fig. 7) is simply a reflection of the predictions in the individual pathways.

4.1.3. dc-level

Wilson's (1997) model predicts the dc-level quite well. That is, inspecting from left to right in Fig. 6, the average level of the probe-threshold-versus-phase curves increases (possibly flattening out at the highest frequency) as did the dc-level in the data (Fig. 2). The ability of Wilson's model to predict the dc-level of the data is critically dependent on a push–pull interaction between the On- and Off-pathways (see Hood & Graham, 1998; Wolfson & Graham, 2000).

4.1.4. Reduced background modulation

Reducing the modulation of the flickering background in Wilson's (1997) model causes the probe-threshold-versus-phase curves to drop slightly and decreases the peak-trough distance slightly (compare the diamond symbols to the square symbols in Fig. 8). This is similar to the data (compare the circle symbols to the triangle symbols in Fig. 4).

4.1.5. Perceived polarity

One possible simple notion is that increments might usually be detected by the On-pathway and decrements by the Off-pathway. Therefore the perception of the probe's polarity might be controlled by which pathway detected the probe. Thus, probe polarity might be misperceived when detected by the 'wrong' pathway (i.e. an increment probe detected by the Off-pathway). Wilson's (1997) model allows a test of this simple notion since it has separate On- and Off-pathways and which pathway controls detection changes as a function of phase and frequency. In Fig. 5, phases in which the On-pathway controls detection have a light gray background and phases in which the Off-pathway controls detection have a dark gray background. These results contradict the simple notion: the misperception data are *not* predicted by which pathway dominates at any given phase. We have no alternative hypothesis at this point.

Note that the pathway that mediates detection is the same for both increment and decrement probes at most phases (compare the light and dark gray background in the top row of Fig. 5 to the background in the bottom row). In general, at the phases when the On-pathway is in control (light gray background in Fig. 5), increment thresholds are higher than decrement thresholds (Fig. 6). And, similarly when the Off-pathway is in control (dark gray background in Fig. 5), decrement thresholds are higher than increment thresholds (Fig. 6).

4.2. Other models to consider

For the sake of breadth, we computed predictions for the five models from Hood et al. (1997), although these models are known to have problems predicting the data of Hood et al (1997). These five models consist of one model from the periodic tradition, one model from the aperiodic tradition, and three models which merge aspects from both traditions. All five models predict very little difference between increment and decrement probe thresholds (not shown). Indeed, the five models predict less of a difference than Wilson's (1997) model which already underestimates the difference seen in the data. The shapes of the difference curves are vaguely U-shaped for the 'Merged 1' and 'Merged 2' models, but not for the other models. These same models were tested with probed-sinewave timing data by Wolfson and Graham (2000). 'Merged 2' could account for some aspects of the timing data, but the others could not account for the timing data at all. Overall, these five models seem less attractive than Wilson's (1997) model.

Snippe et al. (2000) have a new model of light adaptation which predicts quite well their increment probed-sinewave data. The data fit in Snippe et al. is a set of increment probe results, not the increment and decrement probe results discussed above in Section 3.2.2 from Snippe et al. (1998). Though their experiments (Snippe et al., 2000) were run with a very different setup than our own (80% modulation, mean illuminance of 7500 Td, green LEDs, 46' probe, 17° background, 7.5 ms probe duration, three subjects), their data are generally in agreement with our data. Snippe et al.'s (2000) model predicts both the shape of their probe-threshold-versus-phase curves and the dc-level very well. It is particularly interesting that Snippe et al.'s (2000) model predicts the dc-level well since this model does *not* have both On- and Off-pathways. Recall that for Wilson's (1997) model to predict the dc-level, the existence of both pathways, and the push–pull inhibition between them, is essential. In Snippe et al.'s (2000) model the dc-level is mainly due to a divisive contrast gain control which is activated by the temporal contrast of the background. The predictions from Snippe et al.'s (2000) model for increments versus decrements have not yet been computed. Given the model's success on the increment predictions, it seems worth developing.

4.3. Modeling implications

We have presented two lines of argument suggesting that On- and Off-pathways are not important for explaining the difference between increment and decrement probe thresholds. First, in Wilson's (1997) model, either pathway alone can predict the difference between increment and decrement probe thresholds as well as both pathways together. Second, the perceived polarity results cannot be predicted by which pathway in Wilson's (1997) model mediates detection.

Of course, it is still possible that in some other model or hypothesis, On- and Off-pathways would explain the differences between increments and decrements. But we do not know of any such model at present. Thus, it seems worthwhile to consider another explanation for the difference between increments and decrements.

Consider the different effects increments and decrements might have on some saturating nonlinear process. In the conditions where we find that the increment threshold is raised more than the decrement threshold, the system might be pushed by the flickering background into the saturating region of some nonlinearity. Then an increment probe might push the system even further into saturation, producing an elevated threshold relative to a decrement probe, which might pull it away from saturation.

How does the phase of the difference between increment and decrement thresholds relate to the background phase? Is it in phase with the background, as might be true for an instantaneous effect of the background, or is it out of phase? We find that the greatest difference between increments and decrements is on the upswing of the background. The difference thus leads the background modulation by about 90° (or alternately lags it by 270°).

The differential effect of increments and decrements on a saturating nonlinearity could be the mechanism that leads each pathway in Wilson's (1997) model to predict the difference between increment and decrement probe thresholds. It is also possible that this would lead Snippe et al.'s (2000) model to correctly predict the difference between increment and decrement probe thresholds. Snippe et al. (2000) suggest that high thresholds obtained during the upswing of the background are caused by a saturation (NL_2) following subtractive light adaptation. The increment probes might push the system further up into the saturating part of NL_2, and the decrement probes might pull the system down out of the saturating part of NL_2. This might lead the model to predict the difference between increment and decrement probe thresholds reported here (Snippe, personal communication).

4.4. Summary

4.4.1. Probe-threshold-versus-phase curve shape

We measured detection threshold for increment and decrement probes using the probed-sinewave paradigm with background frequencies in the range of 1.2 Hz to 18.8 Hz (Fig. 2). These results were compared to other published results as well as model predictions. The exact shape of the probe-threshold-versus-phase curves varies a great deal in the literature although at low (e.g. 1 Hz) and high (e.g. 30 Hz) frequencies there is more agreement. Wilson's (1997) model generally does not predict the shape of our probe-threshold-versus-phase curves at the middle frequencies (Fig. 2 vs. Fig. 6). At the middle frequencies, the model of Snippe et al. (2000) predicts the shape of the probe-threshold-versus-phase curves they find quite well, and that shape is similar to the shape we find. Both Wilson's (1997) and Snippe et al.'s (2000) models predict the shapes at the low and high frequencies quite well.

4.4.2. dc-level

The dc-level of the probe-threshold-versus-phase curves measured here increases up to 9.4 Hz and is still quite high at 18.8 Hz. It is known to decrease again at higher frequencies. Both Wilson's (1997) and Snippe et al.'s (2000) models predict this change in dc-level quite well although they do so for quite different reasons. In Wilson's (1997) model the existence of both On- and Off-pathways with push–pull inhibition is critical. In Snippe et al.'s (2000) model, the dc-level change is produced by a contrast gain control stage.

4.4.3. Reduced background modulation

Reducing the modulation of the flickering background from 57% to 28.5% does not change the results much (Fig. 4) as is consistent with the predictions from Wilson's model (Fig. 8).

4.4.4. Perceived polarity

We also measured the perceived polarity of both increment and decrement probes (Fig. 5) and the results did not relate, in a simple way, to which pathway in Wilson's (1997) model mediated detection.

4.4.5. Increments versus decrements

We find that increment and decrement probe thresholds in the probed-sinewave paradigm are quite similar (Fig. 2). However, there is a small and systematic difference between increment and decrement probe thresholds (except at the highest frequency), and this difference is characterized by a U-shaped curve of phase (Fig. 3). That is, increment thresholds are higher relative to decrement thresholds during the part of the cycle when the background intensity is increasing. Wilson's (1997) model generally predicts a U-shape for this difference curve, though the model underpredicts the size of the difference (Fig. 7). Further, the individual On- and Off-pathways in the model each predict a U-shaped difference curve. This prediction might be explained by a saturating nonlinearity within a single pathway. The predictions of Snippe et al.'s (2000) model have not yet been computed for the difference between increment and decrement probes but the presence of a saturating nonlinearity in that model may lead to correct predictions.

Acknowledgements

We would like to thank our subjects for their many hours of participation. We would also like to thank Herman Snippe and Paul DeMarco for giving us copies of their increment and decrement results and useful discussions. Portions of this work were presented at the annual meeting of the Association for Research in Vision and Ophthalmology (Wolfson, Graham, & Chowdhury, 2000). The research was supported by National Eye Institute grants EY08459 to Norma Graham and EY06933 to Sabina Wolfson.

References

Adelson, E. H. (1982). Saturation and adaptation in the rod system. *Vision Research*, *22*, 1299–1312.

Battersby, W. S., & Wagman, I. H. (1962). Neural limitations of visual excitability. IV: spatial determinants of retrochiasmal interaction. *American Journal of Physiology*, *203*, 359–365.

Boynton, R. M., Sturr, J. F., & Ikeda, M. (1961). Study of flicker by increment threshold technique. *Journal of the Optical Society of America*, *51*, 196–201.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 443–446.

Crawford, B. H. (1947). Visual adaptation in relation to brief conditioning stimuli. *Proceedings of the Royal Society B*, *134*, 283–302.

DeMarco, P. J., Hughes, A., & Purkiss, T. J. (2000). Increment and decrement detection on temporally modulated fields. *Vision Research*, *40*, 1907–1919.

Geisler, W. S. (1978). Adaptation, afterimage and cone saturation. *Vision Research*, *18*, 279–289.

Graham, N., & Hood, D. C. (1992). Modeling the dynamics of light adaptation: the merging of two traditions. *Vision Research*, *32*, 1373–1393.

Hood, D. C. (1978). Psychophysical and electrophysiological tests of physiological proposals of light adaptation. In J. Armington, J. Krauskopf, & B. Wooten, *Visual psychophysics: its physiological basis* (pp. 141–155). New York: Academic Press.

Hood, D. C., & Finkelstein, M. A. (1986). Sensitivity to light. In K. R. Boff, L. Kaufman, & J. P. Thomas, *Visual psychophysics: its physiological basis* (chapter 5). New York: Academic Press.

Hood, D. C., Graham, N., von Wiegand, T. E., & Chase, V. M. (1997). Probed-sinewave paradigm: a test of models of light-adaptation dynamics. *Vision Research*, *37*, 1177–1191.

Hood, D. C. (1998). Lower-level visual processing and models of light adaptation. *Annual Review of Psychology*, *49*, 503–535.

Hood, D. C., & Graham, N. (1998). Threshold fluctuations on temporally modulated backgrounds: a possible physiological explanation based upon a recent computational model. *Visual Neuroscience*, *15*, 957–967.

Kelly, D. H. (1961). Visual responses to time-dependent stimuli: II. Single channel model of the photopic visual system. *Journal of the Optical Society of America*, *51*, 747–754.

Krauskopf, J. (1980). Discrimination and detection of changes in luminance. *Vision Research*, *20*, 671–677.

de Lange, H. (1958). Research into the dynamic nature of the human fovea-cortex systems with intermittent and modulated light. *Journal of the Optical Society of America A*, *7*, 2223–2237.

Maruyama, K., & Takahashi, M. (1977). Wave form of flickering stimulus and visual masking function. *Tohoku Psychologica Folia*, *36*, 120–133.

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

Shady, S. (1999). Comparing the dynamic mechanisms of light adaptation of the rod and cone systems: Empirical investigation and theoretical analysis. Doctoral Dissertation. Columbia University, New York, NY.

Shapley, R., & Enroth-Cugell, C. (1984). Visual adaptation and retinal gain controls. In N. N. Osborne, & G. J. Chader, *Progress in retinal research* (pp. 263–343). Oxford: Pergamon Press.

Shickman, G. M. (1970). Visual masking by low-frequency sinusoidally modulated light. *Journal of the Optical Society of America*, *60*, 107–117.

Snippe, H. P., Poot, L., & van Hateren, J. H. (1998). Pulse detection on flickering backgrounds: effects of test pulse polarity. *Perception* (Suppl.), *27*, 52b.

Snippe, H. P., Poot, L., & van Hateren, J. H. (2000). A temporal model for early vision that explains detection thresholds for light pulses on flickering backgrounds. *Visual Neuroscience*, *17*, 449–462.

Watson, A. B., & Pelli, D. G. (1983). QUEST: a Bayesian adaptive psychometric method. *Perception and Psychophysics*, *33*, 113–120.

von Wiegand, T. E., Hood, D. C., & Graham, N. (1995). Testing a computational model of light-adaptation dynamics. *Vision Research*, *35*, 3037–3051.

Wilson, H. R. (1997). A neural model of foveal light adaptation and afterimage formation. *Visual Neuroscience*, *14*, 403–423.

Wolfson, S. S., & Graham, N. (2000). Exploring the dynamics of light adaptation: the effects of varying the flickering background's duration in the probed-sinewave paradigm. *Vision Research*, *40*, 2277–2289.

Wolfson, S. S., Graham, N., & Chowdhury, J. (2000). Increment and decrement probes in the probed-sinewave paradigm. *Investigative Ophthalmology & Visual Science*, *41*, abstract #3788, S712.

Wu, S., Burns, S. A., Elsner, A. E., Eskew, R. T., & He, J. (1997). Rapid sensitivity changes on flickering backgrounds: tests of models of light adaptation. *Journal of the Optical Society of America A*, *14*, 2367–2378.