
Adaptation reveals a neural code for the visual location of orientation change

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Abstract. We apply an adaptation technique to explore the neural code for the visual location of textures defined by modulation of orientation over space. In showing that adaptation to textures modulated around one orientation shifts the perceived location of textures modulated around a different orientation, we demonstrate the existence of a neural code for the location of orientation change that generalises across orientation content. Using competitive adaptation, we characterise the neural processes underlying this code as single-opponent for orientation, that is with concentric excitatory/inhibitory receptive areas tuned to a single orientation.

1 Introduction

Among the most important challenges faced by experimental psychologists is explaining perception in ways that are consistent with the known response properties of cortical neurons. The representational approach (Nicols and Newsome 1999) to this challenge is to elucidate neural states that ‘code’ for physical states, and there is a long-standing tradition of adapting sensory processes in order to study the nature of these neural codes. In adaptation studies, the aim is to expose subjects to prolonged stimulation that is narrowband for a particular dimension and to measure perceptual distortions along this dimension in subsequently presented test stimuli. These perceptual distortions are taken to reflect changes in the activity of neurons that code for the stimulus dimension. Adaptation has been used to characterise the neural code for motion, colour, orientation, spatial frequency, and conjunctions between these dimensions (eg Barlow and Hill 1963; McCollough 1965).

With regards to the effects of adaptation on perceived *location*, Köhler and Wallach (1944) demonstrated that presentation of a luminance-defined figure results in a perceived repulsion of the location of a subsequently presented test figure. They interpreted this location aftereffect as evidence of fatigue in neurons selective for the location of adaptation. An alternative explanation by Ganz (1966) involved lateral inhibition between neural activity elicited by the test figure and ‘residual’ neural activity associated with the adaptation figure. This ‘residual’ activity could correspond either to the effects of light adaptation, in which case the influence of adaptation would be analogous to a negative afterimage added to the test figure, or to contrast adaptation (see Georgeson 1991; Hess and Doshi 1995), in which case the contrast polarity of the adapting figure relative to the test figure would be irrelevant.

Common to both types of explanation is the notion that prolonged visual stimulation shifts the distribution of activity of neurons, with this effect being most pronounced for neurons selective for the location (and possibly other dimensions) of the adaptation stimulus. This notion underlies more recent investigations into the neural code for the location of various types of stimuli. For example, Whitaker et al (1997) reported location-specific repulsion effects following adaptation to both luminance-defined (first-order)

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and contrast-defined (second-order) stimuli. They demonstrated that these location aftereffects occurred even when adaptation to global orientation (ie the orientation of the virtual line formed between the misaligned adaptation stimuli) was precluded, thus confirming the existence of a genuine Vernier aftereffect, as distinct from a tilt aftereffect as suggested by earlier researchers (Wolfe 1987; Hess and Doshi 1995) as an alternative explanation.

In the present experiments, we employed the adaptation technique to explore the neural code for the location of second-order structure defined by *orientation change* over space. The location aftereffect was employed as a tool to test for the existence of such a neural code, and to distinguish this code from that for local orientation content. The approach adopted was to manipulate the degree of similarity in global orientation structure between adaptation and test stimuli independently of the degree of similarity in local orientation content between the two.

In these experiments, the adaptation and test stimuli were pairs of vertically separated orientation-modulated textures produced by filtering random visual noise with 2-D filters of narrowband orientation and spatial frequency, and rotating these filters along the horizontal axis according to a Gaussian function. Different versions of these textures were created by varying the starting orientation (the ‘base’) and the direction of rotation of the 2-D filter (determining the ‘peak’ orientation). During adaptation, various pairs of these textures were presented in fixed misalignment (see figure 1), and shifts in the perceived locations of subsequently presented pairs of test textures were measured by having subjects respond to their perceived alignment.

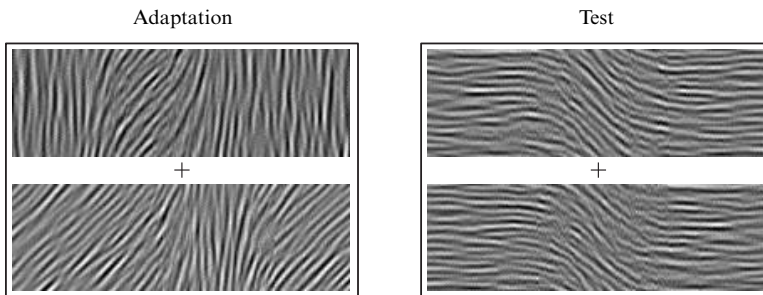


Figure 1. An example of the orientation-modulated adaptation and test textures employed in experiment 2. The example shows the adaptation modulations in left-diagonal misalignment, while the test modulations are in objective alignment. The reader can experience the positional shift due to adaptation by staring for approximately 1 min at the cross between the adaptation textures and then immediately shifting gaze to the cross between the test textures. The reader should perceive the top test modulation to be shifted slightly to the right of the bottom test modulation.

We show that adaptation to an orientation-modulated texture produces a repulsion in the perceived location of a subsequently presented test texture. Surprisingly, this repulsion is observed even when the orientation content of the test texture does not match that of the adapting texture. Together, these results demonstrate the existence of a neural code for the location of *orientation change*. In additional experiments in which orientation-sampled textures are placed in a competitive-adaptation arrangement, we show that the neurons underlying this code are likely to be single-opponent for orientation, that is, they have concentric excitatory/inhibitory receptive areas tuned to a single orientation.

2 General methods

Stimuli were created in Matlab[™] and presented by a Cambridge Research Systems[™] CRS2/3F board. Stimulus configuration and ordering were controlled by custom-written C-programs based on Visionworks[™] graphics routines, and the results were displayed

on a 21-inch EIZO high-resolution monochrome monitor at a viewing distance of 1.5 m, gamma corrected to 32 000 grey levels (from 0 cd m⁻² to 55 cd m⁻²) by a Visionworks[®] calibration system.

2.1 Stimuli and procedures

Stimuli in experiments 1–3 were rectangular patches (2.81 deg wide by 0.89 deg high) filled with orientation-modulated textures of 100% contrast, produced by filtering random visual noise (with a grain of 0.83 min of arc per dot) with 2-D filters of narrowband orientation ($\pm 10^\circ$) and spatial frequency (centred at 12.6 cycles deg⁻¹, bandwidth 10.8 cycles deg⁻¹). The filters were designed in frequency space (sampled at 1.39 cycles deg⁻¹ sample⁻¹) and possessed sharp boundaries between passband and stopband. Convolution kernels were then obtained by the frequency-sampling method (eg Lim 1990) and filtered textures were obtained by convolution with the noise. The orientation content of the textures was modulated along the horizontal axis according to a Gaussian function:

$$\theta(x) = \theta_{\text{base}} \pm 45 \exp(-x^2/2\sigma^2),$$

where $\theta(x)$ is the orientation at location x (x being measured relative to the location of the peak orientation) and $\sigma = 16.6$ min of arc. In all experiments, irrespective of whether or not the adaptation and test textures possessed identical orientation information, the textures differed in terms of their local luminance and contrast distributions because of having different random-noise sources.

Experiments 1–3 followed the same basic procedure:

(i) *Selection of test textures.* Test textures were orientation-modulated textures created (according to the method described above) from a single combination of base orientation (0° —horizontal) and peak orientation (135° anticlockwise from horizontal—ie -45°). Pairs of test textures were separated vertically by a gap of 8.3 min of arc.

(ii) *Selection of adaptation textures.* Adaptation was to pairs of orientation-modulated textures representing various combinations of base and peak orientation (see figure 2, which presents a summary of the adaptation conditions employed for experiments 1–3). In experiment 1 a single combination was employed (base 0° ; peak 135°); in experiment 2a all eight combinations of four base orientations (0° , 45° , 90° , and 135°) by two peak orientations ($\pm 45^\circ$ from the base) were employed; in experiment 2b and experiment 3 six combinations of three base orientations (as in 2a, but excluding 0°) and two peak orientations ($\pm 45^\circ$ from base) were employed; in experiment 2c and experiment 4 a single combination of base orientation (90°) and peak orientation ($+45^\circ$) was employed (note that positive angles indicate anticlockwise rotation and negative angles indicate clockwise rotation from horizontal). Therefore, the test textures were identical in their orientation content to the adaptation textures of experiment 1, one of the eight adaptation textures of experiment 2a, not included in the six adaptation textures of experiments 2b and 3, and orthogonal to the orientation content of the adaptation textures of experiments 2c and 4. Pairs of adaptation textures were separated vertically by a gap of 8.3 min of arc and occupied the same locations on the computer monitor as the test textures.

(iii) *Adaptation phase.* Subjects were required to fixate on the cross placed between pairs of adapting textures for a total of 72 s per block, during which time the adapting textures were randomly replaced ten times with new textures from the selection defined in (ii). In experiments 1, 2a, 2b, 2c, and 4, the orientation profiles of the two adaptation textures were always presented in fixed Vernier misalignment ± 16.6 min of arc (ie separated by 33.2 min of arc) along the horizontal axis (ie 2 standard deviations of the Gaussian profile of the orientation modulation). In this way, the relative positions of the two adaptation textures were always displaced in order to achieve either a

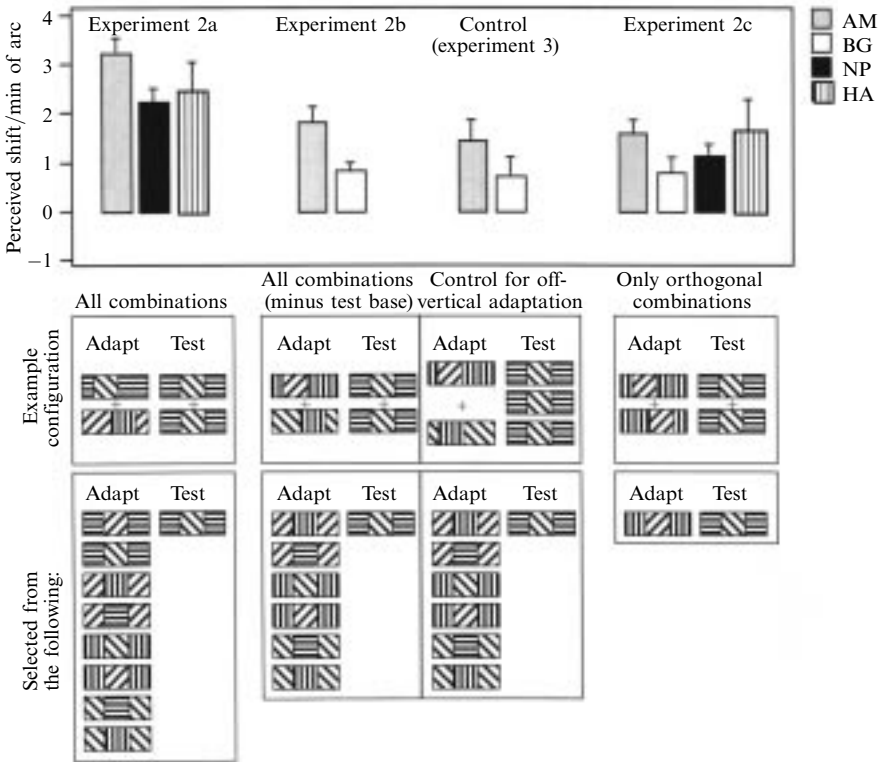


Figure 2. Graph of postadaptation repulsion effects for experiments 2 and 3. In experiment 2, pairs of vertically separated adapting textures were employed in which the peaks of their respective orientation modulations were in vertical misalignment (ie in a left-oblique or right-oblique diagonal configuration). In experiment 3, the pairs of adapting textures were vertically separated to a greater degree and the peaks of their orientation modulations were horizontally displaced in the same direction. Data are plotted (from left to right) for (i) experiment 2a, in which pairs of adapting pairs of textures were randomly selected from a set of eight created by combining base orientations of 0° , 45° , 90° , or 135° , with peaks $+45^\circ$ or -45° from the base; (ii) experiment 2B, in which adapting textures were six of the eight textures of experiment 2a, excluding the two with 0° (horizontal) base orientations; (iii) experiment 3, in which adapting textures were as described in 2b (this experiment was a control for adaptation to off-vertical global orientations—refer to text); (iv) experiment 2c, in which adapting textures were limited to combinations of base and peak orientation that were orthogonal to the tests (90° base and 45° peak). Test textures were of 0° base orientation coupled with 135° peak orientation. In experiments 2a–2c, these tests were vertically arranged into pairs such that their position coincided with the locations of the adaptation textures; in experiment 3, three test textures were vertically arranged such that the outer two coincided with the locations of the adaptation textures while the inner one was in a location that did not receive adaptation. Icons representing examples of adaptation and test textures are presented below each data set, in conjunction with icons representing all the possible textures from which the adaptation and test textures were selected. Response biases were removed by subtracting from the data the average misalignment within the corresponding condition. Data points were then converted such that a positive value indicated repulsion away from the location of the adapting textures (ie on the basis of the adaptation condition, values were multiplied by 1 or -1). Included for each bar are the ± 1 standard error bars.

left-diagonal or right-diagonal configuration. In addition, the absolute positions of the orientation profiles of both adaptation textures were randomised ± 16.6 min of arc along the horizontal axis.

(iv) *Test phase and estimation of direction and magnitude of test misalignment.* Adaptation was immediately followed by a series of ten test trials in which the textures were presented for 0.38 s immediately after which subjects were required to indicate (by button presses)

whether the top orientation modulation appeared to be shifted to the left or right of the bottom orientation modulation. Over the course of one block, consisting of five of these consecutively presented adapt–test pairings, an adaptive staircase procedure (a maximum-likelihood procedure; Best PEST; Pentland 1980) was used to determine for each trial the magnitude and direction (left versus right) of the horizontal position of the upper test relative to that of the lower test, and to estimate the point of subjective alignment of the test textures at the completion of the block.⁽¹⁾

In experiment 5, contrast-modulated (rather than orientation-modulated) textures were employed, and the adaptation procedure involved *two* pairs of adaptation textures in conjunction with one of two pairs of test texture. Details of (and justification for) these stimuli and corresponding procedures are given in the results section for experiment 5.

The two authors and two naïve subjects, all with normal or corrected-to-normal visual acuity, participated in the experiments.

3 Results

3.1 *Experiment 1: The effects of orientation-specific adaptation*

In this preliminary experiment, we sought to confirm the existence of texture adaptation effects by measuring the *combined* effects on perceived location of adaptation specific to absolute orientation content as well as adaptation specific to the shape of orientation change over space. This required that adaptation and test textures contain identical base (0°) and peak (135°) orientations.

For both subjects tested with the above adaptation–test texture combinations, the results of adaptation were in the predicted direction; that is, with the location of test orientation modulations repulsed away from the location of adaptation orientation modulations (AM— 6.13 ± 0.49 min of arc; BG— 4.73 ± 0.54 min of arc).

3.2 *Experiment 2: Evidence of adaptation that is independent of orientation content*

Since orientation content of the test textures in experiment 1 matched that of the adaptation textures, the above effects could be explained on the basis of adaptation of one or both of two putative classes of positionally labelled spatial neuron: orientation-selective neurons that code for *orientation content* by responding to the luminance contrast of a preferred orientation at a particular location, and orientation-opponent neurons that code for *orientation contrast* by responding to a difference in orientation content between two or more locations (in experiment 5 two variants of orientation opponency will be compared).

The aim of the following series of experiments was to distinguish between the relative contributions to adaptation effects from orientation-selective and orientation-opponent neurons. The general rationale was to remove from adaptation effects the contribution of orientation-selective neurons. In experiment 2a alternating adaptation was employed with pairs of textures individually chosen from one of eight orientation modulations whose orientation content was determined by combining one of four different base orientations (0° , 45° , 90° , and 135°) with one of two different peak orientations ($\pm 45^\circ$ from base). The test textures were the same as in experiment 1; that is, with 0° base and 135° peak. Other than the difference in the orientation content of adaptation textures, methods were as described above.

Inspection of the results, presented in figure 2, shows that postadaptation repulsion effects occurred even when the orientation content of adaptation textures did not systematically match that of the test textures.

⁽¹⁾The manipulation of ‘position’ in relation to the adaptation and test textures refers to the horizontal position of the orientation modulation of the textures, not the physical position of the rectangular texture patches. The patches themselves were always in alignment (see figures 1 and 3 for clarification).

In experiment 2b, the orientation overlap between adaptation and test textures was reduced still further by excluding from the adaptation stimuli textures whose base orientation matched that of the test stimuli (ie 0°). The six remaining adaptation stimuli (bases of 45° , 90° , and 135° , with peaks $\pm 45^\circ$ from the base) were employed in conjunction with the same test textures as employed in experiments 1 and 2a. The results (see figure 2) show that postadaptation repulsion effects occurred.

Finally, in experiment 2c, only adaptation stimuli with orientation content orthogonal to the test stimuli were employed. This meant adapting to pairs of textures with a single orientation profile defined by base of 90° and peak of $+45^\circ$. Again, the results (see figure 2) show that adaptation effects occurred.

Overall, the adaptation effects reported in experiment 2 suggest the existence of neural mechanisms, perhaps orientation-opponent neurons, that code for the location of orientation change irrespective of orientation content. We base this conclusion on the fact that luminance or contrast adaptation could not have been involved since there were no variations in these dimensions in our adaptation and test stimuli, and because of the presence of large differences in orientation content between the adaptation and test textures (particularly in experiment 2c).

It is interesting to note that the adaptation effects of experiment 2 were of lesser magnitude than those obtained in experiment 1. As outlined in section 4, this result is consistent with the idea that in experiment 1, where there was complete overlap of orientation content between adaptation and test textures, postadaptation repulsion effects were due to adaptation both of orientation-selective neurons and orientation-opponent neurons, whereas in experiment 2 (especially 2c, where orientation of adaptation and test textures was orthogonal), postadaptation repulsion effects were due exclusively to adaptation of orientation-opponent neurons.

3.3 *Experiment 3: Controlling for adaptation to global, off-vertical orientations*

Before considering further the implications of the adaptation effects uncovered in experiment 2, it was first necessary to discount a possible confound: that the adaptation texture pairs inadvertently adapted neurons with large receptive fields oriented such that they coincided with the angle formed between orientation peaks of the textures. It is conceivable that adaptation of this sort would result in positional displacements of subsequently presented pairs of test stimuli in the global orientation tilted to the opposite side of vertical. A similar suggestion has been made to account for adaptation effects using luminance-defined and contrast-defined adaptation-test combinations (eg Wolfe 1987; Hess and Doshi 1995).

To preclude adaptation to global, off-vertical orientations, we adapted subjects to pairs of *vertically aligned* orientation-modulated textures separated by 69.7 min of arc. The use of aligned adaptation textures meant that adaptation could still occur for position but not for global orientation away from vertical (see Whitaker et al 1997). The effects of adaptation to this configuration were measured by using tests composed of three vertically aligned textures. The placement of the outer test textures coincided with that of the adaptation textures, with the location of their orientation modulations shifted together horizontally by ± 16.6 min of arc from the adaptation modulations (ie 1 standard deviation of the Gaussian profile of each modulation). The placement of the central test texture was such that it occupied the gap, midway between the outer tests, that did not receive adaptation. The location of orientation modulation of this texture was determined by subjects' left/right responses to the direction of misalignment of the texture relative to the outer test textures (after the method described in section 2; see figure 2 legend for a depiction of the adaptation arrangement). Aside from the difference in adaptation and test configurations, texture dimensions and methodologies were as described for experiment 2b.

The results of adaptation to the vertically aligned textures are included in figure 2, and show that positional misalignments were obtained, thus precluding a simple explanation based on adaptation to global, off-vertical orientations.

3.4 Experiment 4: Controlling for artifacts of the filtering process

The filters employed in experiments 1 to 3 to create orientation-modulated textures were designed in frequency space to have the desired bandpass characteristics (described in section 2.1). An anonymous reviewer expressed concern that the presence of ripples in the 2-D frequency response profile of the filters may have introduced spatial-frequency and/or orientation content in the textures that might be correlated spatially with the orientation-modulation. The concern is that subjects may have been adapting to spurious visual content rather than to orientation content or orientation change. Although ripples are a problem inherent in all filtering methods, ours would have been more pronounced since no tapering method was used to introduce a transition band between the filters' passbands and stopbands in frequency space.

In the present control experiment, filters were again designed in frequency space but with three modifications made to significantly reduce the amplitude of ripples in the frequency-response profile: (i) frequency was sampled at a much finer grain ($0.35 \text{ cycle deg}^{-1} \text{ sample}^{-1}$), (ii) a *smooth* transition band between passband and stopband was introduced, and (iii) filtering was performed entirely in frequency space. Specifically, the desired frequency response was given by a squared Gaussian distribution of the following form:

$$H(f, \theta) = \exp\left\{-0.5 \left[\frac{\ln(f/12.6)}{0.416}\right]^4\right\} \exp\left\{-0.5 \left[\frac{\theta - \theta_{\text{centre}}}{10}\right]^4\right\},$$

where $H(f, \theta)$ is the desired frequency response, f is the spatial frequency, and θ is orientation (note: the squaring served to narrow the transition band and more closely approximate the frequency response used in the other experiments). Experiment 2c was then replicated with these filtered textures. In this experiment, only adaptation stimuli with orientation content orthogonal to the test stimuli were employed (ie base of 90° ; peak of 45°).

The repulsion effects obtained were comparable in direction and magnitude to those obtained in experiment 2c. For AM the effect was 1.30 ± 0.47 min of arc (compared with 1.92 ± 0.34 min of arc in experiment 2c); for NP the effect was 1.05 ± 0.34 min of arc (compared with 1.37 ± 0.28 min of arc in experiment 2c). It is unlikely, therefore, that the effects obtained in experiments 1 to 3 can be attributed in a simple fashion to artifacts introduced by the filtering method.

3.5 Experiment 5: Single-opponent versus double-opponent neurons

Having established in experiment 2 the existence of a neural code for orientation change, we sought to characterise the receptive-field organisation of the visual neurons comprising this code. We considered two likely candidates: orientation single-opponent and orientation double-opponent neurons. Single opponency describes neurons with receptive fields arranged into concentric excitatory/inhibitory regions selective for a single orientation (eg vertical-ON centre / vertical-OFF surround). These neurons are analogous to the second-stage filters of Graham and Sutter's (1998) 'complex channels' (Sutter et al 1995). Double-opponency describes the superimposition of two concentric receptive fields of opposite orientation selectivity and response polarity (eg vertical-ON and horizontal-OFF centre / vertical-OFF and horizontal-ON surround).

Although both types of orientation opponency appear to exist (von der Heydt et al 1992; Knierim and Van Essen 1992; Olavarria et al 1992; Sillito et al 1995; Zipser et al 1996), it is generally assumed that double opponency is required to code unambiguously for orientation change (Rubenstein and Sagi 1993; Kingdom and Keeble 1996;

Gray and Regan 1998), since single-opponent neurons respond both to orientation change over space and contrast change over space. Experiment 5 distinguished between the contributions from these two types of neuron by having subjects alternately adapt to two pairs of misaligned textures. These textures contained only portions of the orientation content of the original textures, that is, they were *orientation-sampled* textures. The direction of misalignment between these two orientation-sampled texture pairs was reversed such that equal effects from adaptation to each pair would result in cancellation (figure 3).

One texture pair was produced by filtering out orientations other than those falling within $\pm 10^\circ$ of the peak of a hypothetical orientation-modulated texture. These *grating* textures would stimulate and adapt both single-opponent and double-opponent neurons having central excitatory regions tuned to the orientation peak (see figure 3). The second texture pair was produced by filtering out orientations other than those falling within $\pm 10^\circ$ of the peaks of two orthogonal orientation-modulated textures superimposed on the same location [each at 50% (half) contrast; see figure 3]. These *plaid* textures would stimulate and adapt only single-opponent neurons having central excitatory regions tuned to either orientation peak. These orientation-sampled textures were, in effect, contrast modulations of either a single orientation (in the case of grating textures) or two orthogonal orientations (in the case of plaid textures).

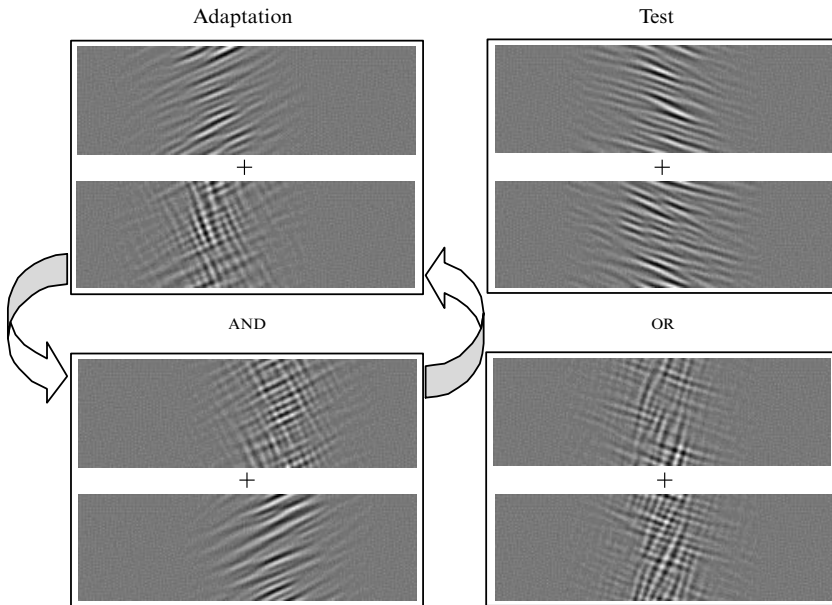


Figure 3. An example of the orientation-sampled adaptation and test textures employed in experiment 5. In the example shown, a left-shifted grating-up/plaid-down test combination is alternated with a right-shifted plaid-up/grating-down test combination, with positional shifts tested with either two grating textures (upper pair in the figure) or two plaid textures (lower pair in the figure).

The rationale behind placing these two types of adaptation stimulus in competition was that resultant shifts in perceived location of test textures would reflect the *additional* contribution to adaptation from double-opponent neurons (which is only possible when grating adaptation is used in conjunction with grating tests). To illustrate the logic of this consider the alternating adaptation configuration depicted in figure 3. The first adaptation texture consists of a pair of left-shifted textures; the upper of these is a grating texture composed of 22.5° orientation, whereas the lower of these is a plaid

texture composed of 22.5° and 112.5° orientations (each at half the contrast). Note that the grating texture should adapt single-opponent neurons tuned to 22.5° as well as double-opponent neurons tuned to 22.5° —centre/ 112.5° —surround, whereas the plaid texture should adapt only single-opponent neurons (those tuned to 22.5° and those tuned to 112.5°) but not double-opponent neurons since their requirement for orientation contrast over space would not be met. Note also that when alternated over time with right-shifted versions of the same textures but in opposite vertical arrangement (ie plaid above, grating below), there should be a cancellation of adaptation of single-opponent neurons, but a residual effect of adaptation of double-opponent neurons. When measured with the appropriate test texture (a grating but *not* a plaid), this should result in a rightwards shift of the upper test texture and a leftwards shift of the lower test texture. Failure to find such a residual effect would contradict the involvement of orientation double-opponent neurons.

The procedure employed for the alternating adaptation experiment was as follows: During each adaptation phase of 72 s, random pairings of grating and plaid adapting textures, both shifted to one side (left or right) of the test locations, were presented in alternation for a total of five cycles. With each alternation, grating and plaid adaptation textures were shifted to the other side of the test locations, and vertical ordering of the two types of texture was reversed. For example, a plaid–top/grating–bottom pairing, with orientation modulations of both shifted to the left of centre, would be alternated with a grating–top/plaid–bottom pairing, with orientation modulations of both shifted to the right of centre.

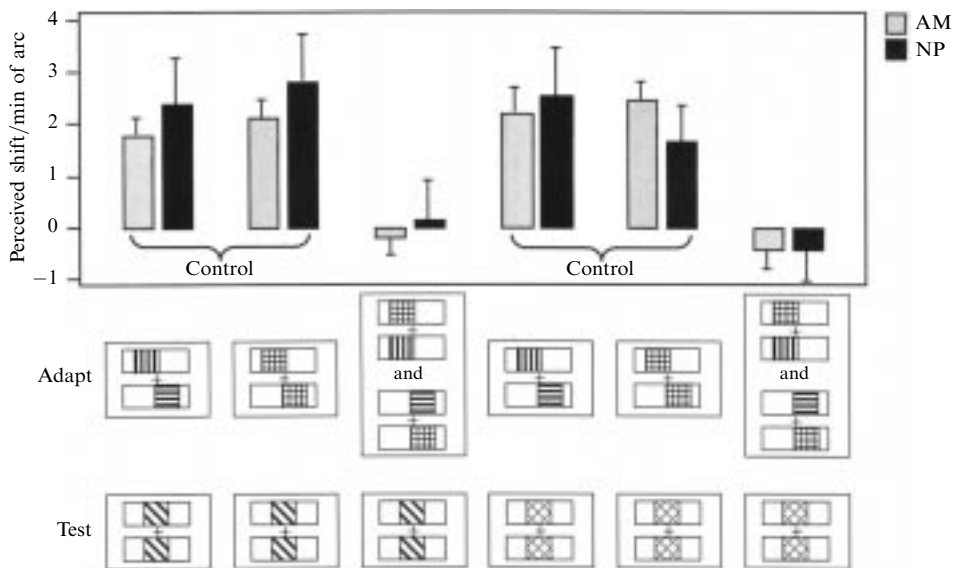


Figure 4. Graph of postadaptation repulsion effects for experiment 5. Data are plotted (from left to right) for (i) grating adaptation and grating test; (ii) plaid adaptation and grating test; (iii) alternating grating and plaid adaptation and grating test; (iv) grating adaptation and plaid test; (v) plaid adaptation and plaid test; (vi) alternating grating and plaid adaptation and plaid test. Icons representing the adaptation and test conditions are presented below each data set. Response biases were removed by subtracting from the data the average misalignment within the corresponding condition. Data points were then converted such that a positive value indicated repulsion away from the location of the adapting textures (ie on the basis of the adaptation condition, values were multiplied by 1 or -1). For data sets (iii) and (vi), the direction of repulsion is taken to be the direction consistent with adaptation of single-opponent neurons. Included for each bar are ± 1 standard error bars.

Within individual blocks, test textures were either both grating textures (top test pair in figure 3) or both plaid textures (bottom test pair in figure 3). The orientation content of the textures was 22.5° and/or 112.5° , versus 67.5° and/or 157.5° . Within each block, the test textures contained the orientation(s) that was/were not used during adaptation. In all other respects, methods were identical to the orientation-modulated experiments.

For the rationale underlying the alternating adaptation experiment to hold, it was first necessary to demonstrate that adapting to each texture pair in isolation, and testing with each texture type separately, produces positional shifts of equal magnitude and in opposite directions. Inspection of the results in figure 4 (identified on the figure as 'control' conditions) confirms this prediction.

Figure 4 also shows the results of the competitive adaptation experiment, with positional shifts assessed separately in grating and plaid tests. Inspection of figure 4 reveals complete cancellation of adaptation effects, suggesting that the same neural mechanisms, presumably single-opponent neurons, are adapted both by orientation-sampled gratings and by plaids.

4 Discussion

There is a growing body of psychophysical evidence consistent with the existence of an explicit code for orientation change based on the operation of orientation-opponent neurons: (i) sensitivity to orientation-modulated textures is well modelled by the operation of neurons tuned to the spatial frequency of orientation change (Kingdom et al 1995; Kingdom and Keeble 1996; Gray and Regan 1998), as is the perceived location of these textures as a function of the skewness of their orientation distributions (Prins and Mussap 2000); (ii) masking of orientation-modulated textures by luminance-modulated gratings is dependent on global structure rather than on local orientation content (Arsenault et al 1999); and (iii) postadaptation detection thresholds for orientation-modulated textures demonstrate selectivity for the axis of orientation modulation (Kwan and Regan 1998).

In the present experiments, we applied the adaptation technique to explore the positional selectivity of putative orientation-opponent neurons. We obtained evidence consistent with the proposition that these neurons are positionally labelled, that is, that they retain the *local signs* (Lotze 1885) of their retinal inputs, presumably by retaining the spatial organisation of these inputs. This might occur in the manner outlined by Lotze (1885, volume 1, pages 319–320) in the context of visually guided motor responses, that is arising by virtue of spatially specific connections between retinal receptors and motor fibres.⁽²⁾ A local-sign explanation fits in well with the results of experiment 3, in which location aftereffects were obtained even when adaptation to global, off-vertical orientation (ie the orientation of the virtual line connecting the peaks of the orientation modulations of the adaptation textures) was prevented.

The results of our experiments demonstrated also that the responses of putative orientation-opponent neurons generalise across the orientation content of textures. The critical result was that postadaptation repulsion effects did not require that the orientation content of test textures match, or even overlap, that of the adaptation textures. This suggests that outputs of orientation-opponent neurons are pooled (perhaps at a higher level) across orientation prior to contributing to the representation of location. If this were not the case then adaptation to orientation-modulated textures would

⁽²⁾Of course, our experiments do not address the issue whether the positional labelling proposed exists exclusively in the form of visually guided motor responses or whether it exists independently in the form of a *perceived* space that our textures occupy. This general issue is explored by Morgan (1977, pages 145–149). In addition, the history of local signs as applied to Vernier acuity is reviewed in detail by Westheimer and McKee (1977).

only repulse the perceived locations of textures of similar orientation content (and no adaptation effects would have occurred in experiment 2c). Just such an early pooling of orientation has been observed in the detection and discrimination of contrast-defined patterns (Dakin and Mareschal 2000; Morgan et al 2000; Mussap 2001).

As to the question of the receptive-field organisation of the underlying neurons, the results of our competitive-adaptation experiment suggest the involvement of neurons that are single-opponent for orientation, and thus argue against the view that orientation double-opponent neurons are required (Rubenstein and Sagi 1993; Kingdom and Keeble 1996; Gray and Regan 1998). This is an interesting finding because it suggests that similar neural mechanisms code for the location of orientation change as well as for the location of contrast change within an orientation band. This in turn highlights the need for the visual system to retain information about orientation content (presumably coded for by the orientation selectivity of the neurons involved) in order to disambiguate orientation change from contrast change. Information about local orientation content would also be required in order for the visual system to disambiguate the *direction* of orientation change (ie clockwise versus anticlockwise) in orientation-modulated textures; something which single-opponent neurons would be unable to determine.

It has been reported that superimposed pairs of orientation-modulated textures of the same base but opposite direction of orientation change produce elevated detection thresholds (Kingdom and Keeble 2000). Since both single-opponent and double-opponent neurons should respond well to such superimposed pairs, this result could be taken as evidence against the idea that orientation opponency underlies detection of orientation-modulated textures. However, Kingdom and Keeble's orientation-modulated components were in anti-phase such that their textures contained *inconsistent*, that is non-parallel, lattice-like patterns of grouping structure. (Their stimuli were, in effect, orientation-*bandwidth*-modulated textures.) Using similar superimposed textures where the components were in-phase and, therefore, the grouping structure was consistent, that is parallel, Prins et al (submitted) demonstrated that such textures are as visible as non-superimposed controls. Therefore, while the results obtained with superimposed textures highlight the importance of local grouping structure to texture perception, they do not necessarily rule out a contribution from orientation-opponent neurons.

While our adaptation study, in using single-component textures with a single direction of local grouping, could not test for grouping effects on texture perception, some previous research has. For example, it has been shown that increasing the number of dots placed along straight paths facilitates detection of global discontinuities in textures formed from these dots (Link and Zucker 1987) and facilitates segmentation of these textures from textures containing random grouping structure (Or and Zucker 1989).

In total, our results point to the existence of a generic code for orientation change over space based on the outputs of orientation single-opponent neurons. This conclusion does not, however, preclude a contribution to texture perception from orientation double-opponent neurons.

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