Adaptation to contingencies in macaque primary visual cortex

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SUMMARY

We tested the hypothesis that neurons in the primary visual cortex (V1) adapt selectively to contingencies in the attributes of visual stimuli. We recorded from single neurons in macaque V1 and measured the effects of adaptation either to the sum of two gratings (compound stimulus) or to the individual gratings. According to our hypothesis, there would be a component of adaptation that is specific to the compound stimulus. In a first series of experiments, the two gratings differed in orientation. One grating had optimal orientation and the other was orthogonal to it, and therefore did not activate the neuron under study. These experiments provided evidence in favour of our hypothesis. In most cells adaptation to the compound stimulus reduced responses to the compound stimulus more than it reduced responses to the optimal grating, and the responses to the compound stimulus were reduced more by adaptation to the compound stimulus than by adaptation to the individual gratings. This suggests that a component of adaptation was specific to (and caused by) the simultaneous presence of the two orientations in the compound stimulus. To test whether V1 neurons could adapt to other contingencies in the stimulus attributes, we performed a second series of experiments, in which the component gratings were parallel but differed in spatial frequency, and were both effective in activating the neuron under study. These experiments failed to reveal convincing contingent effects of adaptation, suggesting that neurons cannot adapt equally well to all types of contingency.

1. INTRODUCTION

Perception of the world can be perturbed after experiencing a potent stimulus for a minute or two, as in the well-known after-effects of seen motion or contrast (Harris 1980*b*). After the discovery of feature-selective neurons in the visual pathway it was natural to attribute such effects to 'fatigue' of neurons specifically sensitive to the potent stimulus (Sutherland 1961); such adaptation was soon demonstrated neurophysiologically in the retina (Barlow & Hill 1963) and is a ubiquitous feature of the response of V1 neurons in the cat (Maffei *et al.* 1973; Vautin & Berkeley 1977; Movshon & Lennie 1979; Ohzawa *et al.* 1982; Carandini & Ferster 1997) and monkey (Sclar *et al.* 1989).

The simple 'fatigue' explanation for perceptual after-effects ran into difficulties when McCullough (1965) showed that there are after-effects, not just to elements of a stimulus, but to contingencies between the elements they contain. In her experiments the colour of adapting gratings was contingent on their orientation—for instance vertical gratings were red while horizontal gratings were green—and this caused vertical black–white gratings to be tinged with green and horizontal ones with red in the period immediately after adaptation. While there may be orientation selective cells that are also colour selective, it has been pointed out (Harris 1980*a*) that almost every contingent coupling that has ever been tested yields contingency-specific after-effects. It becomes difficult to suppose that there are classes of cells selective for every possible contingency.

An alternative explanation is that cortical neurons adapt selectively to contingencies in the pattern of activity they receive, even when they do not initially show selectivity of response to the same contingencies (Barlow & Földiák 1989; Barlow 1990). For example, there may be neurons that are initially selective for red stimuli but not for stimulus orientation. After adaptation to the contingency of 'red' and 'vertical' they would give smaller responses to red vertical gratings than to red horizontal gratings. This could potentially explain the McCullough effect, as it would shift the perceived colour of a white vertical grating towards the complement of red, i.e. green (Barlow & Földiák 1989). In principle, this mechanism of adaptation to contingencies could explain a wide variety of perceptual phenomena (Barlow 1997).

The adaptation of cortical neurons to stimulus contingencies could result from a mechanism that

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increases the amount of mutual inhibition between cells that are simultaneously active. In addition to the contingent after-effects, this mechanism would explain the specificity of adaptation observed in single neurons. For example, adaptation to a spatial frequency on one flank of a neuron's tuning curve depresses the responses to test stimuli on that flank more than on the other flank (Movshon & Lennie 1979; Saul & Cynader 1989*a*,*b*). This selectivity of adaptation could result from the simultaneous activity of the tested neuron and of a population of other neurons, this population varying with the adapting frequency.

Our experiments were intended to test whether neurons in monkey V1 can be adapted to contingencies in the attributes of the stimuli they receive. We measured the contrast responses of the cells using three different stimuli: two drifting gratings and the compound stimulus obtained by summing the two gratings. We subsequently adapted the cells to each of these stimuli in turn, and observed how this adaptation affected the contrast responses. Because of the slow contrast-gain control mechanism known to operate in the primary visual cortex (Ohzawa *et al.* 1982; Sclar *et al.* 1989), we expected that adaptation to compound stimuli would reduce the responses more than adaptation to the individual gratings. The prediction on the hypothesis being tested is that there would be an additional component of adaptation that is caused by, and restricted to, the simultaneous presence of the two components in the compound stimulus. Our results show this is true for some but not all of the stimulus configurations that were tested.

2. METHODS

Methods for single-cell recording in paralysed anaesthetized macaque monkeys in our laboratory have been described elsewhere (Levitt *et al.* 1994). Stimuli were either single drifting gratings or sums of two drifting gratings (compound stimuli), generated by a Truevision ATVista graphics controller (752 × 582 pixels, 107 Hz) and displayed on a gamma-corrected Nanao T560i monitor (mean luminance 72 cd m^{-2}). Gratings were modulated sinusoidally in luminance and had a maximal contrast of 50%. All the stimuli were presented monocularly, had the same mean luminance, and were vignetted by a square window of optimal size for the cell under test, in a surrounding uniform field equal to the mean stimulus luminance.

Vertical microelectrode penetrations were performed 9–10 mm lateral to the midline and 3–4 mm posterior to the lunate sulcus, and often yielded two encounters with the primary visual cortex, with eccentricities first around 2 5° and then around 8 15°. After isolating a cell, we measured under computer control its tuning for the orientation, spatial frequency, temporal frequency, contrast and window size of the vignetted drifting grating stimuli.

The main experimental protocol involved measuring the contrast responses separately to two gratings (G_1 and G_2), and to the sum of the two (G_1+G_2), while the cell was in different adaptation conditions. In the first (control) condition the adapting stimulus was a uniform field. In the subsequent adaptation conditions the adapting stimulus was either G_1, or G_2, or G_1+G_2 (in arbitrary order). Each of these adaptation conditions was preceded by a control condition to ensure that recovery was complete, and followed by rest periods (12–20 min of uniform field stimulation). Adaptation was induced by presenting the adapting stimulus first in a long continuous exposure (generally 30 s), and then for brief (4 s) 'top-up' exposures between test stimuli (Movshon & Lennie 1979). The contrast of the adapting stimuli was 25% or 50% for each component. The contrast responses were measured by presenting the three test stimuli at different contrasts for 4 s each. This measurement was repeated 3–4 times for each adaptation condition, and the order of presentation of the test stimuli was randomized within each repeat. There were five to eight test contrasts, equally spaced in logarithmic scale, usually between 3% and 50%. The complete protocol lasted around two hours.

Adaptation reduces both the response magnitude and the contrast sensitivity of V1 neurons (Albrecht *et al.* 1984; Sclar *et al.* 1989). In an effort to capture both effects with a single measure, we considered an *adaptation index*, whose definition is schematized in figure 1. The adaptation index is the ratio between the sum of the unadapted responses to a given test and the sum of the adapted responses to the same test. These sums were computed over all different test contrasts. In geometric terms, the index is the ratio of the areas under the unadapted and adapted contrast responses. In some experiments we used different test contrasts for the different adaptation conditions, so the ratio was computed from curves fitted to the data, rather than directly from the data. The curves were of the form

$$R + R_0 + R_{\max}\frac{c^n}{\sigma^n + c^n},$$

where R is the estimated mean firing rate, c is the stimulus contrast, R_0 is the firing rate at rest (independent of test stimulus) and σ and n are free parameters

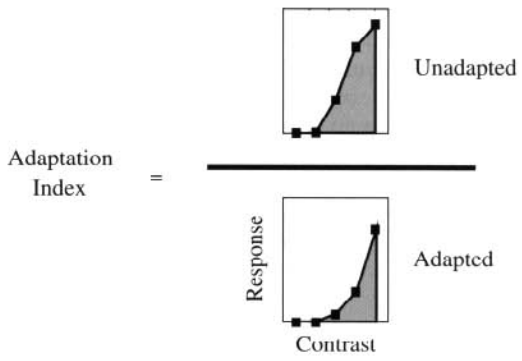

Figure 1. Schematic of the adaptation index. The grey areas in the numerator and denominator lie under the response versus contrast curves measured in two adaptation conditions. In the first condition ('unadapted') the adaptor was a blank field; in the second condition ('adapted') the adaptor was a visual pattern. Contrast is on a logarithmic scale, and response is on a linear scale. The index is 1.0 if adaptation does not affect the contrast responses, larger if it reduces them.

(Albrecht & Hamilton 1982). These curves provided excellent fits to the contrast responses in all adaptation conditions (Albrecht *et al.* 1984; Sclar *et al.* 1989).

3. RESULTS

We recorded from a total of 71 cells from two adult macaque monkeys (*Macaca fascicularis*). We report here on 15 cells (seven complex and eight simple) that (i) were kept for most of the adaptation protocol (around two hours); (ii) gave maximal responses above 10 spikes per second; and (iii) displayed full recovery after the 12–20 min of rest between adaptation conditions.

(*a*) *Different orientations*

In a first series of experiments, performed on eight cells, we chose the two gratings to differ in orientation. Grating G_1 had optimal orientation, and grating G_2 was orthogonal to it, with the same spatial frequency. In these experiments the responses to G_2 were negligible, so we did not measure their dependence on contrast.

An example of the effects of adaptation with these stimuli is illustrated in figure 2. The contrast responses to the preferred grating G_1 are shown in (*a*), and those to the compound stimulus G_1+G_2 are shown in (*b*). In the absence of adaptation (○) the cell gave good responses both to G_1 and to G_1+G_2. Both adaptation to G_1 and to G_1+G_2 were effective in reducing the responses. The responses to G_1 (*a*) were however more reduced by adaptation to G_1 (□) than by adaptation to G_1+G_2 (●). Conversely, the responses to G_1+G_2 (*b*) were reduced more by adaptation to G_1+G_2 (●) than by adaptation to G_1 (□).

Applying the adaptation index to these data, we find that when measured using grating G_1 as a test (*a*) the

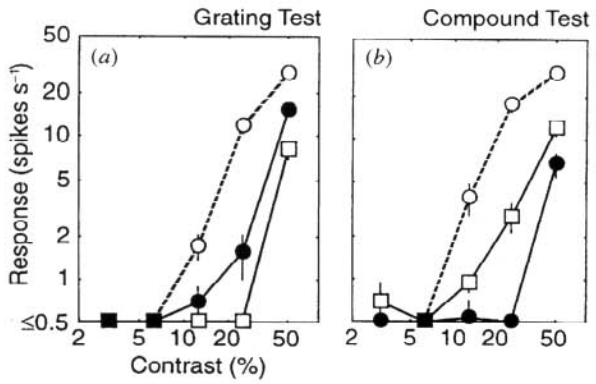

Figure 2. Contrast response functions of a cell to the preferred grating G_1 (*a*) and to the compound stimulus G_1+G_2 obtained by adding an orthogonal grating G_2 (*b*). The responses were measured when the cell was adapted to blank fields (○), to the preferred grating G_1 (□) and to the compound stimulus G_1+G_2 (●). Error bars are ±1 s.e.m. The responses to the preferred grating G_1 were reduced more by adaptation to G_1 itself than by adaptation to the compound stimulus G_1+G_2. Similarly, the responses to G_1+G_2 were reduced more by adaptation to G_1+G_2 itself than by adaptation to G_1 alone.

effects of adaptation to G_1 (adaptation index=4.2) was almost twice as strong as those of adaptation to G_1+G_2 (adaptation index=2.3). Conversely, when measured using the compound stimulus G_1+G_2 as a test (*b*), the effects of adaptation to G_1 (adaptation index=3.0) were almost half as strong as those obtained with adaptation to G_1+G_2 (adaptation index=5.4). These values for the adaptation index also reveal that adaptation to G_1 reduced the responses to G_1 more than the responses to the compound stimulus G_1+G_2 (4.2 vs 3.0) and that adaptation to the compound stimulus G_1+G_2 reduced the responses to G_1+G_2 more than the responses to G_1 (5.4 vs 2.3).

Similar results were obtained in seven of the eight cells tested with gratings differing in orientation (figure 3). The data in (*a*) show the strength of adaptation to the compound stimulus G_1+G_2 on the responses to the preferred grating G_1 (abscissa) and to G_1+G_2 itself (ordinate). For all but one cell, the data lie above the identity line, indicating that adaptation to the compound stimulus G_1+G_2 was in general more effective on the responses to G_1+G_2 itself than on those to the preferred grating G_1.

This observation is consistent with our hypothesis, namely that adaptation to the compound stimulus G_1+G_2 has a component that is specific to the responses to G_1+G_2 itself. Additional evidence in favour of our hypothesis is illustrated in (*b*), where the strength of adaptation on the responses to the compound stimulus G_1+G_2 is plotted for three different adapting stimuli: the orthogonal grating G_2 (□, abscissa), the preferred grating G_1 (○, abscissa), and the compound stimulus G_1+G_2 itself (ordinate). Except for two cells, the data lie above the identity line, indicating that the responses to G_1+G_2 were usually reduced more by adaptation to G_1+G_2 than by adaptation to any of the components alone.

The prevalence of the data points above the diagonal in (*b*) cannot be explained solely by the higher contrast energy of the compound stimulus. This is illustrated in (*c*), where the adaptation indices obtained with the preferred grating G_1 as a test are plotted. Six of the eight circles lie above the diagonal line, indicating that in this condition the compound stimulus G_1+G_2 was quite often a *weaker* adaptor than the preferred grating G_1.

Similarly, the prevalence of the data points above the diagonal in (*a*) cannot be explained by assuming that the responses to the compound stimulus G_1+G_2 were 'more adaptable' than those to the preferred grating G_1. This is illustrated in (*d*), where the adaptation indices obtained with adaptation to the individual gratings are plotted. Only two of the eight circles lie below the identity line, indicating that after adaptation to G_1 the responses to G_1+G_2 were rarely reduced more than those to G_1.

Finally, the specificity of adaptation observed with compound stimuli cannot be ascribed to the sole presence of the orthogonal grating G_2. Indeed, adaptation to the orthogonal grating G_2 was in general quite ineffective compared to the other conditions. For compound tests (*b*), adaptation indices obtained with G_2 as an adaptor were small, between 1 and 2 (□,

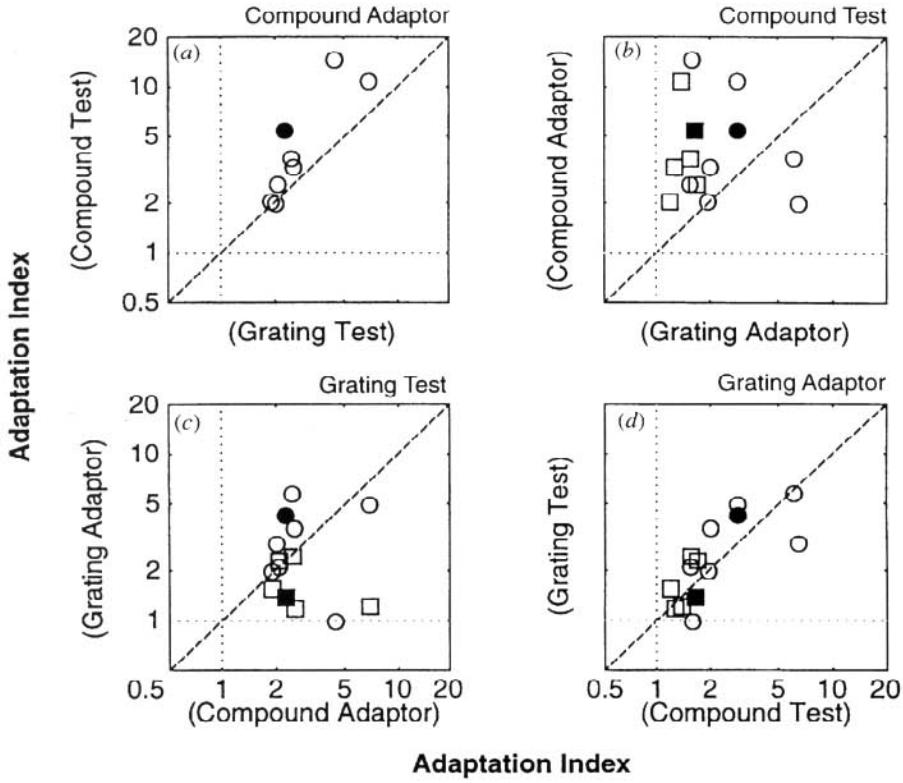

Figure 3. Results of our experiments with gratings differing in orientation. Circles (○), refer to adaptation to the preferred grating G_1, squares (□) to adaptation to the orthogonal grating G_2. Closed symbols (● and ■) refer to the cell in figure 2. Two of the eight cells were not tested with adaptation to G_2. (*a*) Adaptation indices obtained with adaptation to the compound stimulus G_1+G_2 and measured from the responses to the preferred grating G_1 alone (abscissa) and to G_1+G_2 itself (ordinate). (*b*) Adaptation indices measured from the responses to the compound stimulus G_1+G_2, after adaptation to the individual gratings G_1 and G_2 (abscissa) and to G_1+G_2 itself (ordinate). (*c*) Adaptation indices measured from the responses to the preferred grating G_1 alone, after adaptation to the compound stimulus G_1+G_2 (abscissa), and to the individual gratings G_1 and G_2 (ordinate). (*d*) Adaptation indices obtained with adaptation to the individual gratings G_1 and G_2 and measured from the responses to the compound stimulus G_1+G_2 (abscissa) and to the preferred grating G_1 (ordinate). The data points in (*a*) and (*b*) mostly occupy the regions above the identity lines, suggesting that there was a component of adaptation that was selective to, and caused by, the simultaneous presence of two orientations in the visual stimuli.

abscissa). A comparison of the horizontal position of the squares and circles in (*b*) indicates that these indices were in five out of six cells smaller than those obtained with adaptation to G_1. Moreover, all the squares in (*b*) lie above the diagonal, indicating that in six out of six cells the adaptation indices obtained with adaptation to G_2 were smaller than those obtained with adaptation to G_1+G_2. Similar results were obtained with G_1 as a test (□, (*c*)). Besides being quite ineffective, adaptation to the orthogonal grating G_2 had in general similar effects on the responses to G_1+G_2 and on those to G_1 (□, (*d*)).

Taken together, these results indicate that there is a component of adaptation that is specific to, and caused by, the simultaneous presence of the two gratings G_1 and G_2 in the compound stimulus G_1+G_2.

(*b*) *Different spatial frequencies*

The experiments with orthogonal gratings have shown that V1 neurons can adapt to contingencies in the orientations present in a stimulus. To test whether these neurons can adapt to contingencies in other stimulus attributes, we performed a second series of experiments, in which the component gratings differed in spatial frequency rather than in orientation. In these experiments, performed on eight cells, we chose G_1 and G_2 to have optimal orientation and to have spatial frequencies that lie on opposite flanks of the spatial frequency tuning curves of the neuron under study. Both frequencies were chosen so as to be effective in eliciting spikes.

As illustrated in figure 4, the experiments provided little evidence of selective adaptation to these compound stimuli. On average, adaptation to the compound stimulus G_1+G_2 (*a*) affected roughly equally the responses to the individual gratings G_1, G_2 and those to the compound stimulus G_1+G_2. In addition, the responses to G_1+G_2 were in general reduced more by adaptation to G_1+G_2 than by adaptation to the individual gratings G_1 and G_2 (*b*). Because the compound stimuli had higher contrast energy than the individual gratings, this effect may be simply explained

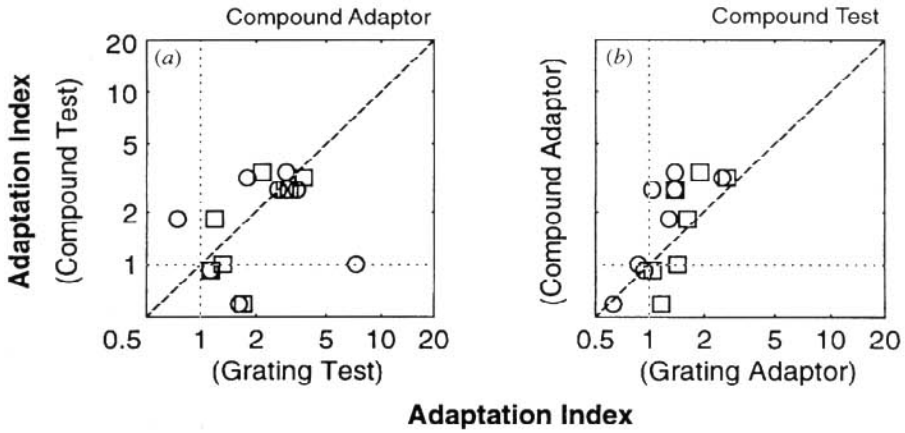

Figure 4. Results of our experiments with parallel gratings. (*a*) Adaptation indices obtained with adaptation to G_1+G_2 and measured from the responses to G_1+G_2 itself (ordinate), to the individual gratings (abscissa). (*b*) Adaptation indices measured from the responses to G_1+G_2, after adaptation to G_1+G_2 itself (ordinate) and to the individual gratings (abscissa). Circles (○) correspond to grating G_1, squares (□) to grating G_2. Because the data points in (*a*) are scattered on both sides of the identity line, these data suggest that neurons in V1 do not display selective adaptation to the simultaneous presence of two spatial frequencies in the visual stimuli.

by the action of the contrast-gain control mechanism known to operate in the primary visual cortex (Ohzawa *et al.* 1982; Sclar *et al.* 1989). Indeed, the responses to the individual gratings were often reduced more by adaptation to the compound stimulus than by adaptation to the gratings themselves (not shown).

The lack of convincing contingent effects of adaptation with parallel gratings suggests that neurons can adapt to contingencies in orientation but not to contingencies in spatial frequency. Nevertheless, there was one aspect of the results with parallel gratings that was consistent with the hypothesis of contingent adaptation. Because in these experiments both components elicited a response when presented alone (we chose G_1 to elicit around twice as many spikes as G_2), we were able to measure the specificity of the individual gratings in reducing the grating responses. From studies of specificity of adaptation in the cat (Movshon & Lennie 1979; Saul & Cynader 1989*a*), we expected to find that adaptation to G_1 would reduce the responses to G_1 more than the responses to G_2, and vice versa. Indeed, we found that given one spatial frequency as an adaptor, the adaptation index measured with the same spatial frequency as a test was on average 30% ($\pm$15% s.e.m., $N = 16$) larger than that measured with the other spatial frequency as a test. Moreover, the responses to a given spatial frequency were reduced by adaptation to the same spatial frequency an average of 26% ($\pm$13%, $N = 16$) more than they were reduced by adaptation to the other spatial frequency. While this selective effect was not large, and was not evident in all experimental protocols (Poirson *et al.* 1995), the specificity of adaptation to individual gratings is consistent with our hypothesis of adaptation to contingencies in the visual stimuli. As mentioned in the introduction, the specificity of adaptation effects could be explained if adaptation resulted from a mechanism that detects simultaneous firing in a population of neurons. The same mechanism would detect contingencies in the attributes of a visual stimulus.

4. DISCUSSION

The results with gratings differing in orientation provide support for our hypothesis: a component of adaptation in these experiments was specific to (and caused by) the simultaneous presence of the two orientations in the compound stimulus. The results with gratings differing in spatial frequency, on the other hand, are less clear. The reason for this could lie either in a true difference between the attributes of orientation and spatial frequency, or in more subtle differences in the experimental protocols employed in the two sets of experiments. In particular, while in the experiments with different orientations one of the two components was optimal, in the experiments with different spatial frequencies the two components were both suboptimal. The smaller responses elicited by these components are reflected in smaller adaptation indices obtained when these components were used as adaptors. This can be verified at a glance by comparing the adaptation indices of figure 3 with those of figure 4. It is conceivable that stimuli eliciting stronger adaptation effects would have provided evidence for contingent adaptation also in the case of stimuli containing different spatial frequencies.

The adaptation behaviour of neurons in the primary visual cortex seems to contain (at least) two different components. A first component is non-specific, i.e. it applies to any visual stimulus used as a test. This component mainly results in a shift to the right of the contrast-response curves (Ohzawa *et al.* 1982; Sclar *et al.* 1989), and has recently been found (in cats) to result from a tonic hyperpolarization of the cells (Carandini & Ferster 1997). A second component is specific—it has different effects on different test stimuli—and was in the present study found to affect the responses to contingencies in the attributes of visual stimuli. This component may result from an interaction between cell populations in the cortex that are selective for the different stimulus attributes. If this

view were correct (experiments involving multiple recording sites would be required to test it), the situation would be remarkably close to that envisioned in a model proposed by Földiák (1990). In this model neurons adjust their firing threshold on the basis of their past history of activity, and adjust their synaptic interactions with other cells in the network in order to minimize simultaneous firing.

In conclusion, our results suggest that cortical neurons can exhibit adaptation that is partially selective to contingencies in the pattern of activity they receive. It is generally agreed that light adaptation in the retina, and contrast-gain control in the visual cortex, discount constant features of input messages and thereby improve the ability of neurons with their narrow dynamic range to represent physical variables that have wide dynamic ranges. A contingency-specific decorrelation mechanism would do the same with regard to the associative structure of sensory messages, and would make the system more sensitive to changes in this associative structure (Barlow & Földiák 1989; Barlow 1990; Földiák 1990; Barlow 1997). The phenomena that von Helmholtz (1910) attributed to unconscious inference suggest that we are indeed sensitive to such changes. This is highly advantageous, for changes in associative structure often signal new causal factors in the environment.

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