Contrast Gain Reduction in Fly Motion Adaptation

Robert A. Harris, David C. O’Carroll,* and Simon B. Laughlin†
Department of Zoology
University of Cambridge
Downing Street
Cambridge, CB2 3EJ
United Kingdom

Summary

In many species, including humans, exposure to high image velocities induces motion adaptation, but the neural mechanisms are unclear. We have isolated two mechanisms that act on directionally selective motion-sensitive neurons in the fly’s visual system. Both are driven strongly by movement and weakly, if at all, by flicker. The first mechanism, a subtractive process, is directional and is only activated by stimuli that excite the neuron. The second, a reduction in contrast gain, is strongly recruited by motion in any direction, even if the adapting stimulus does not excite the cell. These mechanisms are well designed to operate effectively within the context of motion coding. They can prevent saturation at susceptible nonlinear stages in processing, cope with rapid changes in direction, and preserve fine structure within receptive fields.

Introduction

Sensory neurons have a limited signaling range but must code stimulus intensities that may vary over many orders of magnitude. For example, adaptation in retinas shifts the operating range of photoreceptors and neurons to match the prevailing stimulus distribution, thus improving coding efficiency (Shapley and Enroth-Cugell, 1984; Laughlin, 1994). Similar adaptive processes operate in higher-order neurons, but the mechanisms and functions of these processes are less clear. Motion-selective neurons adapt upon exposure to high image velocities (Maddess and Laughlin, 1985; Giaschiet al., 1993; Ibbotson et al., 1998; Mather et al., 1998). What strategies does the visual system use to modify the response properties of motion-sensitive cells?

Motion-sensitive HS cells in the fly lobula plate are particularly amenable for studies of motion processing. We can work with the same readily identifiable neurons in every experiment, which have well-defined roles in the animal’s behavior (Hausen, 1993). Behavioral and electrophysiological studies in many animals, including the fly, indicate that a correlation-based mechanism is used to detect image motion (Hassenstein and Reichardt, 1956; Reichardt, 1961; Barlow and Levick, 1965; Buchner, 1984; van Santen and Sperling, 1985; Wolf- Oberhollenzer and Kirschfeld, 1994). The responses of HS cells are consistent with them being driven by a retinotopic array of correlation-based elementary motion detectors (EMDs; Buchner, 1984).

In flies, prolonged exposure to high image velocities reduces the response magnitude of lobula plate cells and increases their sensitivity to changes in image velocity (Maddess and Laughlin, 1985). Similar changes are observed psychophysically in humans (Thompson, 1981; Clifford and Langley, 1996; Bex et al., 1999). These experiments suggest that adaptation shifts and rescales the operating range of motion-sensitive cells (Maddess and Laughlin, 1985) to match the statistics of the stimulus velocity distribution, so maximizing information transmission (Brenner et al., 2000).

Previous authors suggested that motion adaptation (in insects and mammals) shifts the operating range of the motion pathway to higher image velocities by shortening the delay filter in the EMDs (de Ruyter van Steveninck et al., 1986; Borst and Egelhaaf, 1987; Clifford et al., 1997). However, our recent study (Harris et al., 1999) found little change in the temporal and spatial tuning properties of fly motion-sensitive cells following adaptation, showing that motion adaptation does not significantly alter the inherent velocity optimum of the EMDs. What mechanism does underlie motion adaptation?

Here we demonstrate that motion adaptation induces a profound decrease in the contrast sensitivity of fly motion-sensitive cells. There are two major components of this adaptation: first, an after-potential, antagonistic to recent activity in the cell; second, a contrast gain reduction that is only recruited by moving patterns but is direction insensitive. The two components thus have distinct properties that suggest adaptation at two separate locations in the motion pathway.

Thus, the motion pathway adapts to high speeds not by shifting its inherent tuning in the stimulus (i.e., velocity) domain but by changing its sensitivity to a separate stimulus parameter, image contrast. There are striking parallels between motion adaptation in fly neurons and motion-sensitive units in the mammalian visual system, suggesting that common principles may govern the neural coding of motion in diverse species.

Results

Cell Responses
Intracellular recordings were made from HS cells in the lobula plate of the dronefly *Eristalis tenax* (see Experimental Procedures). Because HS cells respond to visual stimuli with graded changes in membrane potential rather than spikes, we can observe changes in response properties without the severe nonlinearity imposed by a spike threshold. Depending on the direction of motion, visual stimuli depolarize or hyperpolarize HS cells by up to ±12 mV relative to the cell’s resting potential (Figures 1A and 2). Depolarizing graded responses are accompanied by small spikelets that are the result of active so-
The direction tuning of HS is approximately sinusoidal (Hausen, 1982; see also Figure 6B). The largest depolarizing responses are elicited by horizontal progressive (front-to-back) motion, termed the “preferred direction.” The largest hyperpolarizing potentials are elicited by motion in the opposite direction, called here the “anti-preferred direction” and also the “null direction” (Hausen and Egelhaaf, 1989).

Maddess (1986) found evidence for an afterimage mechanism in the fly visual system. Following exposure to stationary or very slowly moving patterns, the afterimage causes profound changes to the response characteristics of wide-field cells (e.g., oscillating responses in response to moving gratings; Maddess, 1986). To avoid the confounding effects of this phenomenon, we only used gratings with moderate or high temporal frequencies (5 Hz or above) in all the experiments described here. A detailed analysis of afterimage effects in hoverfly HS cells is forthcoming (Harris et al., unpublished data).

Contrast Sensitivity before and after Motion Adaptation

Figure 1B plots the response of HS cells to sinusoidal gratings of different contrasts before and after motion adaptation. Both the test and adapting stimuli moved in the preferred direction.

Before and after adaptation, the cell shows a sigmoidal relationship between response and log contrast. The unadapted cell responds to contrasts as low as 4% and saturates at around 20%. Adaptation reduces the contrast sensitivity of the cell. We read from these curves the contrast required to elicit a criterion response from the cell before and after adaptation. The ratio of these contrasts gives the proportional change in contrast sensitivity induced by adaptation, denoted as $\Delta CS_{\text{total}}$ (Figure 3; Table 1).

We used criterion response levels equal to 10% and 50% of the maximum unadapted response level (Figure 1B). Before adaptation, the 10% criterion response (typically found in the range 1–1.5 mV) was elicited by a grating of 5% contrast. After adaptation, a grating of 22% contrast was required, giving a 4.4-fold decrease in overall contrast sensitivity, $\Delta CS_{\text{total}, 10\%} = 4.4$.

Taking similar measurements for the 50% criterion level (around 6 mV), we find a similar decrease in sensitivity, $\Delta CS_{\text{total}, 50\%} = 4.7$.

Three obvious changes in the contrast-response function reduce the contrast sensitivity. (1) Contrast gain reduction: the sigmoidal curve relating response and log contrast is shifted to the right. (2) After-potential: adaptation also induces an after-hyperpolarization. This shifts the contrast-response function vertically downward, decreasing the cell’s contrast sensitivity because a higher contrast is required to elicit a particular criterion response from the cell following adaptation. In Figure 1B, this hyperpolarization is $\sim 1.5$ mV and leaves the cell hyperpolarized relative to its unadapted resting level up to test contrasts of around 25%. (3) Output range...
Table 1. Summary of Changes in Contrast Sensitivity of HS Cells following Adaptation with Motion and Flicker Stimuli

<table>
<thead>
<tr>
<th>Test Stimulus</th>
<th>Adapting Stimulus</th>
<th>ΔCS&lt;sub&gt;total&lt;/sub&gt; 10%</th>
<th>ΔCS&lt;sub&gt;total&lt;/sub&gt; 50%</th>
<th>ΔCS&lt;sub&gt;part&lt;/sub&gt; 10%</th>
<th>ΔCS&lt;sub&gt;part&lt;/sub&gt; 50%</th>
<th>Proportion of Overall Reduction in Contrast Sensitivity Attributable to Gain Reduction 10%</th>
<th>Proportion of Overall Reduction in Contrast Sensitivity Attributable to Gain Reduction 50%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Figure 1 Preferred</td>
<td>Preferred</td>
<td>4.4</td>
<td>4.7</td>
<td>3.4</td>
<td>3.5</td>
<td>71%</td>
<td>68%</td>
</tr>
<tr>
<td>Figure 2 Preferred</td>
<td>Preferred</td>
<td>4.9</td>
<td>6.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.1</td>
<td>3.0</td>
<td>54%</td>
<td>39%</td>
</tr>
<tr>
<td>Preferred Anti-Preferred</td>
<td></td>
<td>1.2</td>
<td>2.6</td>
<td>2.7</td>
<td>3.0</td>
<td>N/A&lt;sup&gt;a&lt;/sup&gt;</td>
<td>N/A&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Anti-Preferred</td>
<td>Preferred</td>
<td>N/A&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.2</td>
<td>4.0</td>
<td>3.5</td>
<td>N/A&lt;sup&gt;a&lt;/sup&gt;</td>
<td>N/A&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Figure 4</td>
<td>Preferred</td>
<td>4.5</td>
<td>4.6</td>
<td>3.6</td>
<td>3.4</td>
<td>74%</td>
<td>66%</td>
</tr>
<tr>
<td>Preferred</td>
<td>Wide-Field Flicker</td>
<td>1.5</td>
<td>1.7</td>
<td>1.3</td>
<td>1.5</td>
<td>60%</td>
<td>71%</td>
</tr>
<tr>
<td>Preferred</td>
<td>Local Flicker</td>
<td>1.9</td>
<td>1.6</td>
<td>1.8</td>
<td>1.6</td>
<td>88%</td>
<td>100%</td>
</tr>
<tr>
<td>Figure 5</td>
<td>Preferred</td>
<td>4.0</td>
<td>3.8</td>
<td>2.8</td>
<td>2.7</td>
<td>60%</td>
<td>61%</td>
</tr>
<tr>
<td>Preferred</td>
<td>Orthogonal</td>
<td>4.0</td>
<td>3.5</td>
<td>3.8</td>
<td>3.4</td>
<td>93%</td>
<td>96%</td>
</tr>
</tbody>
</table>

Experimental data shown in Figures 1–6. ΔCS<sub>total</sub> represents the decrease in the cell’s contrast sensitivity after adaptation, evaluated at criterion response levels of 10% and 50% of the maximum response (see main text and Figure 3). ΔCS<sub>part</sub> is the decrease in contrast sensitivity that can be attributed to the contrast gain reduction alone, i.e., after accounting for the effects of the after-potential. Also shown (final column) is the proportion of the total contrast sensitivity change that can be attributed to the gain reduction (see Equation 2 and main text).

<sup>a</sup>Indicates an unusually large value of CS<sub>total, 50%</sub>, where the hyperpolarizing after-potential depresses the response such that the 50% maximum response level is only attained in the heavily saturated region of the contrast-response function (see Figure 2A, open circles).

<sup>b</sup>Indicates a condition where the value of ΔCS<sub>total, 10%</sub> cannot be defined because the hyperpolarizing after-potential following adaptation depresses the membrane potential below the criterion response level.

<sup>c</sup>Indicates two conditions where it is inappropriate to express ΔCS<sub>part</sub> as a proportion of ΔCS<sub>total</sub> because the after-potential increases the cell’s effective contrast sensitivity and thus acts in opposition to the gain reduction.

Reduction: the output response range of the cell is also reduced following adaptation. Before adaptation, responses to preferred direction motion typically ranged from 0 mV to 11 mV, a total extent of 11 mV. Following adaptation, however, responses typically ranged from −1.5 mV to 6.5 mV, an extent of only 8 mV.

The adapted contrast-response function can be expressed as a transformation of the unadapted contrast-response function, R<sub>unadapted</sub> (contrast):

\[
R_{adapted} (\text{contrast}) = a + b \cdot R_{unadapted} (\text{contrast} \cdot c)
\]

where the variables a, b, and c correspond to the after-potential, output range reduction, and contrast gain reduction, respectively.

This description is a phenomenological classification of the changes associated with motion adaptation. It does not suggest that the three factors are necessarily independent or have different physiological origins. In the next section, we present evidence that the after-potential and contrast gain reduction are the result of two separate adapting mechanisms in the motion pathway.

Contrast Sensitivity for Preferred and Anti-Preferred Direction Motion

Figure 2 shows that a large contrast gain reduction (a rightward shift of the log contrast-response function) is induced irrespective of the direction of motion (preferred or anti-preferred) during either the test or adapting periods.

However, the after-potential induced by adaptation (evident at test contrasts below 10%) depends on the direction of the adapting grating. Preferred direction adaptation depolarizes the cell during the adapting period and, as in Figure 1B, induces a hyperpolarizing after-potential (Figures 2A and 2B, open circles). Conversely, anti-preferred motion hyperpolarizes the cell during the adapting period and induces a weak depolarizing after-potential (typically <0.25 mV; Figures 2A and 2B, open squares). Thus, the after-potential component of adaptation is direction sensitive. All adapting conditions also reduce the total output range of the cell to between 70% and 84% of the unadapted level.

Thus, adaptation to motion in either the preferred or anti-preferred direction reduces the system’s contrast gain (rightward shift of the curve), but the after-potential depends on the direction of the adapting stimulus. This difference indicates that the gain reduction and after-potential are consequences of two different adapting mechanisms in the motion pathway.

Relative Contributions of the Gain Reduction and After-Potential

Given that the gain reduction and after-potential reflect two separate adapting mechanisms, we can estimate their relative contributions to the change in contrast sensitivity. We assume that the overall decrease in contrast sensitivity is primarily the result of rigid vertical downward and horizontal rightward shifts of the curve, attributed to the after-potential and contrast gain reduction components, respectively. Because both the after-potential and contrast gain reduction are likely to have more complex effects on the contrast-response function, this is a first approximation. For example, if the
after-potential were due to an increase in membrane conductance, this would necessarily also decrease the cell’s input-output gain. Our analysis also ignores the small contribution of the output range reduction (see Discussion).

Given these provisos, we determine the relative contributions by evaluating the contrast sensitivity of the cell after correcting for the presence of the after-potential. Consider the experimental data of Figure 1B. The dashed line shows the adapted contrast-response function normalized so that responses to subthreshold contrasts (<3% for the data in Figure 1B) have a mean value of zero. We can now use this “corrected” curve to find the contrast required to elicit the 10% and 50% criterion response levels (Figure 3). Since we have eliminated the after-potential (vertical shift), we obtain the reduction in contrast sensitivity attributable to the “contrast gain reduction” alone (termed $\Delta CS_{\text{gain}}$).

The criterion contrasts on the corrected curve (Figure 1B, dotted line) give $\Delta CS_{\text{gain}}$, 10% = 3.4 and $\Delta CS_{\text{gain}}$, 50% = 3.5. Notice that the total reduction in contrast sensitivity including the after-potential ($\Delta CS_{\text{total}}$) was only around 4.5-fold (see above). The proportion of the total change in contrast sensitivity attributable to the gain reduction is given by:

$$\frac{C_{\text{corrected}} - C_{\text{unadapted}}}{C_{\text{adapted}} - C_{\text{unadapted}}}$$  \hspace{1cm} (1)

where $C_{\text{unadapted}}$ and $C_{\text{adapted}}$ are the contrasts eliciting the criterion response level before and after adaptation, respectively, and $C_{\text{corrected}}$ is the criterion contrast measured from the “corrected” contrast curve (Figure 3). Equation 1 can be rewritten as:

$$\frac{\Delta CS_{\text{gain}} - 1}{\Delta CS_{\text{total}} - 1}$$  \hspace{1cm} (2)

Applying Equation 2, we find that the gain reduction component of adaptation (responsible for the rightward shift of the curve) accounts for ~70% of the change in contrast sensitivity following adaptation with preferred direction motion (see Table 1).

We apply the same analysis to determine whether the magnitude of the contrast gain reduction varies with the direction of the adapting or test stimuli (Figure 2). The results are summarized in Table 1. The magnitude of the contrast gain reduction is similar for all four conditions. On average, the adapting grating induces a 3.5-fold reduction in the system’s contrast gain, irrespective of the direction of motion (preferred or anti-preferred) during either the test or adapting periods.

Note that the proportions calculated only apply to the particular test and adapting stimulus used in our experiments (i.e., drifting sinusoids, 4 s adapting duration at 95% contrast, 20 Hz temporal frequency, and 0.02 cycles/'). The relative contributions of the after-
potential and gain reduction components could depend on the stimuli used.

**Is the Contrast Gain Reduction Driven by Flicker?**
A moving pattern causes local changes in contrast (i.e., flicker) that could reduce the contrast gain. Figure 4 compares the log contrast-response functions of HS cells adapted to either a moving grating, wide-field flicker, or a counter-phasing grating that induces only local flicker. All adapting stimuli had the same temporal frequency and contrast (20 Hz, 95%). The zero-crossings of a stationary counter-phasing grating do not change contrast, so to ensure that all parts of the receptive field were exposed to flicker, the counter-phasing grating was also jumped 90° of spatial phase every two cycles (alternating directions on each jump).

Wide-field and local flicker stimuli induce smaller changes in the contrast-response function of the cell than are induced by the moving grating (Figure 4). Adaptation with preferred direction motion produces a 4.5-fold reduction in contrast sensitivity (consistent with the results of Figure 1B), but adaptation with wide-field or local flicker produces a smaller change, averaging 1.7-fold (see Table 1).

Adaptation with flicker also induces hyperpolarizing after-potentials (Figure 4), although smaller in magnitude than those induced by preferred direction motion. Correcting for the after-potential and calculating ΔCS\text{gain} (Table 1), the contrast gain reduction component of adaptation accounts for ~80% of the total change in contrast sensitivity induced by wide-field or local flicker.

In summary, flicker (local changes in contrast) reduces the contrast sensitivity of the motion pathway, primarily by reducing the system’s contrast gain, but the gain reduction is much smaller than that induced by visual motion of the same temporal frequency and contrast.

**Adaptation with Orthogonal Motion**
Given that the contrast gain reduction is only weakly recruited by flicker (Figure 4) but strongly recruited by both preferred and anti-preferred direction motion (Figure 2), is it also driven strongly by motion in other directions? We measured the contrast-response function before and after adaptation with gratings moving at 90° or 270° to the preferred direction of the cell (termed “orthogonal motion”). Orthogonal motion induces almost no response in the wide-field cell during the adapting period but causes a large reduction in the magnitude

\[
\Delta \text{CS}_{\text{total}} = \frac{C_{\text{adapted}} - C_{\text{unadapted}}}{C_{\text{unadapted}}}
\]

\[
\Delta \text{CS}_{\text{gain}} = \frac{C_{\text{corrected}}}{C_{\text{unadapted}}}
\]

**Figure 3.** Method Used to Quantify Changes in the Cell’s Contrast Sensitivity following Adaptation
The total change in the cell’s contrast sensitivity (ΔCS\text{total}) is given by the ratio of the contrasts required to elicit a criterion response before and after adaptation (C\text{adapted} divided by C\text{unadapted}). We also estimated the change in contrast sensitivity attributable to the “gain reduction” component of adaptation only (ΔCS\text{gain}) (i.e., the component causing the rightward shift of the curve on the log contrast axis). The after-potential is removed by normalizing the adapted curve such that the mean of the subthreshold responses is zero (giving the dashed curve). ΔCS\text{gain} is then determined by taking the ratio of C\text{corrected} to C\text{unadapted}.

**Figure 4.** Contrast-Response Function of HS Cells following Adaptation to Motion or Flicker
Mean and standard errors before adaptation (closed circles, n = 33 trials, 20 cells), after adaptation with preferred direction motion (sinusoidal grating, 20 Hz, 0.1 cycles/°, 95% contrast) (open circles, n = 15 trials, 12 cells), adaptation with wide-field flicker (sinusoidal modulation at 20 Hz, 95% contrast) (open squares, n = 8 trials, 7 cells), and adaptation with local flicker (counter-phasing sinusoidal grating, 95% contrast, 0.1 cycles/°, 20 Hz, see main text) (open triangles, n = 7 trials, 4 cells). Each cell’s responses were normalized to an unadapted resting potential of 0 and a maximum unadapted response of 1.
of response to a subsequent preferred direction test stimulus (Figure 5A). Orthogonal motion induces a large change in the cell’s overall contrast sensitivity similar to that produced by preferred direction adaptation (Figure 5B). A slight hyperpolarizing after-potential is evident after orthogonal adaptation, less than that induced by preferred direction adaptation, but of similar magnitude to that induced by adaptation to flicker (Figure 4). Unlike preferred direction adaptation, orthogonal adaptation does not reduce the final saturation level of the cell.

Table 1 shows that adaptation with orthogonal motion induces a 4-fold decrease in the cell’s overall contrast sensitivity, approximately the same as adaptation with preferred direction motion. Isolating the gain reduction component of adaptation (Figure 3), orthogonal motion has a slightly stronger effect than preferred direction motion, amounting to around a 3.5-fold reduction in contrast gain ($\Delta CS_{\text{gain,}\,10\%} = 3.8$ and $\Delta CS_{\text{gain,}\,50\%} = 3.4$; Table 1). Applying Equation 2, the contrast gain reduction component accounts for $\approx 90\%$ of the total reduction in the cell’s sensitivity following orthogonal adaptation, compared to $60\%$ for preferred direction adaptation.

To confirm that motion presented in any direction causes a similar reduction in the system’s contrast gain, we recorded the responses of a single HS cell to a preferred direction moderate contrast ($30\%$) test grating before and after adaptation with gratings moving in different directions (Figure 6A). All directions of adapting motion cause a similar reduction in response to the test grating, indicating that all adapting directions induce a similar reduction in the system’s contrast sensitivity (Figure 6B).

As expected, adaptation with gratings close to the preferred direction of the cell (around $180^\circ$ in Figure 6B) causes a slightly greater reduction in response magnitude because the response following adaptation reflects the presence of the direction-sensitive after-potential as well as the direction-insensitive contrast gain reduction.

Properties of the After-Potential
The after-potential is antagonistic to the response induced by the adapting stimulus (Figure 2). To see whether the amplitude of the after-potential is related to the level of the cell’s response, we examined data from experiments that followed the same protocol shown in Figure 1A. We plotted the initial response to the first test grating against the after-potential elicited when this stimulus was replaced with a blank mean luminance screen (analysis windows illustrated in Figure 7A). The test stimulus was varied in either contrast (7B), temporal frequency (7C), spatial frequency (7D), or direction (7E).

All four conditions reveal a similar antagonistic relationship between the test-potential and after-potential.
In all conditions, the larger the depolarizing test-potential, the larger the antagonistic (hyperpolarizing) after-potential. The correlation in each condition is highly significant (p < 0.001; see Table 2) with a slope, by linear regression, of approximately -0.15 mV/mV. A homogeneity test (Edwards, 1976) shows that there is no significant difference between the slopes in the different conditions. Thus, our data suggest that, irrespective of how the response is varied, the relationship between depolarizing test-potentials and hyperpolarizing after-potentials is the same to a first approximation.

For stimuli that elicit hyperpolarizing test-potentials, the after-potentials are small and difficult to interpret. For temporal frequency (Figure 7C) and direction (Figure 7E), there is no clear correlation between test-potential and after-potential. The contrast condition (Figure 7B) shows a weak but significant correlation with a shallow slope of -0.05 mV/mV (Table 2). In the spatial frequency condition (Figure 7D), we only used preferred direction motion. We cannot exclude the possibility that depolarizing after-potentials induced by varying grating contrast (Figure 7B) have different properties from the other stimulus conditions. However, any putative relationship between hyperpolarizing test-potentials and depolarizing after-potentials is clearly weak. Thus, similar trends may be hidden in the temporal frequency and direction conditions (Figures 7C and 7E).

The large scatter in the data set may obscure other relationships between the adapting stimulus and the after-potential. In particular, our preliminary investigations indicate that there may be an additional dependency of the after-potential on the temporal and spatial frequency of the adapting stimulus. More extensive experiments using longer adapting periods will be required to establish all of the factors that influence the magnitude of the after-potential.

We conclude that there is currently little evidence to indicate a difference in the after-potentials induced by different types of visual stimuli. The amplitude of the after-potential is correlated with the amplitude of the response produced by the adapting stimulus. Thus, the mechanism for generating after-potentials shows a similar sensitivity to visual stimulus parameters as the HS cell itself, although hyperpolarizing after-potentials are much larger than depolarizing after-potentials.

**Discussion**

We have described three changes in the response functions of wide-field motion-sensitive cells induced by motion adaptation: an after-potential (evidenced as a vertical downward shift of the log contrast-response function), a contrast gain reduction (a horizontal right-
ward shift in the log contrast-response function), and a reduction in the cell’s output response range.

Previous authors have described a gain control mechanism in the fly motion pathway that causes the responses of wide-field cells to be largely independent of stimulus size (Hausen, 1982; Reichardt et al., 1983; Egelhaaf, 1985). This size-dependent mechanism is different from the gain reduction component of motion adaptation described here because it does not generate a steady decay in neural responses during stimulus presentation. Recent work suggests that it is a direct consequence of the wide-field cells taking separate inputs from two mirror-symmetric EMD subunits (Borst et al., 1995; Single et al., 1997).

Table 2. Relationship between Test-Potentials and After-Potentials in HS Cells

<table>
<thead>
<tr>
<th>Stimulus Condition</th>
<th>Hyperpolarizing Test Potentials</th>
<th>Depolarizing Test Potentials</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>r</td>
</tr>
<tr>
<td>Contrast</td>
<td>101</td>
<td>-0.39</td>
</tr>
<tr>
<td>Temporal frequency</td>
<td>48</td>
<td>-0.16</td>
</tr>
<tr>
<td>Spatial frequency</td>
<td>130</td>
<td>—</td>
</tr>
<tr>
<td>Direction</td>
<td>105</td>
<td>0.08</td>
</tr>
</tbody>
</table>

Correlation and linear regression analysis for the data shown in Figure 7. After-potentials induced by hyperpolarizing and depolarizing test-potentials were analyzed separately for each of the four stimulus conditions. Bold type indicates a correlation coefficient (r) significantly different from zero, (r = 0, two-tailed t test, p < 0.001). If r is significant, the linear regression coefficient (slope) is also shown. A homogeneity test (Edwards, 1976) of the slopes for depolarizing test-potentials (far right column) suggests that they are drawn from the same population (F test, degrees of freedom: 3 and 665, p > 0.1).
After-Potentials

The amplitude of the after-potential is closely correlated with the response induced by the adapting stimulus (Figure 7), but it is not clear whether the after-potential is causally dependent on the activity induced during the adapting period or even if the after-potential necessarily originates in the HS cell itself. Further experiments are required to clarify these issues. However, our observations suggest that the after-potential is recruited whenever the cell is driven, irrespective of the particular visual properties of the stimulus (spatial frequency, temporal frequency, contrast, or direction). This is consistent with a purely activity-dependent form of adaptation: the greater the depolarizing activity induced during the adapting period, the larger the hyperpolarizing after-potential.

Antagonistic aftereffects following adaptation have previously been reported in blowfly wide-field cells, and as found in our study, those following preferred direction stimuli were stronger than those following anti-preferred direction stimuli (Srinivasan and Dvorak, 1979; de Ruyter van Steveninck et al., 1986; Dürr, 1998).

What is the origin of the after-potential? Dürr (1998) found a positive correlation between the accumulation of intracellular calcium during the adapting period and the magnitude of the after-potential, and suggests that the after-hyperpolarization may be mediated by calcium-activated potassium conductances in the wide-field cell. This is consistent with our observation that hyperpolarizing after-potentials are closely related to the membrane potential evoked during the adapting period (Figure 7), because calcium accumulation is itself positively correlated with membrane depolarization (Egelhaaf and Borst, 1995; Dürr, 1998). We also found that adaptation with flicker (Figure 4) or orthogonal motion (Figure 5) induces a weak hyperpolarizing after-potential. As far as we are aware, no studies have examined calcium accumulation in response to flicker or orthogonal motion.

Calcium accumulation in HS cells is probably not associated with the other components of adaptation. The contrast gain reduction, output range reduction, and depolarizing after-potential can all be induced by adaptation with anti-preferred motion (Figures 2A and 2B, open squares), which causes no change in the intracellular calcium concentration of wide-field cells (Egelhaaf and Borst, 1995; Dürr, 1998).

Output Range Reduction

The origin of the reduction in the output (voltage) range of the cell following adaptation is unclear. It does not appear to be related to the contrast gain reduction component of adaptation because adaptation with flicker or orthogonal motion induces a profound reduction in contrast sensitivity without a clear reduction in the cell’s final saturation level (Figures 4 and 5). However, the cell’s response range does decrease after adaptation to either preferred or anti-preferred direction motion (Figures 1 and 2). This implies that, like the after-potential, the reduction in output response range is an activity-dependent form of adaptation, only induced by adapting stimuli that cause sustained depolarization or hyperpolarization.

The reduction in output range may be related to the after-potential. Indeed, if hyperpolarizing after-potentials are the result of opening ion channels in the wide-field cell (Dürr, 1988), one would expect to see a decrease in the overall input-output gain of the cell and a reduction in total output range. The size of this gain reduction would depend on the magnitude of the conductance changes involved. Further experiments and modeling are required to determine the properties and physiological origin of the output range reduction.

Our quantitative analysis of the changes in the log contrast-response curve (Figure 3) assumed that the output range reduction has negligible effect on the cell’s overall contrast sensitivity. This is a fair assumption as a first approximation since in any one adaptation condition, $\Delta \text{CS}_{\text{gain}}$, evaluated at 10% criterion response level is approximately equal to $\Delta \text{CS}_{\text{gain}}$ evaluated at 50% criterion level. This pattern is consistent with a rigid rightward shift of the curve: if the function had been compressed vertically, $\Delta \text{CS}_{\text{gain}}$ should increase with increasing criterion level. Thus, we are confident that the output range reduction has only a minor effect on the cell’s overall contrast sensitivity.

Gain Reduction

The largest change in the contrast-response function following motion adaptation is the 3.5-fold reduction in contrast gain (Figure 1), as quantified by our measure $\Delta \text{CS}_{\text{gain}}$ (Figure 3; Table 1). Surprisingly, adapting motion presented in any direction induces a similar gain reduction, including orthogonal motion that evokes no response from the cell during the adaptation period (Figures 5 and 6). However, adaptation with wide-field or local flickering stimuli induces a much smaller reduction in contrast gain (Figure 4). Thus, we conclude that motion adaptation involves a contrast gain reduction component that is primarily driven by moving stimuli, but is direction insensitive. The small reduction in gain induced by flicker (Figure 4) may be due to weak activation of the same contrast gain control mechanism that is recruited by motion or could reflect the existence of a separate, flicker-sensitive, gain control mechanism.

What is the physiological basis for the contrast gain reduction? Maddess and Laughlin (1985) demonstrated that a powerful component of motion adaptation is retinotopic. Our preliminary experiments support this finding—a rightward shift of the log contrast-response curve is observed only when the test stimulus is presented to the same location as the adapting stimulus. This suggests that the gain reduction either occurs in retinotopic elements presynaptic to the wide-field cell or is a localized process occurring on the dendrites of the wide-field cell. Our data do not allow us to be more specific; the gain reduction could occur at any stage of the motion pathway—before, during, or after motion correlation.

The major challenge for any account of adaptation is that motion in any direction induces a large contrast gain reduction (Figures 5 and 6) while flicker does not (Figure 4). Simple activity-dependent models (where the gain of an element is regulated according to its own activity) predict strong adaptation to contrast flicker if the adapting element is located before motion correlation or directional tuning if it is located after correlation.
Our data points to a more complex mechanism for adaptation where the responses of the adapting element are regulated by an external signal that is both motion dependent and direction insensitive. Unfortunately, the anatomy and physiology of the visual pathways leading to the wide-field lobula plate cells is unclear, making it difficult to formulate precise hypotheses about the physiological mechanisms of adaptation.

**Similarities with Mammalian Neurons**

Parallels between adaptation in fly neurons and motion-sensitive units in mammals suggest common principles governing the neural coding of motion in diverse species. In the wallaby NOT (nucleus of the optic tract), Lbbotson et al. (1998) report a decrease in response magnitude following adaptation (Maddess and Laughlin, 1986) accompanied by a shortening of responses to transient image motion (Maddess, 1986; de Ruyter van Steveninck et al., 1986) but no change in temporal frequency optimum (Harris et al., 1999). Thus, motion adaptation in both the blowfly and wallaby seems to have remarkably similar consequences.

Comparison with electrophysiological studies in other mammals is more difficult because despite several studies (Maffei et al., 1973; Vautin and Berlyk, 1977; von der Heydt et al., 1978; Hammond et al., 1985; Marlin et al., 1988), even the basic properties of adaptation to moving patterns remain unclear. Giaschi et al. (1993) note that the only consistent finding has been a reduction in response magnitude with continued exposure to preferred direction motion. Pursuing this topic, Giaschi et al. (1993) report that adaptation with preferred or nonpreferred direction typically reduces the overall gain of simple and complex cells, while simple cells also show evidence of an additional process specific to preferred direction adaptation. This is broadly similar to our results in the fly: both preferred and anti-preferred motions reduce contrast gain, while the after-potential depends on the direction of adapting motion (Figure 2).

**Parallels with Human Psychophysics**

In human observers, prolonged exposure to rapidly moving patterns alters the perceived velocity of subsequently presented stimuli (Thompson, 1981; Stone and Thompson, 1992; Clifford and Langley, 1996; Bex et al., 1999). Perceived velocity also depends on pattern contrast: a high-contrast pattern is perceived as moving faster than the same pattern presented at a lower contrast (Thompson, 1982). Müller and Greenlee (1994) examined the interaction of these two effects and found that motion adaptation reduces the effect of contrast on perceived velocity.

If we assume that the responses we record in wide-field cells are analogous to the “perceived speeds” measured by Müller and Greenlee (1994), fly neurons (Figure 1B) mirror the psychophysical observation that increasing pattern contrast increases perceived velocity (Thompson, 1982). Furthermore, the gain of the relationship between pattern contrast and wide-field cell response is greatly reduced following adaptation, just as Müller and Greenlee (1994) find the relationship between contrast and perceived speed to be reduced. To our knowledge, Müller and Greenlee’s (1994) method has not been used to study other adapting directions. It would be interesting to know whether our finding that the decrease in contrast gain is direction independent (Figure 5) also holds for the human visual system.

**Adaptation and Coding**

Our previous work (Harris et al., 1999) demonstrates that motion adaptation does not alter the inherent velocity optimum of fly motion detectors. Instead, adaptation involves at least two components (the after-potential and gain reduction), both of which reduce the system’s contrast sensitivity. Why does the system adapt to high image speeds by reducing its sensitivity to contrast?

The correlation model of motion detection suggests that each correlator contains an expansive nonlinearity (multiplication). This would make the correlator output particularly sensitive to the magnitude of the input signals and so potentially vulnerable to saturation. We suggest that the after-potential and gain reduction serve to release the motion pathway from this saturation, allowing it to maintain high sensitivity across a wide range of stimulus conditions. The after-potential acts antagonistically to recent activity in the cell, repositioning the cell’s responses within the available signaling range. By analogy with the retina (Laughlin, 1994), this type of subtractive mechanism may exploit correlations in continuous signals, reduce redundancy, and maintain the operation of synapses in favorable regions of their input-output functions.

Similarly, the gain reduction component of adaptation scales down the magnitude of signals in the motion pathway. Our data does not demonstrate whether gain reduction occurs before or after motion correlation, but if the correlator nonlinearity is to be protected from saturation, the gain control should act on the inputs. Furthermore, since the output of the correlators depends on the spatiotemporal correlation between the input signals as well as their magnitude, this gain control would be best regulated by the magnitude of the correlator output, not the magnitude of the inputs. This is consistent with our observation that adaptation is recruited by motion but not flicker (Figure 4). The fact that fly and mammalian neurons exhibit similar forms of adaptation suggests that the limited signaling capacity of individual neurons is a serious constraint at the levels at which motion is extracted. Adaptation mechanisms that regulate input amplitude to protect vulnerable nonlinear operations from saturation could be useful in a wide variety of neural circuits.

**The Advantages of Nondirectional Adaptation**

Why are HS cells and apparently some cortical neurons (Giaschi et al., 1993) strongly adapted by motion that does not strongly excite them? For a fly, prolonged exposure to just one component of high-speed optic flow is unlikely in a behavioral context. Instead, high retinal image speeds are likely to be experienced during chasing or escape behavior, which will transiently generate many forms of optic flow. Thus, if the fly experiences high velocity in one direction, it is likely to experience high velocities in other directions, too. Instead of adapting individual detectors based on their own activity, perhaps it is more appropriate to adapt all detectors simul-
taneously when any of them are strongly activated. Such “system-wide” adaptation also preserves the relative activity between different detectors, perhaps simplifying subsequent neural processing.

A nondirectional “system-wide” mechanism has the additional advantage that it preserves patterns of relative sensitivity and direction tuning within a neuron’s receptive field. Maps of the local direction selectivity of several classes of wide-field cell provide strong evidence that wide-field cells constitute a system of matched filters for decomposing visual flow fields in order to recover information about self-motion (Krapp and Hengstenberg, 1996; Krapp et al., 1998; Krapp, 1999). A similar role has been ascribed to cells in area MST of the primate visual cortex (Duffy and Wurtz, 1991a, 1991b).

This argument assumes that other wide-field cells (tuned to different components of optic flow) behave in a similar way to HS—i.e., greatly reducing their gain following adaptation with motion presented in any direction. Our preliminary experiments on another class of wide-field cells (VS) indicate that they do indeed share this property.

Finally, Brenner et al. (2000) recently presented another fly wide-field cell, H1, with a random sequence of image velocities drawn from distributions with zero mean but different variances. Brenner et al. suggest that H1 maximizes information transmission by dynamically rescaling its input-output function to match the variance of the velocity stimulus. This “adaptive rescaling” requires an adaptation process that is sensitive to changes in the variance of the velocity stimulus, even though the mean image velocity remains zero. We note that the contrast gain reduction component of motion adaptation described here has suitable properties because it is recruited by high image velocities in any direction (Figures 5 and 6). Thus, the gain reduction mechanism will be recruited strongly when either the mean or the variance of the stimulus velocity distribution becomes large.

Experimental Procedures

Intracellular recordings were made from HS cells in male and female drone flies (Eristalis tenax) collected from the wild near Cambridge. We used aluminium silicate glass electrodes filled with 2 M Potassium Acetate (tip resistance 120 MΩ). Further details of the experimental procedure are given in O’Carroll et al. (1997).

Stimulus Presentation

Sinusoidal gratings were generated with a Picasso Image Synthesizer (Innisfree) and presented on a CRT (Tektronics 608, frame rate 300 Hz, mean luminance 40 cd/m²). Stimuli were presented to the ipsilateral eye only: an occluding mask was placed in front of the contralateral eye. The stimulus monitor was located ~70 mm from the eye and positioned to best fill the cell’s receptive field. Further details in O’Carroll et al. (1997).

Cell Selection

Cells were included in this study if they (1) showed both depolarizing and hyperpolarizing graded responses, with spikelets evident during depolarizing responses, (2) showed the largest depolarizing responses for horizontal progressive (front-to-back) motion, (3) showed responses to high-contrast preferred/anti-preferred direction gratings in excess of ~10 mV, and (4) had large receptive fields extending over 60° horizontally and 40° vertically. These criteria are all consistent with the selection of HS cells (Hauser, 1982). All HS cell types (HSN, HSNE, HSE, and HSS; Hauser, 1982; O’Carroll et al., 1997) showed similar responses to the adaptation protocols used in the study.

Contrast-Response Protocol

The following protocol was used to determine the contrast-response function of a wide-field cell before and after motion adaptation. A sinusoidal test grating (5 Hz, 0.1 cycles/°) was presented for 1 s at the test contrast. The screen was then blanked to mean luminance for 500 ms and followed by presentation of the adapting stimulus, a high-contrast (95%) sinusoidal grating (0.02 cycles/°, 20 Hz), for 4 s. For experiments where we investigated the effects of adapting grating direction (Figures 5 and 6), the adapting grating had the same spatial frequency as the test grating (0.1 cycles/°). After the adapting period, the test grating was immediately represented for 1 s. The screen was blanked to mean luminance for at least 5 s before the beginning of the next trial.

This protocol was repeated for between 12 and 20 different test contrasts between 0% and 95%, and repeated between 1 and 3 times for each test contrast. We defined the cell’s response to the test gratings as the mean membrane potential between 100 and 300 ms following stimulus onset (windows illustrated in Figure 1A). Our conclusions do not depend critically on the choice of analysis windows—similar results are found using any window located between 50 and 500 ms following stimulus onset.

For the data shown in Figure 4, flickering stimuli were used to adapt the cell. Further details are given in the main text and the caption of Figure 4.

Measurement of After-Potential

Data from the same protocol (Figure 1A) was used to study the relationship between the potential evoked by the first test stimulus and the subsequent after-potential (Figure 7). The test-potential and after-potential were defined as the mean membrane potential between 50 and 250 ms following stimulus onset (windows illustrated in Figure 7A). Again, our conclusions do not depend critically on this choice of window.

Test gratings varied in either contrast (12–20 different values, between 0% and 95%), temporal frequency (10–15 values, between 5 and 75 Hz), spatial frequency (20 values, between 0.01 cycles/° and 1 cycle/°), or orientation (32 values, between 0° and 348°). For each experiment, all other parameters were held constant at 5 Hz temporal frequency, 0.1 cycles/° spatial frequency and ~30% contrast.

Acknowledgments

This work was supported by the BBSRC, the Rank Prize Fund, and a Wellcome Trust Mathematical Studentship to R. Harris.

Received April 12, 2000; revised September 11, 2000.

References


