Asymmetric dynamics of adaptation after onset and offset of flicker

H. P. Snippe
Department of Neurobiophysics, University of Groningen, Groningen, The Netherlands

L. Poot
Department of Neurobiophysics, University of Groningen, Groningen, The Netherlands

J. H. van Hateren
Department of Neurobiophysics, University of Groningen, Groningen, The Netherlands

We measured human psychophysical detection thresholds for test pulses which are superimposed on spatially homogeneous backgrounds that have abrupt onsets and offsets of high-contrast 25 Hz flicker. After the onset of the background flicker, test thresholds reach their steady-state levels within 20-60 ms. After the offset of the background flicker, test thresholds remain elevated above their steady-state level for much longer durations. Adaptation after onsets and offsets of background flicker is modeled with a divisive gain control that is activated by temporal contrast. We show that a feedback structure for the gain control can explain the asymmetric dynamics observed after onsets and offsets of the background contrast. Finally, we measure detection thresholds for tests presented on steadily flickering backgrounds as a function of the contrast of the background flicker. We show that the divisive feedback model for contrast gain control can describe these results as well.

Keywords: contrast adaptation, divisive gain control, feedback model, ideal observer

Introduction

The natural input to the visual system consists of signals that contain large variations not only in local luminance, but also in local contrast (Buiatti & van Vreeswijk, 2003; van Hateren, 1997; Ruderman, 1994). This poses a problem to the visual system because its neurons have a limited dynamic range which may well be smaller than the large variations in the input. The solution to this problem is well known: the visual system has gain controls both for luminance (Crawford, 1947; Fain, Matthews, Cornwall, & Koutalos, 2001; Geisler, 1978; Hayhoe, Benimoff, & Hood, 1987; Perlman & Normann, 1998) and for contrast (Baccus & Meister, 2002; Chander & Chichilnisky, 2001; Rieke, 2001; Shapley & Victor, 1978).

In the present paper our focus is on contrast gain control. When the visual system encounters inputs with low contrast (locally in space and/or time), it will pass these small contrasts with high gain, thus protecting the resulting signals against noise further on in the visual system. However, in an environment with high contrast, such a high contrast gain could well be inappropriate because it would lead to a saturation of the dynamic range that is available to the visual system, and hence to a loss of information. Thus, for these high contrasts it would be beneficial for the visual system to reduce its contrast gain in order to escape such a saturation. A reduction of the contrast gain that is induced by the background yields a reduced visibility of the test signal, compared to the visibility of the same test superimposed on a background with low (or zero) contrast. This reduced visibility for tests presented on backgrounds of high contrast yields detection thresholds for the test signal that are elevated compared to the detection threshold for the test presented on a background with zero contrast. These elevations of test thresholds have been measured using the so-called probe-sinewave paradigm (Hood, Graham, von Wiegand, & Chase, 1997; Snippe, Poot, & van Hateren, 2000; Wu, Burns, Elsner, Eskew, & He, 1997). In these experiments, detection thresholds for brief test pulses superimposed on flickering (spatially homogeneous) backgrounds are measured for various moments of presentation of the test pulse relative to the flicker cycle of the background. Detection thresholds depend on the precise timing of the test pulse relative to the modulation of the background luminance. This dependence can be understood as a consequence of dynamic processes of light adaptation in the visual system (Snippe et al., 2000). When the test thresholds are averaged over a full cycle of the background flicker (to average out these effects of light adaptation), the averaged threshold is systematically elevated above the detection threshold measured for a test pulse superimposed on a steady (nonflickering) background with a luminance equal to the time-averaged luminance of the flickering backgrounds. Snippe et al. (2000) show how this threshold elevation can be explained by a process of contrast gain control in the visual system.
In the present paper, we study the dynamics of such a contrast gain control, by measuring detection thresholds for tests that are presented shortly after an onset of the background flicker (Wolfson & Graham, 2000; Snowden, 2001), and also after the offset of the background flicker (Foley & Boynton, 1993). The comparison of threshold dynamics after the onset and the offset of the background contrast is especially interesting in view of the ideal-observer calculations of DeWeese & Zador (1998). These authors show that a statistically optimal observer can adapt faster after increments of the contrast than after decrements of the contrast. The present measurements are consistent with their prediction for an ideal observer: we find substantially faster adaptation after the onset of the background contrast than after the offset of the background contrast. This match between the psychophysical results and the predictions for the ideal observer strengthens the belief that contrast gain control in the human visual system is functionally appropriate.

Methods

Apparatus and psychophysical procedure

The experimental set-up was identical to that described in Snippe, Poot & van Hateren (2000). Stimuli were presented monocularly through a Maxwellian view system, using two green (563 nm) Toshiba TLGD 190P light-emitting diodes (LEDs) as light sources. One LED provided a spatially homogeneous circular adaptation field of diameter 17°. The other LED was used for foveal presentation of a concentric, sharp-edged test stimulus with a diameter of 46 arcmin and a duration of 7.5 ms. A PC controlled the LED intensities at a rate of 400 Hz, through a 12-bit digital-to-analog converter. The LED outputs were linearized on-line using the photodiode-feedback design of Watanabe, Mori & Nakamura (1992). We collected psychophysical thresholds using a modified yes-no method, as described in Poot, Snippe & van Hateren (1997).

Observers

Eight observers took part in this study, 5 male and 3 female. Ages ranged between 21 and 42 years. Observers used their normal optics to obtain good acuity. All observers were aware of the purpose of the experiments.

Temporal dynamics of the stimuli

In the main experiment, the background stimulus consisted of alternating periods (of duration 1.28 s) of a 25 Hz sinusoidal flicker of 80% contrast, and a constant luminance of 7500 Td equal to the average luminance level of the sinusoid (Figure 1). Brief (7.5 ms) incremental test pulses were superimposed on this background at times \( \tau \) (positive or negative) relative to the beginning or the end of the sinusoidal flicker. Threshold strength for detection of the test pulse was measured as a function of \( \tau \).

Test thresholds were measured for four different versions of the background stimulus (Figure 2). In the different versions the flicker started at a different phase of the sinusoid (0, 90, 180 and 270 deg). This procedure resulted in four detection thresholds for the test at each value of \( \tau \). Because the luminance on which the test pulse is superimposed differs for the four different backgrounds (Figure 2), these four thresholds will be different (typically varying by a factor 2-3 during continuous 25 Hz flicker of 80% contrast; see Figure 1 in Snippe et al., 2000). These differences in thresholds can be understood as effects due to the dynamics of light adaptation (Snippe et al., 2000). However, in the present paper we are interested in dynamic effects of contrast gain control, rather than light adaptation.

![Figure 1. Temporal sequence of the background. A 25 Hz sinusoidal flicker with a contrast of 0.8 is alternated continually with a constant luminance of 7500 Td. Both alternating periods have a duration of 1280 ms.](image)

![Figure 2. The four phase conditions used for the background, here shown with test pulses superimposed at a delay \( \tau = 40 \) ms after the onset of the flicker of the background. The lowest curve (flicker onset at phase 0 deg) shows the luminance as used in the experiments; the other three curves have been vertically displaced for clarity.](image)
duce any effects of light adaptation we average the four thresholds obtained at each value of $\tau$. This allows us to obtain an uncluttered picture of the effects of the onset of the background contrast, independent of the precise luminance conditions of the 25 Hz carrier. The same averaging procedure was performed at contrast offset, since phase effects may still influence the thresholds after flicker has stopped.

We used a modulation frequency of 25 Hz for the background stimulus, because for continuous flicker the elevation of test thresholds is close to maximal at this frequency (Snippe, Poot & van Hateren, 2000). A second reason for choosing a high frequency of the background flicker is that the influence of the discontinuity in luminance which occurs when flicker begins or ends at a phase of 90 or 270 degrees is smaller at high frequencies, because of low-pass filtering early in the visual system (Levinson, 1968). A third reason is that the threshold modulations induced by light adaptation are smaller at 25 Hz than at lower frequencies (Snippe et al., 2000), and thus have less influence on the present results.

Results

Asymmetric dynamics after onset and offset of flicker

In Figure 3, phase-averaged detection thresholds for tests presented around the onset (A) and the offset (B) of the background flicker are shown for two individual observers, and for the results averaged over the 8 observers who performed this experiment. A large asymmetry in the speed of adaptation after the onset and the offset of flicker is evident. After the onset of flicker, thresholds reach their steady state (the phase-averaged threshold level during continuous flicker) within approximately 40 ms. Although not shown in Figure 3, this is the case not only for the phase-averaged thresholds, but also for each of the four phase conditions separately. After the offset of the background flicker, however, thresholds at $\tau = 40$ ms are still much elevated above the steady state level for tests presented on a steady background. Denoting the measured threshold for observer $i$ at time $\tau$ after contrast offset as $M_i(\tau)$, and the

![Figure 3. Detection thresholds for test pulses presented near the onset (A) and the offset (B) of the background flicker for two individual observers (LP and JK), and for the results averaged over all the 8 observers who performed the experiment. The step functions included in each graph indicate the steady-state thresholds: the low level of each step function is the steady-state threshold for a test superimposed on a constant background, and the high level of each step function is the steady-state threshold for a test superimposed on a background with a continuous flicker of contrast 0.8. To reduce scatter in the data for the average observer due to differences in the steady state thresholds of the individual observers, thresholds $M(\tau)$ for the average observer are obtained as follows. First the raw data $M_i(\tau)$ for each observer $i$ are scaled relative to that observer’s steady state thresholds, resulting in scaled data $m_i(\tau) = (M_i(\tau) - M_i^-) / (M_i^C - M_i^-)$, with $M_i^-$ the steady state threshold for that observer obtained with a constant background, and $M_i^C$ the steady state threshold obtained with a flickering background. Next, at each delay $\tau$ the scaled data $m_i(\tau)$ are averaged over observers. Finally, to facilitate comparison of these averaged data to the data obtained for the individual observers, the averaged data $m(\tau)$ are rescaled to $M(\tau) = M^- + (M^C - M^-) m(\tau)$, with $M^-$ and $M^C$ the observer-averaged steady state thresholds. Note the logarithmic scale of the vertical axis, and the different time scales of the horizontal axes.]
steady-state threshold of this observer for a test presented on a steady background as \( M_i \), the normalised threshold elevation \( E_i(\tau) \) above the steady state level can be quantified as

\[
E_i(\tau) = \frac{M_i(\tau) - M^-}{M^-}.
\]  

At \( \tau = 40 \) ms after contrast offset, threshold elevations \( E_i(40) \) for our observers range from 1.3 to 3.5; the arithmetic mean of their threshold elevations is \( 2.2 \pm 0.3 \) (SE; \( n = 8 \)).

A further asymmetry between adaptation after contrast onset and offset is that steady state is reached only during the “on” period of the contrast stimulus and not during the “off” period. After the onset of contrast, thresholds reach steady state within approximately 40 ms. But after the offset of contrast, a slow adaptation component appears to take over after about 80 ms, and the threshold curves flatten. At \( \tau = 640 \) ms after contrast offset, threshold elevations \( E_i(640) \) above the steady-state level are still quite high (range \( E_i(640) = 0.1-0.7 \); mean \pm s.e.m. = 0.38 \pm 0.08). Thresholds do not further decline much below the level obtained at \( \tau = 640 \) ms within the remaining 640 ms of steady background before flicker is switched on again.

Threshold recovery after contrast offset does not behave as a simple exponential decay (Figure 4, dashed lines). Instead (Figure 4, full lines), a power law recovery produces an excellent fit to the data at \( \tau \geq 20 \) ms:

\[
E(\tau) = \left( \frac{\tau_1}{\tau} \right)^\gamma.
\]  

The value of the power exponent \( \gamma \) ranges approximately between 0.5 and 1 for our observers (Table 1).

<table>
<thead>
<tr>
<th>Observer</th>
<th>( \gamma )</th>
<th>( \tau_1 ) (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RV</td>
<td>0.67\pm0.06</td>
<td>90\pm5</td>
</tr>
<tr>
<td>HS</td>
<td>1.06\pm0.07</td>
<td>116\pm12</td>
</tr>
<tr>
<td>LP</td>
<td>0.62\pm0.12</td>
<td>104\pm18</td>
</tr>
<tr>
<td>JB</td>
<td>0.57\pm0.07</td>
<td>273\pm61</td>
</tr>
<tr>
<td>JK</td>
<td>0.63\pm0.08</td>
<td>92\pm10</td>
</tr>
<tr>
<td>JH</td>
<td>0.63\pm0.14</td>
<td>153\pm42</td>
</tr>
<tr>
<td>LT</td>
<td>1.06\pm0.06</td>
<td>63\pm8</td>
</tr>
<tr>
<td>SW</td>
<td>0.54\pm0.08</td>
<td>84\pm12</td>
</tr>
<tr>
<td>Average Observer</td>
<td>0.65\pm0.05</td>
<td>122\pm9</td>
</tr>
</tbody>
</table>

Table 1. Estimates of the parameters \( \gamma \) and \( \tau_1 \) in Equation 2. Values shown are means and SDs of the power exponent \( \gamma \) and the time-parameter \( \tau_1 \) in Equation 2 for each of the individual observers, and for the average observer defined in the Caption of Figure 3.

Figure 4. Threshold elevation (Equation 1) as a function of the time \( \tau \) after the offset of the background flicker for two individual observers, and for the results averaged over all observers. In accordance with Equation 1, the threshold elevation \( E(\tau) \) for the average observer is \( E(\tau) = (M(\tau) - M^-)/M^- \), with \( M(\tau) \) and \( M^- \) defined in the legend of Figure 3. The straight lines are the best power-law fits (Equation 2) to the data. Exponential functions (dashed lines) yield unacceptable fits to the data.
Control experiments

Tapered contrasts

Some of our observers show overshoots of their thresholds for test pulses presented at times near the onset and offset of the contrast (e.g., Figure 3A, LP). This could be caused by luminance artifacts due to the abrupt (instantaneous) onset and offset of the contrast (Levinson, 1968). To test this possibility, we repeated the experiment for observer HS, but now using a more gradual (tapered) onset and offset of the flicker contrast:

\[ C_{on}(t) = \frac{1}{2} C \left( 1 + \sin 2\pi \frac{t}{T} \right), \quad -\frac{T}{4} \leq t \leq +\frac{T}{4} \]  

(3)

\[ C_{off}(t) = \frac{1}{2} C \left( 1 - \sin 2\pi \frac{t}{T} \right), \quad -\frac{T}{4} \leq t \leq +\frac{T}{4}. \]  

(4)

Between \( t = -T/4 \) and \( t = +T/4 \), for \( C_{on}(t) \) the flicker contrast gradually increases from 0 to its full value \( C = 0.8 \). Likewise, at flicker offset \( C_{off}(t) \) gradually decreases from \( C = 0.8 \) at \( t = -T/4 \) to \( C = 0 \) at \( t = +T/4 \). We used \( T = 120 \) ms, which should be sufficient to remove any luminance artifacts due to the onset and offset of the contrast. Nevertheless, detection thresholds for the test pulse show overshoots at the contrast onset and offset also for these tapered contrasts (Figure 5). Also the asymmetric dynamics of thresholds after contrast onsets and offsets is equally strong for tapered and non-tapered (instantaneous) contrast switches. Thus we conclude that the asymmetric dynamics reported in Figure 3 is not caused by potential artifacts due to the instantaneous onsets and offsets of flicker contrast.

Noise carriers

The long tail of threshold elevation at contrast offset in our experiments could be a peculiarity of using a harmonic signal (25 Hz flicker) as the contrast carrier. To check the robustness of the result, one of the observers (RV) measured test thresholds after the offset of a background contrast of which the luminance values were samples of Gaussian noise, rather than harmonic modulations. Sample time (10 ms) and r.m.s. contrast (0.57) of the luminance noise were chosen such that during the noise, test thresholds were on average close to the phase-averaged threshold obtained with continuous 25 Hz flicker. As shown in Table 2, at 80 ms and 320 ms after the offset of the noise, threshold elevations above the steady-state for zero contrast are somewhat larger than after the offset of 25 Hz flicker (a difference that is not accounted for in the models that we present later in this paper). However, from the experiment we can conclude that the long tail of threshold elevations after the offset of stimulus contrast is not limited to backgrounds with harmonic flicker. Further, since the offset of noise is free from luminance artifacts (Koenderink & van Doorn, 1978), the present results confirm that the long-term elevation of thresholds after the offset of harmonic flicker is not due to a luminance artifact for these stimuli.

<table>
<thead>
<tr>
<th>( \tau ) (ms)</th>
<th>flicker</th>
<th>noise</th>
</tr>
</thead>
<tbody>
<tr>
<td>80 ms</td>
<td>1.09±0.12</td>
<td>1.45±0.14</td>
</tr>
<tr>
<td>320 ms</td>
<td>0.49±0.08</td>
<td>0.89±0.11</td>
</tr>
</tbody>
</table>

Table 2. Threshold elevations \( E(\tau) \). Values shown are means and SDs of the threshold elevations \( E(\tau) \), defined in Equation 1, for observer RV at two delays \( \tau \) after the offset of background flicker, respectively background noise.

Contrast increments and decrements

In the first part of the Results we reported asymmetric dynamics of adaptation after contrast onsets and offsets, i.e. contrast steps in which the low contrast equals zero. To test whether this result generalises to contrast steps in which the low contrast is unequal to zero, two of our observers measured test thresholds after contrast increments (from \( C \)
test thresholds have reached the steady state, but at these times \( \tau \) the test thresholds are still substantially elevated above the steady state level after a decrement step of the background contrast. Thus asymmetric adaptation occurs not only after contrast onsets and offsets, but also more generally after contrast increments and decrements.

**Divisive gain control**

In this Section we present models for contrast gain control that can explain the psychophysical results. Our aim here is not to obtain a detailed quantitative correspondence with the psychophysical data. Rather, we concentrate on explaining the main trends of the present data with simple divisive models for contrast gain control. In divisive gain control, the output \( O(t) \) of the gain control equals the input \( I(t) \) divided by the control (adaptation) signal \( A(t) \):

\[
O(t) = \frac{I(t)}{A(t)}.
\]

Divisive gain control has been observed both in the retina (Baccus & Meister, 2002; Berry, Brivanlou, Jordan, & Meister, 1999; Kim & Rieke, 2001; Wilke, Thiel, Eurich, Greschner, Bongard, Ammermüller, & Schwegler, 2001) and in the visual cortex (Albrecht, Geisler, Frazor, & Crane, 2002; Carandini, Heeger, & Movshon, 1997). A further reason to study divisive models for contrast gain control is that the divisive control signal \( A(t) \) has a particularly simple relation to the thresholds \( p(t) \) measured for the test pulse in our psychophysical experiments. When a test pulse \( p \) is superimposed on a background \( I \), the resulting output of the divisive gain control equals \( (I + p)/A \). Hence the extra output \( \Delta O \) generated by the test pulse \( p \) equals \( p/A \). Using the traditional assumption (Fechner, 1860; Meier & Carandini, 2002) that the test pulse attains its detection threshold \( M \) when it generates a fixed extra output \( \Delta O \) at detection threshold

\[
\Delta O = \frac{M}{A} = \text{constant.}
\]

Thus the detection threshold \( M \) of the test pulse will be proportional to \( A \), the value of the divisive gain control. Hence we can relate the dynamics \( M(t) \) for the detection thresholds measured in our experiments to the dynamics of the adaptation signal \( A(t) \) in a model of divisive gain control.

Does the adaptation signal \( A(t) \) in a divisive gain control structure have the asymmetric dynamics that we see in our experiments: faster response at contrast onset than at contrast offset? Actually, it does not for a simple feedforward gain control (Figure 7a) in which the dynamics of \( A(t) \) is governed by the contrast \( C(t) \) of the input signal \( I(t) \):

\[
t_0 \frac{dA}{dt} = C_I(t) - A(t).
\]
The form of Equation 7 is such that $A(t)$ is a low-pass filtered version of $C(t)$. This can be readily seen by Fourier transforming the equation, yielding $1/(1 + i\omega \tau_o)$ as the transfer function between the frequency domain versions of $C$ and $A$. Equation 7 yields identical dynamics for $A(t)$ (an exponential response with time constant $\tau_o$) at the onset and the offset of the contrast $C(t)$. This would still be the case if a small positive constant $\varepsilon$ would be added to the right-hand-side of Equation 7 (such that $A$ attains a finite steady-state value $\varepsilon$, rather than zero, for a constant background $C_I = 0$). Although the resulting dynamics of adaptation is symmetric for these simple feedforward models, more complicated models for feedforward gain control can certainly respond with asymmetric dynamics to contrast onsets and offsets. However, rather than exploring such feedforward models, we will concentrate on a feedback structure (Victor, 1987) for contrast gain control (Figure 7b). In such a feedback structure the dynamics of the adaptation signal $A(t)$ is governed by the contrast $C(t)$ of the output $O(t)$ of the gain control loop, rather than by the contrast $C(t)$ of the input $I(t)$. The reason for exploring feedback structures is that they show asymmetric behavior already for a simple first order dynamics of $A(t)$:

$$\tau_o \frac{dA}{dt} = C(t) - A(t).$$

Equation 8

Using the divisive nature of the gain control: $C(t) = C(t)/A(t)$, Equation 8 can be rewritten by multiplying both sides of the equation with $A(t)$, and using the identity $A \frac{dA}{dt} = 1/2 A^2 \frac{dA}{dt}$:

$$\frac{1}{2} \tau_o \frac{dA^2}{dt} = C(t) - A^2(t).$$

Equation 9

Figure 7. Schematic feedforward (a) and feedback (b) divisive models for contrast gain control. The boxes labeled ‘Demodulation’ perform a demodulation of the flicker present in $I(t)$ respectively $O(t)$. The boxes labeled ‘LP’ perform a low-pass filtering of the resulting contrast signal. This yields $A(t)$, the adaptation signal that divides the input $I(t)$ to produce the output $O(t) = I(t)/A(t)$ of the gain control loop.

Equation 9 shows that for the first-order feedback dynamics of Equation 8, the square $A^2(t)$ of the adaptation signal $A(t)$ is a low-pass filtered version (with time constant $\tau_o / 2$) of the input contrast $C(t)$, hence

$$A(t) = [C(t)]_{\text{low-pass}}^{\frac{1}{2}}.$$

Equation 10

The solid lines in Figure 8 show that the dynamics of the resulting adaptation $A(t)$ is asymmetric for onset versus offset steps in the input contrast $C(t)$. The asymmetric dynamics for $A(t)$ seen in Figure 8 can be simply explained. At contrast onset the adaptation $A(t)$ is initially low, hence the output contrast $C(t) = C_I/A(t)$ is large (representing an overshoot in $O(t)$). This provides an especially strong drive to the dynamics in Equation 8. At contrast offset there is no similarly strong undershoot in the output contrast $C(t)$, which explains the observed asymmetry in $A(t)$ seen in Figure 8.

Although the solution (Equation 10) of Equation 8 reacts fast at contrast onset, there is still a discrepancy of its response at contrast offset when compared with our psychophysical results. After a contrast offset ($C(t) = C_I = 0$ for $t > 0$), the solution $A(t)$ of Equation 8 is an exponential: $A(t) = A(0) \exp(-t/\tau_o)$, which does not provide a good fit to our data (see Figure 4). However, by only slightly modifying the structure of Equation 8 we can obtain a low-pass filtering which yields the observed power-law behavior:

$$\tau_o \frac{dA^n}{dt} = C^n(t) - A^m(t).$$

Equation 11

Note that Equation 8 represents a special case of Equation 11, with $n = m = 1$. However, contrary to Equation 8, for $m > 1$ Equation 11 has a power-law solution for $A(t)$ after

Figure 8. Dynamics $A(t)$ of the gain control after onsets (from $C = 0$ to $C = 1$; increasing curves $A(t)$) and offsets (from $C = 1$ to $C = 0$; decreasing curves $A(t)$) of the contrast. The solid lines are the solutions of Equation 8. The dashed (dotted) lines are the solutions of Equation 11 with respectively $n = m = 2$ and $n = m = 3$. The parameter $\tau_o$ in Equations 8 and 11 has been set to 100 ms.
contrast offset:
\[ A_{\text{eff}}(t) = \frac{A(0)}{\left(1 + (m-1) \cdot A(0)^{-(m-1) \cdot t/\tau_0}\right)^{1/(m-1)}}. \] (12)

For large enough \( t \), the recovery of \( A_{\text{eff}}(t) \) in Equation 12 behaves as a power law \((1/t)^{1/(m-1)}\), thus (by using Equation 6) a power-law recovery with power exponent \(1/(m-1)\) is predicted for the test thresholds. Therefore, \(1/(m-1)\) corresponds to the steepness parameter \( \gamma \) defined in Equation 2 (strictly speaking, Equation 1 is not defined for the present model because \( M_i = 0 \), but this can be easily resolved by adding a small constant to the adaptation signal \( A(t) \) in Figure 7b). The typical range 0.5-1 obtained for \( \gamma \) in the psychophysical experiments thus corresponds to values \( m = 2 - 3 \) in Equation 11. The dashed and dotted lines in Figure 8 show the solution of Equation 11 to steps of the input contrast \( C(t) \), for the choice \( n = m = 2 \), respectively \( n = m = 3 \). The response dynamics is much faster after a contrast onset than after a contrast offset, and the response to the contrast offset shows a prolonged elevation as was seen in the psychophysical data. To further understand the behavior of Equation 11, note that for \( n = m = 2 \) its right-hand-side can be rewritten as \([C_0(t) + A(t)][C_0(t) - A(t)]\). Hence, dividing both sides of Equation 11 by \( C_0(t) + A(t) \), it can (for \( n = m = 2 \)) be rewritten as
\[ \frac{\tau_0}{C_0(t) + A(t)} \frac{dA}{dt} = C_0(t) - A(t). \] (13)

Hence for \( n = m \) the adaptation signal \( A \) increases in proportion to the square root of the flicker contrast \( C_f \). For \( n < m \) the relation between \( A \) and \( C_f \) would be more compressive than a square root, and for \( n > m \) it would be less compressive (i.e. more linear).

In order to test these predictions, we obtained detection thresholds for test pulses presented on backgrounds with steady flicker as a function of flicker contrast \( C_f \) for four observers. Thus in this experiment, contrary to Figure 1, the flicker now was “on” throughout the duration of the experiment. As in the previous experiments, we determined detection thresholds for the test pulse presented at four moments in the flicker cycle of the background (at phase 0, 90, 180 and 270 degrees). Reported (phase-averaged) thresholds are the mean of these four thresholds.

Figure 9 shows the phase-averaged threshold as a function of the flicker contrast \( C_f \) for two observers. Results for the other two observers who performed this experiment were similar, as were results for observer SW obtained for two different values of the flicker frequency (\( f = 6.25 \) Hz and \( f = 12.5 \) Hz). As expected from Equation 14, thresholds are a compressive function of the flicker contrast \( C_f \) over most of the contrast range. An exception are the re-

Detection thresholds for pulses on backgrounds with steady contrast

As was shown above, threshold recovery after the offset of contrast constrains the power exponent \( m \) of \( A(t) \) in Equation 11 to values \( m = 2 - 3 \). Estimates of the power exponent \( n \) of \( C_0(t) \) in Equation 11 can be obtained from the steady-state behavior \((dA/dt = 0)\) of Equation 11 that is attained for backgrounds with a steady contrast \( C_i \) (i.e. with steadily flickering backgrounds). Using the relation \( C_0 = C_i /A \), the steady-state solution of Equation 11 is
\[ A = C_i^{n/(n+m)}. \] (14)

\[ \text{Figure 9. Detection thresholds for two observers for tests presented on continuously flickering backgrounds, as a function of the flicker contrast of the background. Solid lines are the fits of the model of Figure 10 (Equation 15). Parameters of the fits: SW, } \sigma = 0.24, n/m = 0.94; \text{ JB, } \sigma = 0.12, n/m = 0.78. \]
sults at low \( C_l \) \((C_l \leq 0.05)\), where the threshold function is accelerating, rather than compressive. This behavior can be accommodated in a divisive feedback structure for contrast gain control by assuming that the output \( O(t) \) of the divisive gain control consists of a deterministic part \( I(t)/A \) plus an additive noise \( N(t) \) with standard deviation \( \sigma \) (see Figure 10). Then, assuming that the noise \( N(t) \) is uncorrelated with \( I(t)/A \),

\[
C_o = \sqrt{\left(\frac{C_l}{A}\right)^2 + \sigma^2}.
\]  

(15)

Figure 10. A dynamic model for contrast gain control that includes an internal noise \( N(t) \) after the divisive gain control.

The model of Figure 10 yields a non-zero value \( \sigma \) for the adaptation signal \( A \) when the contrast \( C_l \) at the input equals zero (i.e. for a non-flickering background). An alternative (and closely related) way to obtain a non-zero \( A \) at zero input contrast would be to include an additive constant in the feedback path of Figure 10. Each of these possible elaborations of the model of Figure 7b would prevent a division by zero when the input contrast \( C_l \) becomes zero for long durations. The lines in Figure 9 show that the model of Figure 10 can provide a good fit to the data over the complete range of flicker contrast \( C_l \). Using Equation 15, we determined the values for \( n/m \) in Equation 11 that yield optimal (minimal \( \chi^2 \)) fits to the steady-state data. Results as shown in Table 3 indicate that on average \( n/m \approx 1 \), hence \( n \approx m \). Altogether we conclude that a feedback structure for divisive gain control, as indicated by Equation 11 with \( n \approx m \approx 2-3 \), can explain both dynamic and steady-state results of contrast adaptation.

## Discussion

### Adaptation after contrast onsets

Fast adaptation after the onset of contrast was shown in previous psychophysical experiments. Wu et al. (1997) show that detection thresholds for brief test pulse reach steady state approximately 10-30 ms after the onset of a 9.4 Hz flicker of the background. Snowden (2001) shows that the detection thresholds for a 10 ms test pulse reach a steady plateau within 100 ms of the onset of a 16 Hz flicker of the background. From a theoretical analysis of their data, Foley and Boynton (1993) conclude that adaptation (desensitization) after the onset of background contrast occurs on a time-scale of 10-50 ms. These timescales of adaptation after the onset of contrast are similar to our results in Figure 3a. From their results on contrast discrimination under dynamic contrast conditions, Dannemiller and Stephens (1998, 2000) conclude that contrast gain control is much slower, with an integration time of at least 125 ms. However, in their model Dannemiller and Stephens take into account only the effects of the spatial contrast of their adapting stimuli, and ignore the temporal contrast that is induced by the instantaneous switch between adapting stimuli with different spatial contrast. It can be shown that when this temporal contrast is taken into account, the results of Dannemiller and Stephens are in fact fully compatible with a fast contrast gain control. Fast gain control after contrast onsets has also been observed in physiological studies, both in the retina (Baccus & Meister, 2002) and in the visual cortex (Albrecht et al., 2002).

### Adaptation after contrast offsets

In comparison to adaptation after the onset of contrast, adaptation is slower after the offset of contrast. At \( \tau = 640 \) ms after the offset of a flicker that had a duration of 1280 ms, we still find threshold elevations \( E = 0.1 - 0.7 \). Similar threshold elevations are reported in Figure 4 of Foley and Boynton (1993) after the offset of flicker of durations of 200 ms and 2000 ms. That the dynamics of adaptation is slower after decrements of contrast than after increments of contrast was predicted by DeWeese and Zador (1998) for ideal observers. In fact, in Snipe and van Hateren (2003) we show that the dynamics of adaptation after the offset of contrast seen in our experiments is close to what would be expected for an ideal (statistically efficient) estimate of the

<table>
<thead>
<tr>
<th>Observer</th>
<th>( n/m )</th>
<th>( m )</th>
<th>( n )</th>
</tr>
</thead>
<tbody>
<tr>
<td>SW</td>
<td>0.94±0.15</td>
<td>2.85±0.28</td>
<td>2.68±0.50</td>
</tr>
<tr>
<td>JB</td>
<td>0.75±0.08</td>
<td>2.75±0.22</td>
<td>2.07±0.28</td>
</tr>
<tr>
<td>HS</td>
<td>1.37±0.18</td>
<td>1.94±0.06</td>
<td>2.66±0.36</td>
</tr>
<tr>
<td>RV</td>
<td>0.65±0.13</td>
<td>2.49±0.13</td>
<td>1.62±0.39</td>
</tr>
</tbody>
</table>

Table 3. Estimates of the power exponents \( n \) and \( m \) in Equation 11. Values shown are means and SDs for four observers of the power exponents \( n \) and \( m \) in Equation 11, and of their ratio \( n/m \). The estimates for \( n/m \) are determined from the fit of Equation 15 to the psychophysical data obtained with steady contrasts of the background. The estimates for \( m \) are determined from the estimates of \( \gamma \) in Table 1, using the relation \( \gamma = 1/(m - 1) \), hence \( m = 1 + (1/\gamma) \). Finally, \( n \) is estimated from the values of \( n/m \) and \( m \) as \( n = (n/m) \times m \).
background contrast. However, it is known that for human observers the speed of recovery from adaptation decreases with increasing duration of the adapting contrast (Greenlee, Georgeson, Magnussen, & Harris, 1991; Rose & Lowe, 1982). It is at present unclear if this aspect of recovery from contrast adaptation can also be understood from the ideal-observer calculations of DeWeese & Zador (1998).

**Demodulation of flicker**

Contrast C describes the size of the fluctuations of a signal \( S(t) \) around its mean. We assume that the mean of \( S(t) \) equals zero, which is reasonable if \( S(t) \) is a signal in the visual system at a stage when processes of subtractive light adaptation and/or temporal high-pass filtering have occurred. Then a dynamic contrast \( C(t) \) for \( S(t) \) can be defined by writing \( S(t) = C(t)s(t) \), a product of a carrier signal \( s(t) \) with zero mean and unit variance and a contrast envelope \( C(t) \). Extracting the contrast \( C(t) \) of a signal \( S(t) \) hence amounts to demodulating the effects of the carrier \( s(t) \). Such a demodulation can be approximately attained in various ways. Perhaps the simplest way is through a full-wave rectification of \( S(t) \) (Victor, 1987). A more precise demodulation can be obtained by combining \( S(t) \) with its first and second order temporal derivatives (Snippe et al., 2000).

Yet another method of demodulation combines \( S(t) \) with its Hilbert transform (quadrature partner) \( S_H(t) \), by using the relation \( C(t) = (S^2(t) + S_H^2(t))^{1/2} \) (Adelson & Bergen, 1985; Klein & Levi, 1985; Morrone & Owens, 1987). Because the Hilbert transform is not a causal operation, an exact Hilbert transform cannot be implemented in real time. However, a causal Hilbert transform can be approximated using band-pass filters. In the present paper, we have suppressed the exact form of the demodulation operation, since the qualitative dynamics of Equation 11 (including the asymmetry at contrast onsets and offsets) does not depend on the method used for demodulation. A fully quantitative model for contrast gain control, however, would have to specify the operation used for demodulation.

**Effects of contrast on the temporal response function**

In the present paper we model contrast adaptation with a divisive gain control in which the output \( O \) of the gain control equals the input \( I \) divided by the gain control signal \( A \), i.e. \( O = I/A \). In fact, however, it is known that contrast gain control acts not only through a divisive operation, but also through a change of the temporal response of the visual system. Contrast speeds up the visual system (Baccus & Meister, 2002; Benardete, Kaplan, & Knight, 1992; Chander & Chichilnisky, 2001; Kim & Rieke, 2001; Shapley & Victor, 1978; Stromeyer & Martini, 2003). To keep the modeling as simple as possible, we have ignored this dependence. Ignoring the effect of contrast on the shape of the temporal response function has the advantage that it yields a simple relation (Equation 6) between the psychophysical detection thresholds \( M \) and the adaptation signal \( A \) in the model. Including the effects of contrast on the shape of the pulse response would necessitate a description of which aspect of the response to the test pulse (e.g. the peak, variance, area, etc.) is most important for its detection. When such a more quantitative model would be desired, however, the effects of contrast on the temporal response can be incorporated by assuming that the relation between the output \( O \) and the input \( I \) of the contrast gain control is dynamic, rather than simply divisive. For instance, \( O \) could be an adaptively low-pass filtered version of \( I \) (Carandini & Heeger, 1994; Fuortes & Hodgkin, 1964; Sperling & Sondhi, 1968):

\[
\tau_L \frac{dO}{dt} = I - AO .
\]

Note that a gain control that is purely divisive, \( O = I/A \), corresponds to a value \( \tau_L = 0 \) in Equation 16. Alternatively, \( O \) could be an adaptively high-pass filtered version of \( I \) (Victor, 1987):

\[
\tau_H \frac{dO}{dt} = \frac{dI}{dt} - AO .
\]

Assuming that the adaptation signal \( A \) is related to \( O \) through Equation 11, both Equation 16 and Equation 17 can yield an adaptation after contrast onsets and offsets that is asymmetric, similar to the results shown in Figure 8 for a purely divisive contrast gain control. A quantitative analysis of the effects of Equations 16 and/or 17 on the detectability of brief test pulses, however, is beyond the aim of the present paper.

**Conclusions**

We have shown that adaptation after onsets of flicker is much faster than adaptation after offsets of flicker. This behavior of human observers is in good accord with theoretical predictions for statistically optimal observers (DeWeese & Zador, 1998; Snippe & van Hateren, 2003). The asymmetric dynamics of adaptation after onsets and offsets of contrast can be implemented in a natural way using a feedback structure for contrast gain control.

**Acknowledgements**

We wish to thank our observers Johan Kruseman, René van der Veen, Lila Thymiati, Sri Wahyuni and Joep Bontemps for their input during the experiments. Commercial relationships: none.

Corresponding author: H. P. Snippe;
email: h.p.snippe@phys.rug.nl.
References


