Adaptation in single units in visual cortex:
The tuning of aftereffects in the temporal domain

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Abstract

Adaptation-induced changes in the temporal-frequency tuning and direction selectivity of cat visual cortical cells were studied. Aftereffects were induced largely independent of direction. Adapting in either direction reduced responses in both directions. Aftereffects in the direction opposite that adapted were only slightly weaker than were aftereffects in the adapted direction. No cell showed any enhancement of responses to drifting test stimuli after adapting with moving gratings. Adapting in a cell's null direction usually had no effect. Dramatic differences between the adaptation characteristics of moving and stationary stimuli were observed, however.

Furthermore, aftereffects were temporal frequency specific. Temporal frequency-specific aftereffects were found in both directions: adapting in one direction induced frequency-specific effects in both directions. This bidirectionality of frequency-specific aftereffects applied to the spatial domain as well. Often, aftereffects in the direction opposite that adapted were more narrowly tuned.

In general, adaptation could shift a cell's preferred temporal frequency. Aftereffects were most prominent at high temporal frequencies when testing in the adapted direction. Aftereffects seemed to be more closely linked to temporal frequency than to velocity matching.

These results constrain models of cortical connectivity. In particular, we argue against schemes by which direction selectivity is generated by inhibiting a cell specifically when stimulated in the nonpreferred direction. Instead, we argue that cells receive bidirectional spatially and temporally tuned inputs, which could combine in spatiotemporal quadrature to produce direction selectivity.

Keywords: Adaptation aftereffects, Temporal frequency, Direction selectivity, Intracortical inhibition, Cortical organization

Introduction

The nervous system actively processes temporal information. Retinal responses are altered by a contrast gain control mechanism acting in the temporal domain (Shapley & Victor, 1981). The lateral geniculate nucleus relays spatial responses largely unchanged from the retina to the cortex, but modifies temporal properties (Mastronarde, 1987; Humphrey & Weller, 1988). Visual cortical cells, in turn, show markedly different responses to high stimulus speeds than do their dominant geniculate afferents (Orban et al., 1985). The spatial behavior of visual cortex has without doubt been more closely investigated than the temporal behavior.

The previous article (Saul & Cynader, 1989) described spatial aspects of adaptation in cortical units, studied using methods which revealed aftereffects in every cell. Aftereffects were specific to the adapting stimulus, implying that extrinsic mech-

anisms (Vautin & Berkley, 1977) underly the phenomenon. We further suggested that intracortical mechanisms are responsible. In this paper, we describe novel results on the temporal-frequency tuning of adaptation aftereffects in single cells.

Some previous studies of adaptation in visual cortex have noted the direction selectivity of aftereffects (von der Heydt et al., 1978; Movshon et al., 1980; Saul & Daniels, 1985; Hammond et al., 1985; 1986; 1988; Marlin et al., 1988), although some authors have observed varying degrees of bidirectionality (Vautin & Berkley, 1977; von der Heydt et al., 1978; Movshon et al., 1980). Single unit studies have often linked this selectivity to the motion aftereffect, in which unidirectional adapting induces apparent motion in stationary targets. Using the methods described in the previous paper, we observed bidirectional aftereffects.

Psychophysicists have used adaptation to isolate mechanisms in the visual system (Sekuler & Ganz, 1963; McCollough, 1965; Pantle & Sekuler, 1969; Blakemore & Campbell, 1969; Blakemore et al., 1970; Julesz, 1971; Tolhurst, 1972; Carpenter & Blakemore, 1973; Stecher et al., 1973; Dealy & Tolhurst, 1974; Pantle, 1974; Levinson & Sekuler, 1975). The same technique

can be adapted to the physiological study of single cell response properties. Adapting in one direction reduces the responses of presumably all cells which respond to that direction. One can then test the response properties of a cell in the absence of the normal input from other cells.

In the discussion, we speculate on the mechanisms generating adaptation aftereffects, and consider implications of our results for cortical connectivity.

Methods

The physiological preparation, recording and stimulation techniques, and data analysis are as described in the preceding paper (Saul & Cynader, 1989). Recordings were obtained from cat visual cortex, area 17. Surgical anesthesia was induced by i.v. injection of sodium thiopental, and continued during recording sessions with a mixture of nitrous oxide and oxygen supplemented with pentobarbital sodium. EEG, ECG, body temperature, and expired CO_2 were continuously monitored and maintained at appropriate levels.

Single units were isolated with glass-insulated platinum–iridium microelectrodes inserted through the intact dura. Recording stability was essential for the long runs necessary in this study, and runs were terminated if responses became erratic or if the physiological state of the animal varied significantly.

Cells were first mapped by hand to determine the receptive-field location and the optimal orientation. *Direction* will refer to the two opposite senses of movement possible at the fixed, optimal orientation. *Direction-selective* cells have a null direction, which evokes no response or which reduces any spontaneous activity present. *Direction-biased* cells produce at least twice as many spikes for stimulation in one direction (the *preferred* direction) as in the opposite (*nonpreferred*) direction. *Bidirectional* cells have similar responses in the two directions. Assignment (for convenience) of preferred and nonpreferred labels to the two directions is arbitrary for bidirectional cells. *Temporal frequency* or *drift rate* will mean the number of cycles of the sine wave grating passing a given point each second. By convention, positive and negative drift rates will be assigned to the two directions of motion, with negative drift rates signifying the nonpreferred direction. Stationary stimuli in this study were gratings which were flashed on and left standing. That is, the contrast was raised from zero to some fixed level (with a rise time on the order of milliseconds) and maintained at that fixed contrast throughout the trial. No attempt was made to match the spatial phase of stationary stimuli to the receptive field.

Experiments consisted of alternating adapting and test trials. An adapting trial consisted of either low-contrast stimulation, for purposes of obtaining subsequent control data, or high-contrast stimulation, to obtain subsequent adapted response levels. The spatial and temporal frequencies and the direction of the adapting trials were varied. A test trial followed each adapting trial. The parameters of the test trials were varied across a set of test conditions in each run. For each test condition, the responses to that condition were extracted for those trials following each given adapting condition. Conditions were sometimes pooled across a stimulus dimension. Means and standard errors were computed for the responses to each test condition contingent on the prior adapting condition. Comparisons were often made between control and adapted responses by means of the t-statistic between them. These t-scores served as an objective index of the strength of adaptation aftereffects.

Results

Direction

In several previous investigations using different experimental designs, direction-selective adaptation aftereffects have been observed (von der Heydt et al., 1978; Movshon et al., 1980; Saul & Daniels, 1985; Hammond et al., 1985, 1986, 1988; Marlin et al., 1988). There are two aspects of directionality for adaptation effects: 1) one can compare the responses in each direction following adapting in one direction; and 2) one can compare the effects of adapting in each of the two directions. For instance, adapting visual cortical neurons in one direction can lead to a relative enhancement of responses to stimulation in the opposite direction (von der Heydt et al., 1978; Hammond et al., 1985; Saul & Daniels, 1985; Marlin et al., 1988). Comparing the effects of adapting in each direction, one finds that aftereffects match the adapting stimulus, so that the adapted direction is most affected (Hammond et al., 1985; 1988; Marlin et al., 1988). Although we confirmed such observations in a broad sense, we were surprised to find that under the adapting regime used in the present experiments, aftereffects tended to be bidirectional. Adapting in one direction generally reduced responses in both directions. Thus, adapting in each direction resulted in similar effects.

Individual examples

We compared the responses to testing in each direction under three conditions: control, and adapted in each direction. For cells which responded in both directions, adapting in either direction induced adaptation aftereffects in both directions. Figure 1A shows an example of a complex cell which gave similar responses in the two directions. Test responses were strongly reduced by adapting in either direction. A very slight bias can be seen for stronger aftereffects when adapting and test directions match. This bias is insignificant here, especially compared to the large depression of responses created by adapting either in the same or in the opposite direction as that tested.

Even direction-biased cells showed bidirectional adaptation effects. Figure 1B shows an example of a cell whose preferred-direction response was affected most strongly by adapting in the preferred direction, but which also showed deficits in both directions following adapting in the nonpreferred direction. Adapting in the nonpreferred direction was as potent as adapting in the preferred direction when testing the nonpreferred direction, despite the weaker evoked responses. Therefore, a bias might exist for stronger aftereffects when adapting and test directions are the same, as reported by previous studies, if each direction had been adapted at equivalent contrasts. This cell was also adapted and tested with stationary flashed gratings. Stationary gratings evoked about the same response magnitude as gratings drifting in the nonpreferred direction, but the adaptation characteristics were very different. Adapting with a stationary grating had no effect (or induced a slight enhancement) on the test responses to moving gratings. On the other hand, moving gratings had little effect on the stationary tests. Only when adapting and test gratings were both stationary or both moving did aftereffects occur.

The directionality of adaptation aftereffects must be viewed in terms of the underlying directionality of the cell. Direction-selective cells must be treated separately from cells which show responses for both directions. For a cell which has a true null direction, bidirectional aftereffects could only be shown by
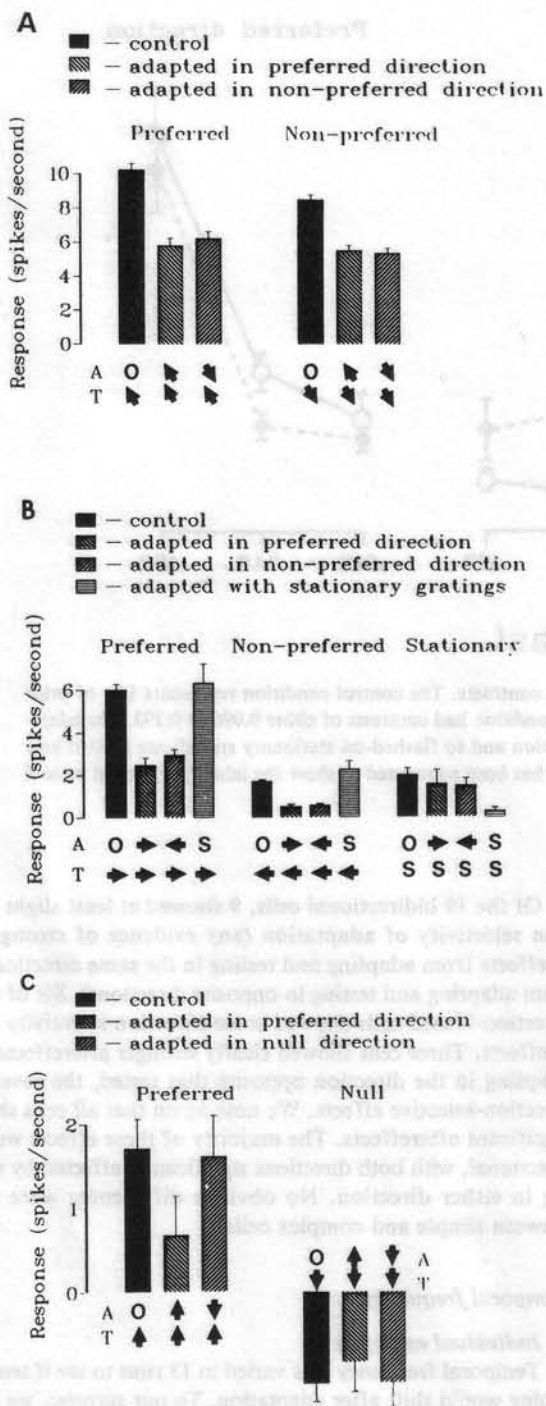
A
- control
- adapted in preferred direction
- adapted in non-preferred direction

B
- control
- adapted in preferred direction
- adapted in non-preferred direction
- adapted with stationary gratings

C
- control
- adapted in preferred direction
- adapted in null direction

Fig. 1. Evoked responses (spontaneous activity has been subtracted) to each direction of motion of drifting gratings are shown under three conditions of adaptation: control, and adapted in each direction. Adapting (A) and test (T) conditions are labeled for each histogram bar by an arrow, an O for control adapting conditions, or by an S for stationary stimuli. A, a complex cell showing little direction preference was tested at a contrast of 0.15 and a spatial frequency of 0.3 cpd. Drift rates of the test stimuli were 1.92, 3.84, 5.76, and 7.68 Hz. Test trials were 4.267 s long. Adapting trials lasted 17.067 s, and had contrasts of 0 or 0.30, a spatial frequency of 0.3 cpd, and drift rates of 1.92 and 5.76 Hz. B, responses in a direction-biased simple cell to gratings drifting in each direction and to stationary gratings are plotted for prior adapting in each direction, with stationary gratings, and with a blank screen. Adapting contrast was 0.15, test contrast was 0.075. Moving gratings had temporal frequencies of 1.2, 2.4, and 3.6 Hz. Adapting trials lasted 15 s. C, this direction-selective complex cell was tested at contrasts of 0.012, 0.024, and 0.048, at spatial frequencies of 0.15, 0.3, 0.45, 0.6, and 0.75 cpd, and at a temporal frequency of 2.4 Hz. The adapting trials had contrasts of 0.012 (control) and 0.096 (adapted), spatial frequencies of 0.45 and 0.75 cpd, and drift rates of 2.4 Hz. Adapting trials were 30 s long. The responses in the null direction were below the average spontaneous rate.

In Fig. 2, contrast-response curves from another direction-selective complex cell are shown for stimuli which drifted in the null direction, stimuli which were flashed on and left standing for 5 s, and stimuli which drifted in the preferred direction. Three contrasts were tested, and the cell was adapted for 10 s at low contrast (control) or at higher contrast (adapted) with gratings drifting in the *null* direction. The cell was inhibited by stimulation in the null direction. Adapting in the null direction induced no change in the test responses in this direction. However, a small decrease in responsiveness was found in the preferred direction. Interestingly, this cell showed an enhancement in responses to a stationary grating which was flashed on and left standing for 5 s (see Discussion). We never observed enhanced responses to drifting gratings following adapting with drifting gratings. Adapting with stationary gratings sometimes enhanced test responses, however (e.g. Fig. 1B).

Population results

The degree of direction selectivity of aftereffects can be gauged by plotting the directions against each other as in Fig. 3. Population results across 38 cells are illustrated in these plots. For each cell, the data were analyzed as in Fig. 1 to obtain responses in each direction under the three conditions of adaptation (control, adapted in the preferred direction, and adapted in the nonpreferred direction—only one direction was adapted or tested in some runs, giving different sample sizes for the different plots in Fig. 3). For each test direction, the ratios of adapted to control responses were computed for each adapting direction (Marlin et al., 1988). Thus, when both directions were tested and adapted, four ratios were obtained (PP, PN, NP, and NN, where P and N stand for preferred and nonpreferred directions, the first letter indicates the adapting direction, and the second letter indicates the test direction). In Fig. 3A, the two ratios based on adapting in the preferred direction are compared. The horizontal axis indicates the ratio for testing the preferred direction (PP), the vertical axis for testing the non-preferred direction (PN). The diagonal line divides the data between those cells which were more affected in one of the two test directions: points above and to the left of the line were

adapting in the null direction and observing a loss of response in the preferred direction. Although we have observed this behavior in one neuron (Fig. 2), most direction-selective cells showed no effect from adapting in their null direction. The complex cell illustrated in Fig. 1C was inhibited by stimulation in the null direction. No changes were evident following adapting in the null direction. Adapting in the preferred direction induced aftereffects in the preferred direction. A slight improvement in the activity in the null direction was seen following preferred direction adapting, but this change was not significant. In most cells, aftereffects were induced only when adapting stimuli excited the cell.
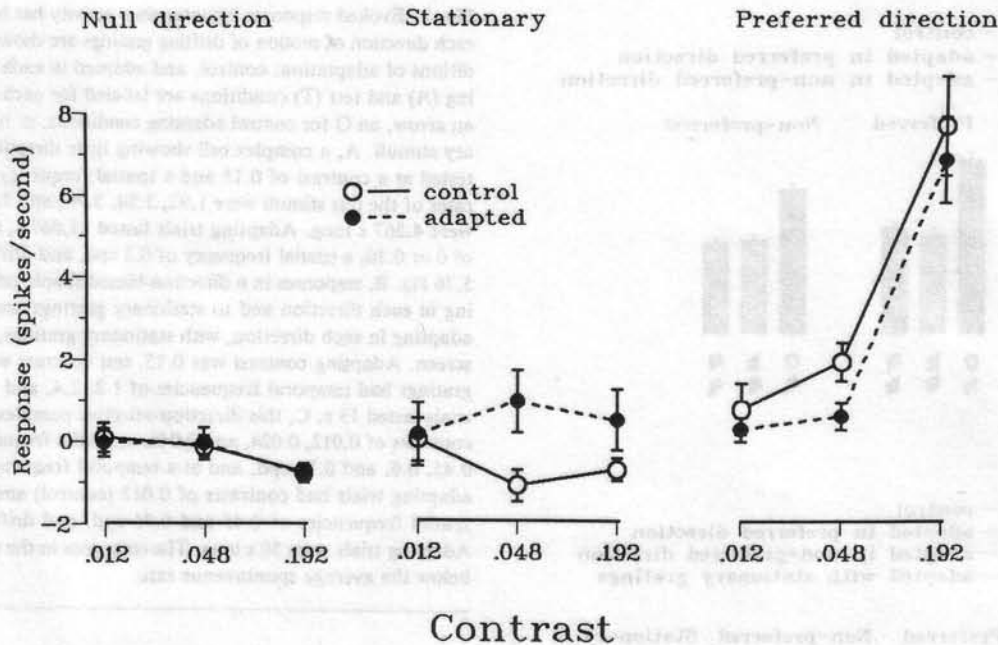
Fig. 2. Data from a direction-selective complex cell, tested at three contrasts. The control condition represents 10 s of prior stimulation at a contrast of either 0.012 or 0.024, while the adapted condition had contrasts of either 0.096 or 0.192. The adapting stimuli all drifted in the null direction. Responses in each direction and to flashed-on stationary stimuli are plotted as a function of test contrast. The spontaneous firing rate of 3.2 spikes/s has been subtracted to show the inhibition evoked by null direction and stationary stimulation.

more affected in the adapted, preferred direction. The center of gravity of these points (0.54, 0.57) falls barely into this region, suggesting some direction specificity of the aftereffects. However, the predominant effect of adapting in the preferred direction was to reduce responses in both directions, pushing the points toward the center of the plot. Note that all points lie to the left of 1.0 (although one exceptional point from a strongly direction biased cell fell at 1.14, −0.71). Adapting in the preferred direction almost invariably reduced responses in the preferred direction.

The plot in Fig. 3B is similar to Fig. 3A, but for the other two ratios (NP and NN), based on adapting in the nonpreferred direction. This plot shows a bias for stronger aftereffects when testing the adapted, nonpreferred direction, as the center of gravity lies at (0.66, 0.54), in the lower right half of the plot. This means that adapting in the nonpreferred direction reduced nonpreferred direction responses to 54% of their control values, and preferred direction responses to 66% of their control values, on average. The same four ratios are replotted in the alternative format in Figs. 3C and 3D, by reversing the roles of adapting and testing. In Fig. 3C, the two ratios based on testing the preferred direction (PP and NP) are compared. The points lie mostly above the diagonal, as adapting in the preferred direction was much more effective than adapting in the nonpreferred direction. The asymmetry in Figs. 3B and 3C is due to the relative ineffectiveness of nonpreferred direction adapting in reducing the response in the preferred direction. Adapting in either direction reduced the nonpreferred direction responses roughly equally, as seen in Fig. 3D. We note again, however, that adapting in each direction at equivalent contrasts may alter this symmetry, by making the effects of adapting in the nonpreferred direction more profound.

Of the 19 bidirectional cells, 9 showed at least slight direction selectivity of adaptation (any evidence of stronger aftereffects from adapting and testing in the same direction than from adapting and testing in opposite directions). Six of the 14 direction-biased cells showed some direction selectivity of aftereffects. Three cells showed clearly stronger aftereffects from adapting in the direction opposite that tested, the reverse of direction-selective effects. We note again that all cells showed significant aftereffects. The majority of these effects were bidirectional, with both directions significantly affected by adapting in either direction. No obvious differences were noted between simple and complex cells.

Temporal frequency

Individual examples

Temporal frequency was varied in 13 runs to see if temporal tuning would shift after adaptation. To our surprise, we found a remarkable degree of selectivity of aftereffects in the temporal domain. In Fig. 4, temporal-frequency (drift rate) tuning curves are shown for four conditions: control, and adapted at three temporal frequencies. Each of the adapting stimuli evoked similar responses from this direction-selective complex cell, and depressed test responses strongly. The control tuning curve (solid line and open circles) shows a slight preference for low temporal frequencies, but is broadly tuned. Adapting at 1.8 Hz (filled circles) drastically reduced the response to testing at 1.8 Hz, leaving the responses to higher frequencies relatively unaffected. Adapting at 3.6 Hz (filled squares) reduced the responses to all drifting test gratings, but left a notch in the tuning curve at the adapting frequency. The 5.4-Hz adapting trials induced aftereffects primarily at higher temporal frequencies
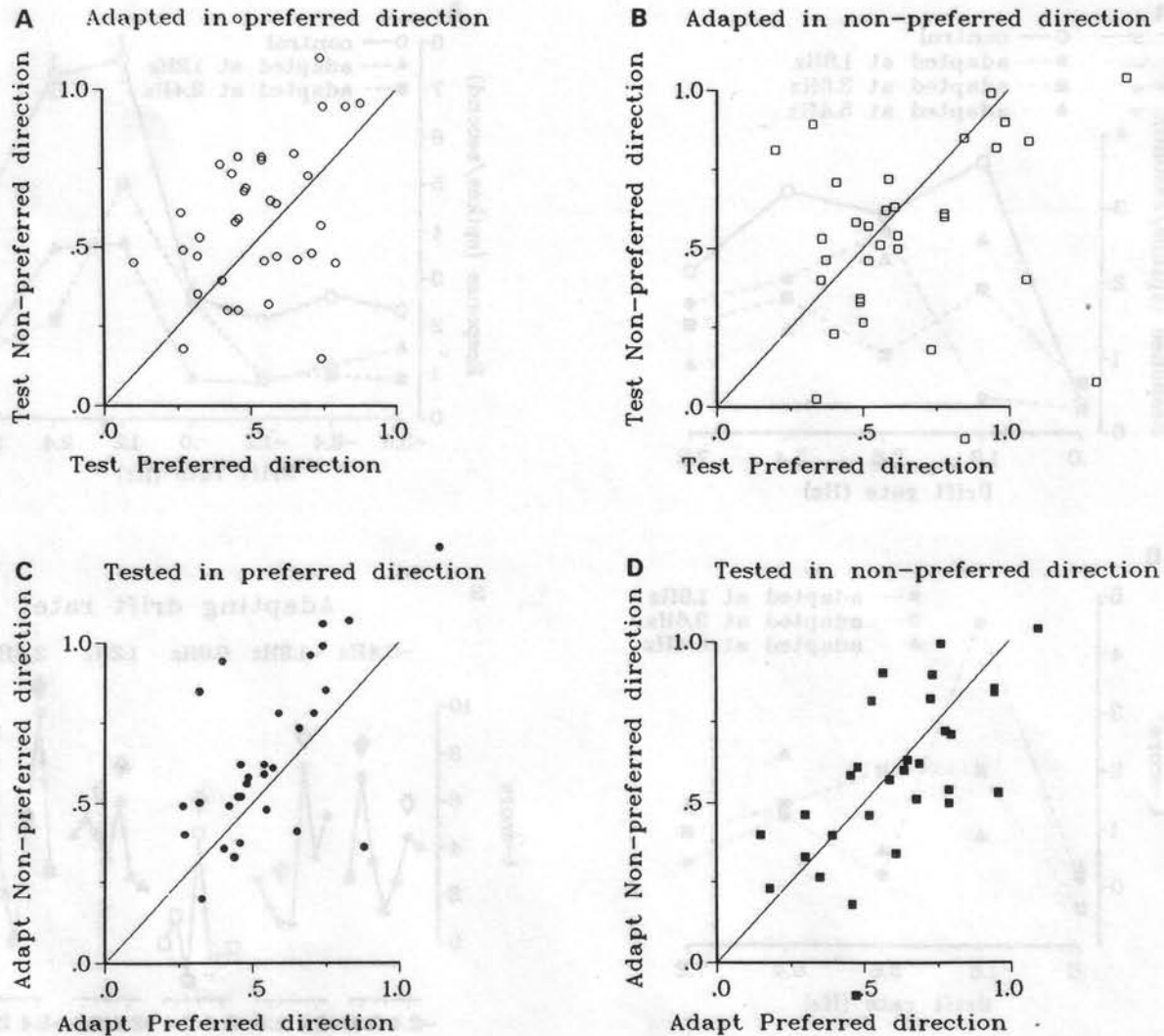
A Adapted in preferred direction

B Adapted in non-preferred direction

C Tested in preferred direction

D Tested in non-preferred direction

Fig. 3. Population results on the directional asymmetry of adaptation aftereffects are illustrated by plotting the ratios of adapted to control responses. A small ratio corresponds to a strong aftereffect. Contrasts and frequencies were pooled to compute these data. Diagonal lines show equal effects in both directions. A, adapted to control ratios for testing in the preferred direction (horizontal axis) *versus* testing in the nonpreferred direction (vertical axis) are shown for the case when the adapting stimuli drifted in the preferred direction. The center of gravity in this plot lies at (0.54, 0.57), $N = 37$. B, similar to A, but for adapting in the nonpreferred direction. Most points lie below and to the right of the diagonal, as the adapted, nonpreferred direction has smaller ratios than does the preferred direction which was opposite the adapted direction. The center of gravity is at (0.66, 0.54), $N = 32$. C and D, the same data as in A and B are replotted by reversing the placements of adapt and test. The horizontal axis gives the ratio of adapted to control responses where the adapting stimuli drifted in the preferred direction. The vertical axis represents the ratio for nonpreferred direction adapting. In C, the responses to testing in the preferred direction are shown, and in D the nonpreferred direction test responses are given. The centers of gravity are at (0.56, 0.67) in C, and at (0.57, 0.56) in D, $N = 31$.

(filled triangles), thereby sharpening the tuning curve. The aftereffects of adapting at 1.8 Hz, 3.6 Hz, and 5.4 Hz are clearly tuned and match the adapting temporal frequency. As described in the previous paper (Saul & Cynader, 1989), we computed the *t*-scores between the control and adapted points as a measure of the strength of aftereffects. Figure 4B shows the *t*-scores for each of the adapting temporal frequencies. Although noisy, each of these curves peaks at the adapting frequency.

Figure 5 shows the results of another run in which adapting and test temporal frequencies were varied. This cell was a strongly direction-biased simple cell. The three curves in Fig. 5A represent the responses following zero contrast adapting, and

adapting at 1.2 Hz and 2.4 Hz in the preferred direction. Each of these adapting temporal frequencies was very effective at driving the cell, and induced strong response decrements at most test frequencies. Note, however, that the 2.4-Hz adapting (filled squares) changed the tuning considerably by depressing the responses to 2.4 Hz well below the responses to 1.2 Hz. Although difficult to see in this plot, the opposite direction was similarly affected. By plotting the *t*-scores at each point on the abscissa, we can normalize the response differences to better reveal the effects in the nonpreferred direction. These *t*-scores are shown in Fig. 5B for adapting drift rates of −2.4 Hz, −1.2 Hz, 0.0 Hz, 1.2 Hz, and 2.4 Hz, where negative drift rates corre-
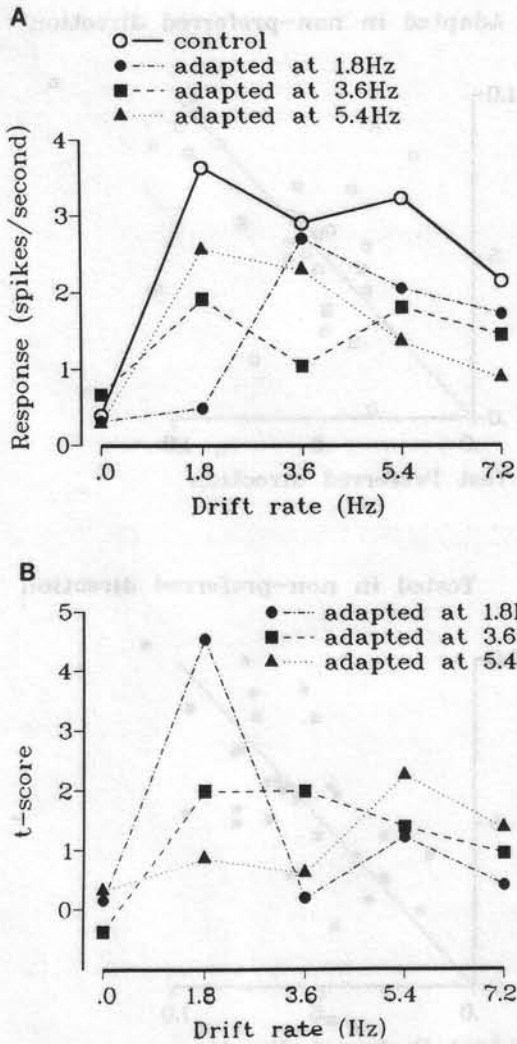
A

B

Fig. 4. Temporal-frequency tuning curves from a complex cell. Only the preferred direction is shown. Test trials had a contrast of 0.05. Adapting trials lasted 10 s. Control responses were derived from trials following stimulation at low contrast (0.01), while adapted responses were preceded by a contrast of 0.15. Spontaneous firing rates have been subtracted. Mean firing rates during the 5 s test trials are shown in A. A measure of the strength of aftereffects is plotted in B. These are the *t*-scores between the control and adapted points shown in A.

A

B

Fig. 5. Temporal-frequency tuning curves from a simple cell. Seven drift rates were tested at a contrast of 0.075 and a spatial frequency of 0.7 cpd. Adapting trials lasted 15 s, had a contrast of 0 or 0.15, a spatial frequency of 0.7 cpd, and temporal frequencies of 0, and 1.2, 2.4, and 3.6 Hz in each direction. Negative drift rates correspond to the nonpreferred direction, positive numbers to the preferred direction. A, the control and two of the adapted tuning curves are shown. The control responses were collected during test trials which followed 0 contrast adapting trials, while the adapted responses occurred during test trials which followed stimulation with high-contrast gratings drifting at 1.2 or 2.4 Hz in the preferred direction. B, the tuning of aftereffects is plotted using the *t*-scores computed between control and adapted responses. The number above each curve and the open arrow indicate the drift rate of the corresponding adapting stimulus. The filled arrows indicate the temporal frequency of the adapting stimulus, but in the opposite direction.

spond to motion in the nonpreferred direction. Large *t*-scores indicate strong aftereffects; note that responses are significantly reduced at most frequencies, with *t*-scores commonly above 4. Each curve is peaked at the adapting temporal frequency (arrows). *These peaks can occur in either direction,* however. For the 2.4-Hz adapting stimuli (filled squares and circles), both directions were strongly and specifically affected. Adapting at 1.2 Hz (asterisks and triangles) induced the strongest aftereffects (as measured by this *t*-score index) at 1.2 Hz in the nonpreferred direction, independent of the direction of the adapting grating. Note that adapting at 1.2 Hz in the preferred direction (triangles) caused a severe reduction in overall responses (see Fig. 5A), despite the relative lack of tuning of aftereffects. Adapting with a stationary grating (open squares)
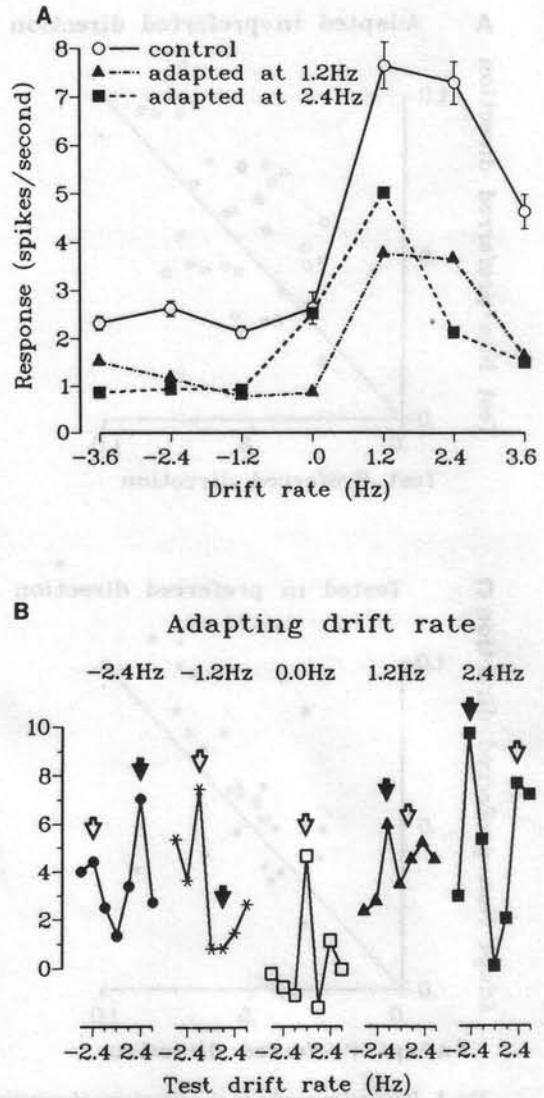
reduced responses to stationary grating tests alone. We repeatedly observed frequency-specific aftereffects which were independent of direction. Gratings drifting at a given rate in either direction appeared to share a common behavior with respect to adaptation, which differed from the behavior of stationary grat-

ings or of gratings drifting at a different rate. Some direction selectivity appears in these curves, in the effects at frequencies higher than the adapting frequency. Aftereffects at higher frequencies are larger in the same direction than in the opposite direction.

In the accompanying paper (Saul & Cynader, 1989), we noted a bias for lower spatial frequencies to be more susceptible to adaptation. Some of the temporal-frequency data suggested that aftereffects were stronger at higher temporal frequencies. An example is shown in Fig. 6. This direction-selective complex cell preferred higher drift rates, as seen in the control tuning curve. This curve was replicated by adapting in the null direction and with stationary stimuli (not shown). Adapting in the preferred direction reduced the response at the highest drift rate tested, independent of the adapting frequency.

Population results

We analyzed the temporal data as we described for the larger sample of spatial data (Saul & Cynader, 1989). From the control and adapted tuning curves as in Figs. 4–6A, we derived *t*-scores as in Figs. 4–6B. The horizontal axis was then centered on the adapting frequency and transformed to a log scale indicating how many octaves separated the test and adapting stimuli. The 197 points obtained in this way are plotted in Fig. 7A. Both drift directions are included in this figure. Very few points fall below 0.0, as responses were almost always reduced by prior adapting stimulation. Fifty percent of the points have *t*-scores above 2.0. These 197 points are averaged over octave-wide bins in Fig. 7D. The strongest aftereffects clearly occurred near the adapting frequency.

In Figs. 7B and 7E, the same data is plotted, but only points where the same direction was adapted and tested are included. Evidence for a high-frequency bias comes out in Fig. 7E. The points 1 and 2 octaves above the adapting frequency are much higher than the points 1 and 2 octaves below ($P > 0.9995$, $df = 86$, *t*-test). The effects of testing the direction *opposite* that adapted are shown in Figs. 7C and 7F. The tuning of aftereffects for these 74 points is narrower than the tuning shown in Fig. 7E for the *same* direction as was adapted. For adapting and testing in opposite directions, aftereffects appeared to be stronger at test frequencies below the adapting frequency ($P > 0.9995$, $df = 48$).

Bidirectional, frequency-specific aftereffects

Adaptation thus appears to induce specific aftereffects in the temporal-frequency domain. Matching of temporal frequency can occur independently of direction, so that adapting at a given frequency in one direction reduces the responses in the opposite direction at the same temporal frequency. We found such bidirectional, temporal-frequency selectivity of adaptation aftereffects even in strongly directionally biased cells. This result implies that such cells are influenced by bidirectional, temporal-frequency selective mechanisms.

Similar observations were made in the spatial domain. We found that adapting at a given spatial frequency in the nonpreferred direction induced specific aftereffects in the preferred direction, although not to the same degree or with the same tuning as did adapting in the preferred direction. An example is shown in Fig. 8. All test trials were in the preferred direction. The control spatial-frequency tuning curve (open circles) peaks
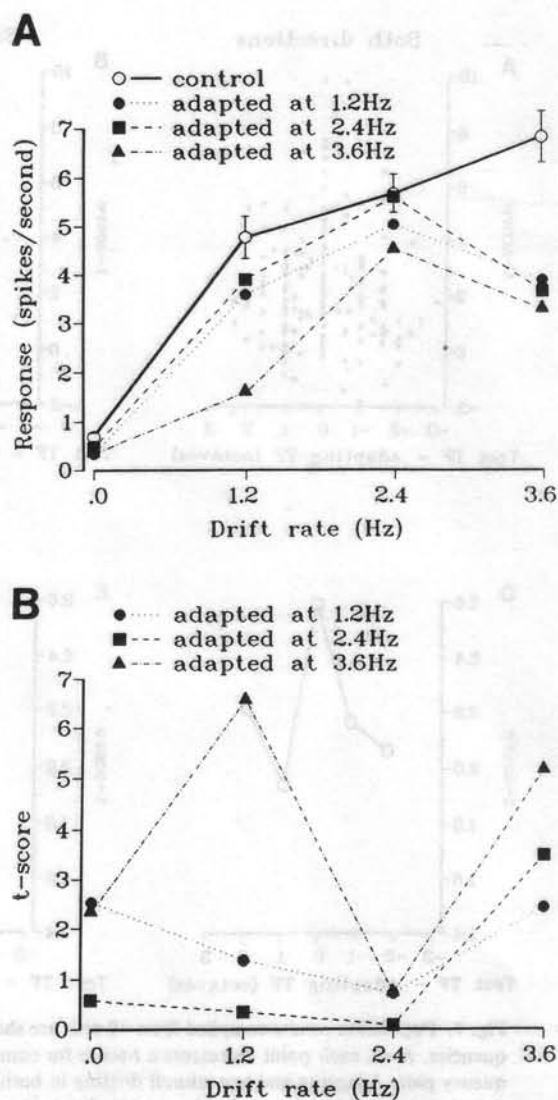

Fig. 6. Temporal-frequency tuning curves from a complex cell, plotted as in Fig. 4. This cell was tested only up to 3.6 Hz, although it responded to higher frequencies. Adapting at 1.2, 2.4, or 3.6 Hz reduced the response at 3.6 Hz. All stimuli drifted in the preferred direction. Adapting trials lasted 10 s, had a contrast of 0.0015 (control) or 0.15 (adapted), and a spatial frequency of 0.175 cpd. Test trials had a contrast of 0.096, and spatial frequencies of 0.075–0.275 cpd.

at 0.225 cpd. The two adapted tuning curves shown were both obtained by adapting at 0.225 cpd, in the same, preferred direction (triangles) or in the opposite, nonpreferred direction (squares). This directionally biased simple cell was strongly affected by preferred direction adaptation, with a broad, asymmetric tuning of the aftereffects. Adapting in the nonpreferred direction induced strong but narrowly tuned aftereffects. At most frequencies, no significant changes were observed after adapting in the nonpreferred direction (see *t*-scores in Fig. 8B). Two of the points (0.225 cpd and 0.325 cpd) were significantly reduced, however. If only the unaffected frequencies (0.025, 0.125, and 0.425 cpd) had been tested, or if the effects were averaged across all frequencies, the adaptation effects would appear to be direction selective. In general, the tuning of af-
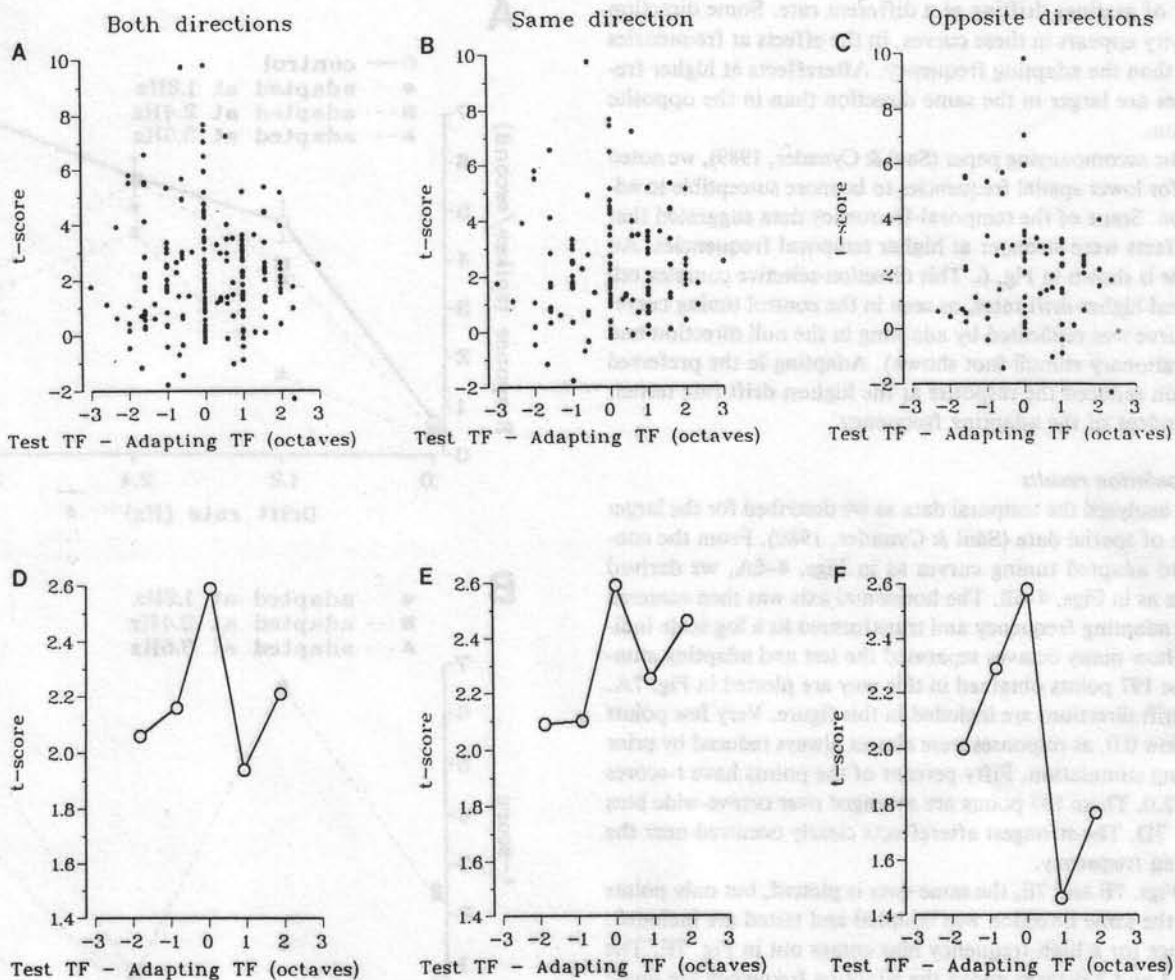
Fig. 7. Population results compiled from 10 cells are shown as *t*-scores *versus* distance between test and adapting temporal frequencies. A–C, each point represents a *t*-score for comparing adapted to control responses at a particular adapting/test frequency pair. Adapting and test stimuli drifting in both the same and the opposite directions are included in A, while B and C include only points from adapting and testing in the same or opposite directions, respectively. Sample sizes in A, B, and C are 197, 123, and 74, respectively. D–F, the points in A–C were averaged over octave-wide bins, to indicate the net tuning of aftereffects in the population. Similar tuning was seen by plotting medians rather than means, or by plotting the proportion of *t*-scores greater than 2.0.

tereffects was narrower in the direction opposite that adapted than in the same direction.

Speed or frequency specificity of aftereffects?

Because we varied the temporal and spatial frequencies of the drifting grating stimuli, we have analyzed the data in terms of temporal and spatial frequencies. However, adaptation aftereffects could be speed specific, rather than frequency specific. We varied *both* spatial and temporal frequencies in 6 experiments, and analyzed the data to see if the aftereffects were dependent on speed. Adapting and test stimulus pairs were assigned to one of nine space/time positions based on whether the test stimulus was half an octave below, within, or above the adapting stimulus in spatial and in temporal frequencies. Adapted responses were compared to control responses using the *t*-score, and *t*-scores for each stimulus combination were averaged over all 6 cells. These averaged *t*-scores are shown in Table 1. A slight preference for lower spatial frequencies is evi-

dent (these numbers are consistent with the results of the larger samples illustrated in Fig. 5C of the preceding paper and Fig. 7D above). If aftereffects were strongest when adapting and test speeds matched, a compensation should occur when spatial and temporal frequencies covary. Raising (or lowering) both spatial and temporal test frequencies keeps the speed of the test stimulus similar to the speed of the adapting stimulus. The relatively low *t*-scores of 2.2 and 1.5 along the diagonal indicate that matching of adapting and test speeds did not induce stronger aftereffects. Note that matching of adapting and test temporal frequencies, on the other hand, induced strong aftereffects independently of the spatial-frequency match. The effects of adaptation appear to be temporal-frequency selective, rather than speed selective.

Discussion

Spatial-frequency tuning, contrast sensitivity, direction selectivity, and temporal-frequency tuning can be altered by adapt-
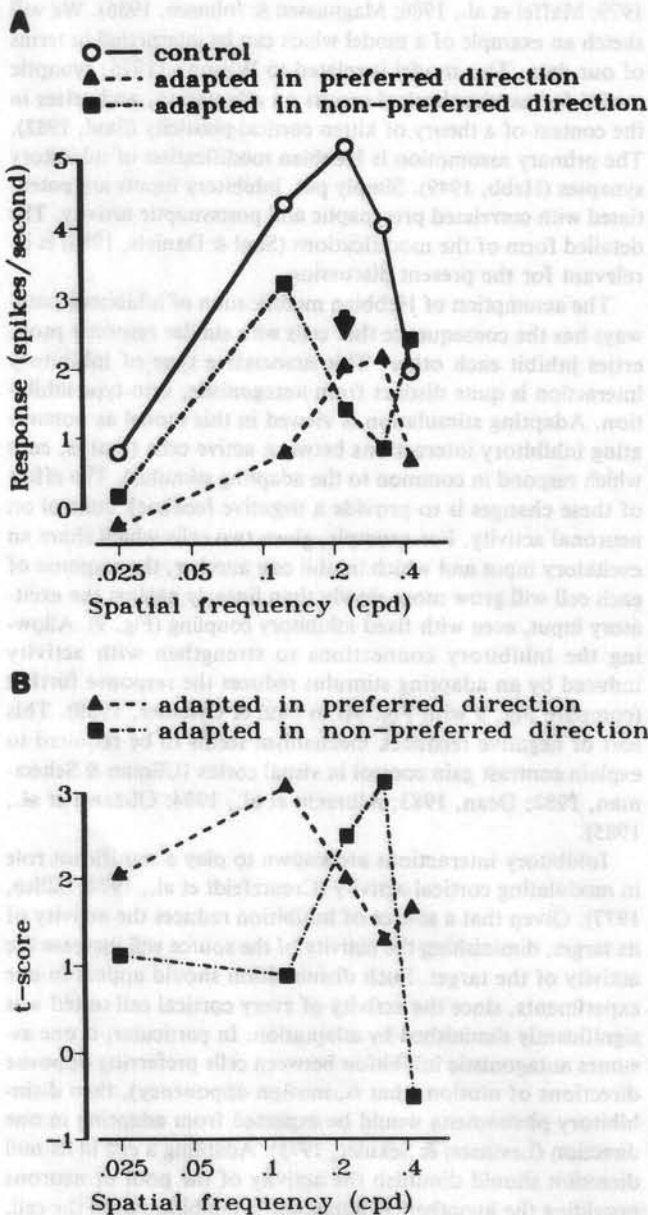
A

B

Fig. 8. Spatial-frequency tuning curves from a direction-biased simple cell. Only the responses in the preferred direction are shown. Temporal frequency was 2.4 Hz. Each point is derived from pooling all contrasts tested (0.003, 0.009, 0.027, 0.081, and 0.243). Adapting spatial frequency was 0.225 cpd (arrow). Adapting trials had contrasts of 0.003 (control) or 0.096 (adapted). The spontaneous firing rate of 0.87 spikes/s has been subtracted. The *t*-scores are plotted in B.

ing with appropriate gratings. Adaptation of visual cortical units in the temporal-frequency domain had not been previously reported. Adaptation shows a remarkable degree of selectivity for the drift rate of moving gratings. Even more remarkably, this selectivity is independent of direction. Adapting with gratings drifting in either direction reduced test responses in both directions. Specificity for spatial and temporal frequency was present in both directions, with a tendency for the tuning of aftereffects to be narrower in the direction opposite that adapted.

Some cells showed losses primarily at temporal frequencies which were higher than the adapting frequency (at least when

Table 1. *Averaged t-scores as a function of spatial and temporal frequencies*[a]

	Test spatial frequency-adapting spatial frequency (octaves)		
	less than −0.5	within 0.5	greater than 0.5
Test temporal frequency-adapting temporal frequency (octaves) — less than −0.5	2.2	2.3	1.7
within 0.5	2.4	3.0	2.5
greater than 0.5	2.4	2.3	1.5

[a]Averages are based on samples of between 14 and 34 *t*-scores obtained in runs where both spatial and temporal frequencies were varied. Each run contributed at least one *t*-score to each of the 9 bins. Most runs contributed several points because of different combinations of adapting and test stimuli which fell into the same bin.

testing and adapting in the same direction). Adaptation therefore resulted in stronger effects at lower frequencies in space (Saul & Cynader, 1989) and stronger effects at higher frequencies in time over the entire sample. These asymmetries imply a preferential loss of response to high stimulus speeds (lower left-hand corner of Table 1). Such a finding in single units corresponds to the psychophysical observation of shifts in apparent speed of test targets following adapting to a moving stimulus (Thompson, 1981).

Thompson (1983) suggested that only two temporal channels accounted for the processing of stimuli up to 24 Hz in the human visual system. Presuming that cats would show analogous psychophysical behavior, our results seem contradictory. Single units showed narrow tuning of aftereffects in the temporal domain, as though many narrowly tuned channels provided inputs to these cells (Mandler, 1984). The uncertain relation between the cortical responses in cats and human perceptions makes the apparent contradiction potentially resolvable. We explored a restricted range of frequencies in this study, since most cells in cat area 17 respond poorly above 8 Hz. The two-channel model may have a substrate involving cells and areas beyond the limits of our investigation. Our data imply the existence of narrowly tuned bidirectional mechanisms in at least some cat striate cortical cells, but do not exclude a two-channel model at the level of psychophysics.

Hammond et al. (1985, 1988), Saul and Daniels (1985), and Marlin et al. (1988) emphasized the direction-specific nature of adaptation. Adapting in one direction decreases the response to testing in that direction. The responses in the opposite direction are sometimes enhanced (von der Heydt et al., 1978; Saul & Daniels, 1985; Hammond et al., 1985, 1986; Marlin et al., 1988). The present experiments are consistent with a degree of direction specificity, but we emphasize the bidirectionality of many of the observations. Vautin and Berkley (1977), von der Heydt et al. (1978), and Movshon et al. (1980) also noted bidirectional effects, at least in bidirectional cells. We found that the adapted direction was most affected, but the opposite direction was also influenced, often with greater specificity. These bidirectional aftereffects were seen even in strongly direction-biased cells, and the entire population showed little direction

selectivity of aftereffects. The variability of directionality over time requires control and adapted responses to be collected more or less simultaneously, as we attempted in this study. We also tried to avoid possibly artificial indices of directionality (such as the commonly used ratio (P-N)/(P+N)) when measuring aftereffects, relying on simple responses to single test stimuli. Finally, we tested across a range of parameters, and found that responses to only a subset of this range were reduced. Failure to consider this specificity could lead to failure to observe aftereffects in the opposite direction, especially since the tuning was generally narrower than in the same direction. The fact that aftereffects in the direction opposite that adapted were specific to the adapting frequency implies that bidirectional frequency-specific mechanisms underlie the adaptation effects. We conclude that even highly direction-biased cells receive bidirectional spatially and temporally tuned inputs.

We observed enhanced responses following adapting only under exceptional circumstances. The data in Fig. 2 illustrate some of the problems in interpreting enhanced responses. The response to a stationary grating was enhanced by adapting in this cell's null direction. This observation suggested a direct correlate to the motion aftereffect. Adapting in the null direction perhaps made the stationary grating appear to move in the opposite direction, which was the cell's preferred direction. The cell signaled this by firing. It might then be conceivable that the diminished response to testing the cell in the preferred direction could be attributed to a speed-sensitive mechanism, as though the apparent speed of the grating following adapting in the null direction were faster than optimal. Such reasoning fell apart under closer scrutiny, however. First of all, the cell was poorly tuned for speed sensitivity. Secondly, the enhanced response was entirely due to an increase in the onset discharge. These observations suggest that the enhanced responses involve a release from the inhibition generated during the adapting trials, or some other transient mechanism. Previous reports of enhanced responses from adapting in the opposite direction (von der Heydt et al., 1978; Saul & Daniels, 1985; Hammond et al., 1985, 1986; Marlin et al., 1988) have failed to show that such enhancement is a robust effect which persists above control levels for several seconds. Nonetheless, cells which are released from inhibition following adapting in their null direction could contribute to the motion aftereffect.

Theoretical implications

What sorts of mechanisms could underlie the adaptation effects we report here? One could suppose that adaptation simply reflects the fatigue of excitatory inputs. However, it would be difficult to reconcile the strength of aftereffects in the nonpreferred direction with the weak excitatory influence of the nonpreferred direction in many of these cortical neurons. In addition, the tuning of adaptation aftereffects in the temporal domain is much sharper than the tuning of single units, and in the spatial domain the asymmetric tuning of aftereffects does not match the tuning of the excitatory inputs which would presumably be driven by the adapting stimulus (Saul & Cynader, 1989). Finally, a fatigue mechanism predicts disinhibitory phenomena which do not occur, as we discuss below.

Alternatives to the fatigue mechanism have been suggested by many authors, mostly involving inhibitory inputs (Dealy & Tolhurst, 1974; Wilson, 1975; Heggelund & Hohmann, 1976; Lovegrove, 1976; Vautin & Berkley, 1977; Movshon & Lennie,

1979; Maffei et al., 1986; Magnussen & Johnsen, 1986). We will sketch an example of a model which can be interpreted in terms of our data. This model is related to Wilson's (1975) synaptic model for psychophysical results on adaptation, and arises in the context of a theory of kitten cortical plasticity (Saul, 1982). The primary assumption is Hebbian modification of inhibitory synapses (Hebb, 1949). Simply put, inhibitory inputs are potentiated with correlated presynaptic and postsynaptic activity. The detailed form of the modifications (Saul & Daniels, 1986) is irrelevant for the present discussion.

The assumption of Hebbian modification of inhibitory pathways has the consequence that cells with similar response properties inhibit each other. This associative type of inhibitory interaction is quite distinct from antagonistic, veto-type inhibition. Adapting stimulation is viewed in this model as potentiating inhibitory interactions between active cells (that is, cells which respond in common to the adapting stimulus). The effect of these changes is to provide a negative feedback control on neuronal activity. For example, given two cells which share an excitatory input and which inhibit one another, the response of each cell will grow more slowly than linearly against the excitatory input, even with fixed inhibitory coupling (Fig. 9). Allowing the inhibitory connections to strengthen with activity induced by an adapting stimulus reduces the response further (compare Fig. 9 with Fig. 9B in Saul & Cynader, 1989). This sort of negative feedback mechanism seems to be required to explain contrast gain control in visual cortex (Ullman & Schectman, 1982; Dean, 1983; Albrecht et al., 1984; Ohzawa et al., 1985).

Inhibitory interactions are known to play a significant role in modulating cortical activity (Creutzfeldt et al., 1974; Sillito, 1977). Given that a source of inhibition reduces the activity of its target, diminishing the activity of the source will increase the activity of the target. Such disinhibition should appear in our experiments, since the activity of every cortical cell tested was significantly diminished by adaptation. In particular, if one assumes antagonistic inhibition between cells preferring opposite directions of motion (that is, motion opponency), then disinhibitory phenomena would be expected from adapting in one direction (Levinson & Sekuler, 1975). Adapting a cell in its null direction should diminish the activity of the pool of neurons providing the hypothetical antagonistic inhibition onto the cell, so that subsequent testing in the adapted, null direction would reveal enhanced responses. We never observed enhancement of test responses in the adapted direction. Cells in cat area 17 do not appear to show opponent motion responses. Rejecting the assumption of antagonistic inhibition in favor of the associative-inhibition model described above can explain the absence of disinhibition, since potentiation of mutually inhibitory connections between similarly responding cells diminishes the activity in all the cells.

The absence of disinhibitory effects from adaptation implies that a simple antagonistic-inhibition model of direction selectivity fails. How then can we explain our observations of frequency-specific, bidirectional aftereffects in direction-biased cells? We inferred that direction-biased cells receive bidirectional inputs, some of which are presumably excitatory. Inhibiting one direction of a bidirectional excitatory input appears to depend on antagonistic inhibition. Independent evidence suggests that direction selectivity is generated not by vetoing one direction based solely on the direction, but instead by combin-
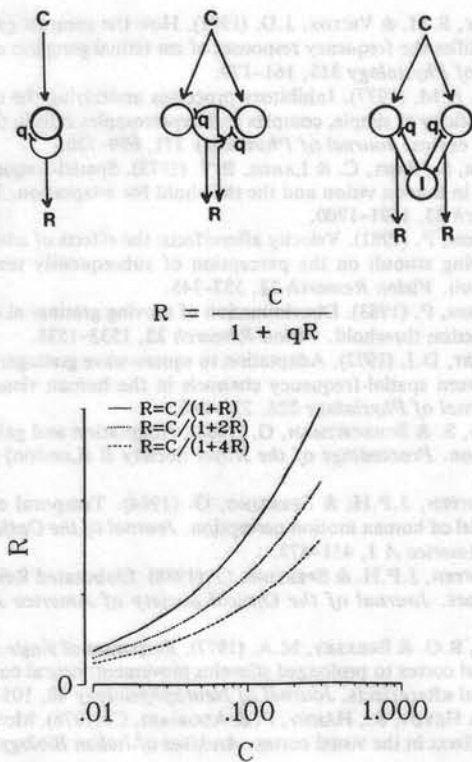
Fig. 9. Computed contrast-response functions from a simple associative-inhibition model. The model is schematized using three anatomical organizations which could produce the hypothetical responses. The essence of the model is negative feedback, which is seen most simply as self-inhibition, but could be generated as well by mutual inhibition or mediated via an interneuron (I). The output R is derived from cells which are excited by input proportional to the contrast C. Inhibitory interactions have a gain q, so that $R = C/(1 + qR)$. Therefore, $R = (1/2q)(-1 + \sqrt{(1 + 4qC)})$, so that response grows as the square root of contrast. Response is inversely proportional to the square root of the inhibitory gain. Adapting at high contrast is hypothesized to increase this inhibitory gain. The three curves represent three levels of inhibition, corresponding to three states of adaptation. These theoretical curves are meant to resemble the data of Fig. 9B of the preceding paper (Saul & Cynader, 1989).

ing bidirectional inputs in spatiotemporal quadrature, where two inputs are a quarter cycle out of phase with each other both in space and in time (Reichardt, 1961; van Santen & Sperling, 1984, 1985; Watson & Ahumada, 1985; Adelson & Bergen, 1985; Nakayama, 1985; Shadlen & Carney, 1986). In order to achieve these phase relationships, frequency specificity must be roughly matched between the inputs. Spatiotemporal quadrature models therefore should be subject to bidirectional, frequency-specific adaptation. The presumed bidirectional spatially and temporally tuned intracortical inputs underlying the adaptation aftereffects observed in direction-biased cells would correspond to the projections from a separable stage to a directional stage in these models. The fully opponent stage of these models does not correspond with any of our striate cortical cells, for the reasons discussed above. On the other hand, the intracortical locus of adaptation effects implies that direction-selective cortical neurons receive separable inputs from cortical cells, as opposed to receiving only direct thalamic inputs.

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