Adaptation to global structure induces spatially remote distortions of perceived orientation

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Adapting neurons at early stages of cortical visual processing to an oriented grating pattern suppresses responses to nearby orientations, causing a shift in the population response to subsequently viewed stimuli and an illusory distortion of perceived orientation: the classic tilt aftereffect. Perception of stimuli that are presented at unadapted spatial locations or that have a substantially different spatial frequency to the adapting stimulus remains veridical however by virtue of the fact that they stimulate a population of neurons distinct to those affected by adaptation. Here, we demonstrate that adapting to complex visual patterns containing circular or radial structure induces distortions of perceived orientation with markedly different characteristics to those traditionally reported. These novel effects occur in remote, unadapted spatial regions and are immune to manipulations of spatial frequency, rendering them incompatible with direct orientation-specific adaptation in early visual cortex. Rather, our results are most readily explained by a recurrent network in which global form encoding mechanisms that combine orientation information across space actively inhibit the local orientation detectors over which they pool.

Keywords: adaptation, orientation, global form, feedback connections


Introduction

Processing in the visual cortex is typically characterized within a hierarchical feedforward framework, where each successive stage combines or pools information from the preceding stage (Felleman & Van Essen, 1991; Fukushima, 1980; Riesenhuber & Poggio, 1999, 2000). At the first stage of processing in primary visual cortex (V1), neurons encode relatively simple image features, such as the orientation and spatial frequency of lines and edges falling within a small region of the visual field. The subsequent convergence of inputs into successive levels of analysis produces neurons with progressively larger receptive fields, preferences for increasingly complex stimulus attributes and greater tolerance to changes in stimulus position and scale. For encoding of spatial form, this analysis appears to be carried out along a pathway of cortical areas projecting ventrally from V1, culminating in highly complex, object-based representations in inferotemporal cortex (Fujita, Tanaka, Ito, & Cheng, 1992; Kobatake & Tanaka, 1994; Tsunoda, Yamane, Nishizaki, & Tanifuji, 2001). A parallel, though not strictly independent, cortical pathway projects dorsally from V1 to parietal cortex and is thought to specialize in motion analysis (see Born & Bradley, 2005; Maunsell & Newsome, 1987; Merigan & Maunsell, 1993; Ungerleider & Mishkin, 1982).

Throughout the visual processing hierarchy neurons adapt to their input, giving rise to a rich variety of perceptual aftereffects, ranging from distortions of low-level stimulus properties such as orientation (Gibson, 1933; Gibson & Radner, 1937), spatial frequency (Blakemore, Nachmias, & Sutton, 1970; Blakemore & Sutton, 1969), motion (see Mather, Verstraten, & Anstis, 1998) and color (McCollough, 1965; Webster & Mollon, 1991) to complex high-level attributes such as facial identity (Leopold, O’Toole, Vetter, & Blanz, 2001; Leopold, Rhodes, Müller, & Jeffery, 2005; Webster & MacLin, 1999) and object viewpoint (Fang & He, 2005). Furthermore, recent physiological evidence demonstrates that the effects of adaptation at one level can be inherited by subsequent processing stages (Kohn & Movshon, 2003). In contrast, it is unknown whether activity at higher levels of analysis can exert a reciprocal influence on the adapted state of neurons in preceding stages. Feedback connections are known to exist in comparable numbers to feedforward connections in visual cortex (Felleman, Xiao, & McClendon, 1997; Rockland, Saleem, & Tanaka, 1994; Rockland & Van Hoesen, 1994; Zeki & Shipp, 1989); however, it is unclear what role (if any) they play in neural adaptation.

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One of the most widely studied and best understood perceptual adaptation phenomena is the tilt aftereffect. First described over 70 years ago, it is a robust, misperception of stimulus orientation that occurs following extended viewing of a simple oriented line or grating patch (Campbell & Maffei, 1971; Gibson, 1933; Gibson & Radner, 1937; Mitchell & Muir, 1976; Muir & Over, 1970; Ware & Mitchell, 1974). The magnitude and direction of the tilt aftereffect vary systematically as a function of the relative angle between adapting and test stimuli. For angles less than 60 deg, the perceived orientation of the test stimulus is repelled away from that of the adaptor, with peak effect typically occurring with an angle of around 15 deg. A weaker, attractive effect is sometimes found when the orientations of adapting and test stimuli are separated by 75–80 deg.

There is considerable converging evidence that the neural locus of tilt aftereffects induced by luminance-defined stimuli resides in early visual cortex. Physiological studies of orientation-tuned cells in V1 have shown that adaptation results in suppression of responses near the adapting orientation (Dragoi, Sharma, & Sur, 2000; Maffei, Fiorentini, & Bisti, 1973; Müller, Metha, Krauskopf, & Lennie, 1999). This suppression, when implemented in population-based orientation coding models, predicts comparable perceptual misperceptions to those measured psychophysically (Clifford, Wenderoth, & Spehar, 2000; Jin, Dragoi, Sur, & Seung, 2005; Wainwright, 1999). Further evidence for a link with V1 can be drawn from analysis of the conditions under which tilt aftereffects do not occur. As a general rule, perceptual aftereffects only arise when the population of neurons activated by a test stimulus includes some or all of those affected by adaptation. Because each V1 neuron only responds to a spatially restricted portion of the visual field, adapting and test stimuli presented at different locations will activate largely independent populations of neurons and should therefore result in little or no aftereffect. Consistent with this prediction, it has been shown that the tilt aftereffect is tightly tuned for position, occurring only when the location of the test stimulus overlaps with the adapted spatial region (Gibson & Radner, 1937). Tilt aftereffects also diminish as the spatial frequency of adapting and test patches is decoupled (Ware & Mitchell, 1974) in a manner consistent with the band-pass spatial frequency tuning of neurons in V1 (De Valois, Albrecht, & Thorell, 1982).

There is, however, reason to believe that not all tilt aftereffects can be explained by processing intrinsic to V1. Tilt aftereffects have been demonstrated using “illusory” or “subjective” contours, distinct surface boundaries that are perceived despite the absence of any luminance cue (e.g., Berkley, Debruyyn, & Orban, 1994; Paradiso, Shimojo, & Nakayama, 1989; van der Zwan & Wenderoth, 1995). These stimuli contain little or no Fourier energy at the orientation of the perceived edge and have been shown to elicit selective responses in V2 but not V1 (von der Heydt, Peterhans, & Baumgartner, 1984; but see Ramsden, Hung, & Roe, 2001; Sheth, Sharma, Rao, & Sur, 1996). In contrast to the specificity of traditional tilt aftereffects, these effects exhibit a degree of cue invariance, transferring between contours defined by a variety of different attributes (Berkley et al., 1994; Cruickshank & Schofield, 2005; Hawley & Keeble, 2006; Paradiso et al., 1989).

In this study, we investigate the properties of tilt aftereffects induced by adaptation to stimuli containing global orientation structure requiring additional processing beyond that carried out in early visual cortex. In contrast to the simple Cartesian gratings and contours typically used in studies of the tilt aftereffect, non-Cartesian stimuli such as concentric or radial patterns comprise multiple orientations. Encoding structure of this type requires extensive pooling of local orientation information across space, processes that cannot be accomplished in V1 (Smith, Bair, & Movshon, 2002) or V2 (Smith, Kohn, & Movshon, 2007). Rather, neural populations capable of selectively encoding global orientation structure first appear at intermediate levels of the form processing hierarchy, such as visual area V4 (Gallant, Braun, & Van Essen, 1993; Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Gallant, Shoup, & Mazer, 2000; Wilkinson et al., 2000). According to a traditional hierarchical feedforward framework, mechanisms underlying the tilt aftereffect should be unaffected by processing at these subsequent stages of form analysis. Here, we demonstrate that this is not the case, and that global orientation structure contained within an adapting stimulus can exert a marked influence on the adapted state of local orientation coding mechanisms.

### Methods

#### Observers

Five adult observers completed each of the experiments: two were authors (NWR and BSW) and three were naive to the specific purposes of the study. All had normal or corrected-to-normal visual acuity.

#### Stimuli

Visual stimuli were preloaded on a Cambridge Research Systems ViSaGe and displayed at a viewing distance of 32.6 cm on a gamma-corrected Mitsubishi Diamond Pro 2045U CRT monitor (1024 × 768 resolution, 100 Hz framerate, 47 cd/m² background luminance).

#### Adapting patterns

A variety of different adapting patterns were used, the details of which are summarized below:
a. **Full concentric adaptor.** 2 c/deg, 100% contrast concentric grating with a radius of 25.6 deg. The contrast of the outer edge was ramped off via a quarter cycle cosine function over 1.6 deg.

b. **Spatially remote concentric adaptor.** Identical to (a), with the exception of the addition of a zero-contrast annulus covering eccentricities of 8.5 to 11.5 deg. Beyond the inner and outer edges of the annulus, contrast was ramped back to 100% via a quarter cycle cosine function over 2 deg. Apart from where otherwise stated, the spatial frequency of the carrier grating was 2 c/deg.

c. **Local adaptor patch.** Small wedge of the concentric adaptor (a), restricted to a region within inner and outer radii of 8.5 and 11.5 deg and between polar angles of 0 and 30 deg relative to fixation.

d. **Spatially remote radial adaptor.** Radial grating, the frequency of which (126 cycles per circumference) was chosen such that the local spatial frequency at 10 deg eccentricity was equal to that of the test stimulus (2 c/deg). A similar contrast envelope was used for the spatially remote concentric adaptor (b), except for an additional zero-contrast central region introduced to avoid spatial aliasing (zero contrast for eccentricities <3.33 deg, 2 deg cosine ramp).

e. **Spatially remote Cartesian adaptor.** 2 c/deg grating oriented 15 deg from vertical, constrained by an identical contrast envelope to that described above for the spatially remote concentric adaptor (b).

### Test stimuli

Test stimuli were Gabor patches consisting of a 2 c/deg sine phase grating multiplied by a Gaussian contrast envelope ($\sigma = 0.5$ deg, 50% peak contrast) and were presented at an eccentricity of 10 deg in the top-right quadrant of the display. In an initial experiment measuring the angular dependence of tilt aftereffects, test stimuli were presented at one of 7 positions, forming polar angles of 0, 15, 30, 45, 60, 75, and 90 deg relative to fixation. All positions were randomly interleaved within a run of trials.

In subsequent conditions, test patches were presented at the position along the iso-eccentric arc at which the local (physical or implied) orientation of the adapting pattern was 15 deg from vertical. Spatial frequency tuning was investigated by fixing the spatial frequency of the test patch and by manipulating the spatial frequency of the adapting pattern across different testing sessions.

### Procedure

Observers were required to maintain fixation on a small dot at the center of the screen while the adapting pattern was presented (Figure 1A). In order to avoid the build up of a retinal afterimage, all adapting patterns were counter-phase flickered at 2.5 Hz. Following a period of adaptation (30 s initial, 3 s top-up between each trial), a small Gabor test patch was presented briefly at one of a number of locations along an iso-eccentric arc in the upper-right quadrant of the display. Observers judged whether the test patch was oriented clockwise or counter-clockwise of vertical.

Tilt aftereffects were quantified by measuring the shift in subjective vertical: the physical orientation required to elicit equal proportions of clockwise and counter-clockwise responses (Figure 1B). Test patch orientation was controlled via a method of constant stimuli with 30 trials at each of 7 different orientations. The step size between successive test orientations was fixed for each observer, whereas the entire range was offset where required so as to capture the full psychometric function.

For each observer, proportions of “clockwise” responses were fit with a logistic function of the form

$$P(\text{clockwise}) = \frac{1}{1 + e^{-\frac{X_{PSV}-\text{JND}}{\text{JND}}}}$$

where $X$ indicates the orientation of the test patch, PSV indicates the point of subjective vertical, and JND is a slope parameter defining one just noticeable difference. Tilt-aftereffect estimates were obtained by calculating the change in the PSV relative to a baseline condition with no adaptation.

### Results

**Adaptation to concentric structure induces TAEs at unadapted locations**

Adaptation to a full concentric pattern produced tilt aftereffects that, plotted as a function of the local (tangential) orientation of the adaptor at the test location, exhibit a profile comparable to that previously demonstrated using simple Cartesian grating stimuli (Figure 2, red symbols) (Campbell & Maffei, 1971; Mitchell & Muir, 1976; Muir & Over, 1970; Ware & Mitchell, 1974). However, whereas traditional tilt aftereffects typically require spatial overlap between adaptor and test, tilt aftereffects following adaptation to concentric structure do not. When an annular ring encompassing each of the test sites was removed from the adapting stimulus, significant repulsive tilt aftereffects remained for all observers (Figure 2, blue symbols).

**Distinct spatial frequency tuning profiles of traditional and spatially remote TAEs**

A key property of global form mechanisms is that they pool across local orientation detectors with preferences for different spatial scales, resulting in broad tuning for spatial...
frequency (Achtman, Hess, & Wang, 2003; Dakin & Bex, 2001). We reasoned that if the global stage of analysis plays a role in producing spatially remote tilt aftereffects, these effects should also be broadly tuned. Figure 3 compares the spatial frequency tuning of spatially remote tilt aftereffects to those produced using a local adapting stimulus. Consistent with previous findings (Ware & Mitchell, 1974), tilt aftereffects following local adaptation were band-pass tuned, with the largest effects occurring when adaptor and test spatial frequencies were equivalent (Figure 3, black symbols). In striking contrast, manipulations of spatial frequency had no systematic effect on the magnitude of spatially remote tilt aftereffects induced by adaptation to a concentric pattern (Figure 3, blue symbols). This difference in spatial frequency tuning produces a reversal of the relative magnitude of effects induced by the two types of adapting stimuli. With an equivalent adapting/test spatial frequency (21 c/deg), TAEs following local adaptation were, on average, ~2.5 times larger than spatially remote effects. However, local tilt aftereffects were an equivalent factor smaller than spatially remote aftereffects when the adapting spatial frequency was three octaves lower than that of the test stimulus (23 c/deg).

Spatially remote TAEs require adaptors containing complex global orientation structure

In order to further test the specificity of the spatially remote tilt aftereffects, we next experimented with different forms of adapting stimuli. To enable direct compar-
ison between conditions, the test stimulus was presented at a position where the local orientation implied by adapting stimulus was 15 deg from vertical. As shown in Figure 4, similar magnitude effects were found when the adapting stimulus contained radial, rather than concentric structure. However, adaptation to an oriented Cartesian grating of comparable size produced little or no effect. Together, these results suggest that spatially remote tilt aftereffects occur only when the adapting stimulus contains global structure, the encoding of which requires pooling of different orientation signals across space.

**Discussion**

Mirroring the tuning properties of orientation-selective neurons in V1, tilt aftereffects obtained with grating stimuli are both restricted to the adapted location and are band-pass tuned for spatial frequency. In direct contrast, the present study demonstrates that adaptation to stimuli containing circular or radial structure produces novel tilt aftereffects that are characterized by neither of these properties. Clearly, these spatially remote, spatial frequency-insensitive distortions of perceived orientation must arise through neural mechanisms that are at least partially distinct from those mediating traditional tilt aftereffects. Here, we consider the plausibility of three classes of explanation for these effects: (i) adaptation occurring within V1, (ii) adaptation in extrastriate cortex, or (iii) adaptation mediated by feedback from extrastriate cortex to V1.

**Hypothesis 1: Adaptation in V1**

As discussed earlier, perceptual aftereffects are thought to be limited to situations in which the population of neurons used to encode a particular test stimulus overlaps...
with those affected by adaptation. With this in mind, it is tempting to simply dismiss the possibility that spatially remote tilt aftereffects could result from adaptation in V1 since adapting and test stimuli that are presented at different spatial locations ought to activate different neurons at this level. However, more detailed consideration is required.

First, it is important to note that spatial segregation of adaptor and test stimuli does not guarantee complete independence between active neuronal populations in V1. Indeed, given that observers could have made small eye movements during or after adaptation, it is reasonable to assume that some common neuronal activation by adapting and test patterns might have occurred. Making a quantitative estimate of the degree of co-activation is difficult for a number of reasons, not least the variability of V1 classical receptive field size estimates with different stimuli and methods of characterization (for a discussion, see Cavanaugh, Bair, & Movshon, 2002). Regardless, we can be confident that an artifact of this sort does not explain our results. If the spatially remote stimulus were to directly adapt the classical receptive fields of a relatively small proportion of the neurons subsequently involved in encoding the test stimulus, the resulting aftereffect should be a reduced magnitude version of that obtained with a spatially superimposed adaptation. Accordingly, this explanation predicts that effects obtained using local and spatially remote adaptors should exhibit comparable spatial frequency tuning profiles—a prediction that is clearly at odds with our findings.

An additional consideration is the potential role of surround effects in V1. It is well established that neural responses elicited by stimuli presented within a V1 classical receptive field can be modulated by the presence of stimuli in surrounding areas. These modulatory effects can be facilitatory or suppressive in nature (Blakemore & Tobin, 1972; Fries, Albus, & Creutzfeldt, 1977; Hubel & Wiesel, 1965; Kapadia, Ito, Gilbert, & Westheimer, 1995;
Nelson & Frost, 1978) and have been linked to a variety of perceptual phenomena including contour integration (Field, Hayes, & Hess, 1993), filling-in (Toth, Rao, Kim, Somers, & Sur, 1996), and texture segmentation (Lamme, 1995). Might it be possible that adaptation of V1 surround mechanisms underlie spatially remote tilt aftereffects? For this explanation to hold, surround adaptation would have to suppress responses elicited from within the classical receptive field. However, available evidence suggests that surround and classical receptive field mechanisms are independently adaptable (Cavanaugh et al., 2002; Webb, Dhruv, Solomon, Tailby, & Lennie, 2005). That is, the primary effect of surround adaptation is to reduce the modulatory effect of stimuli presented subsequently in the surround. Since our small test stimuli provide minimal stimulation of surround mechanisms, it is therefore unlikely that surround adaptation would produce any effect. Furthermore, even if surround adaptation did alter the response to stimuli within the classical receptive field, it is questionable that it would produce similar effects to those we report. Large stimuli covering substantial regions of the surround invariably exert a suppressive influence on the response of V1 neurons. Surround adaptation might therefore be expected to result in a reduction of suppression, precisely the opposite of what is required to produce a repulsive tilt aftereffect.

Hypothesis 2: Adaptation beyond V1

Although traditional tilt-aftereffect properties closely mirror tuning characteristics in early visual cortex, the lack of positional specificity and broad spatial frequency tuning of tilt aftereffects following adaptation to globally structured stimuli suggests the involvement of areas higher in the form processing hierarchy. An interesting parallel can be found in the literature on motion adaptation, where aftereffects with contrasting...
properties are reported to occur depending on the nature of the test stimulus used. Motion aftereffects measured with static test stimuli are typically restricted to the adapted location (Anstis & Gregory, 1965; Masland, 1969) and are tuned for spatial frequency (Cameron, Baker, & Boulton, 1992; Over, Broerse, Crassini, & Lovegrove, 1973). In contrast, studies using dynamic (flickering or drifting) test stimuli have reported motion aftereffects that occur in unadapted spatial regions (Snowden & Dubé, 1992) and are more broadly tuned for spatial frequency (Ashida & Osaka, 1994). The prevailing view is that these differences most likely reflect adaptation at different levels of motion analysis in the cortex; it is thought that static motion aftereffects are a manifestation of adaptation of local motion detectors in early visual cortex, whereas their dynamic counterparts result from adaptation in higher dorsal stream areas such as V5/MT, which integrate local motion information across space.

As described earlier, studies using adapting contours defined by changes in stimulus attributes other than luminance have reported tilt aftereffects that are less tightly coupled to the properties of the adapting stimulus (Berkley et al., 1994; Cruickshank & Schofield, 2005; Hawley & Keeble, 2006; Paradiso et al., 1989). The discovery of these “cue-invariant” effects has prompted the suggestion that adaptation mechanisms capable of producing tilt aftereffects might exist in V2, where robust neuronal responses to these types of contours are found. In light of the fact that orientation signals contained within stimuli in the present study were all luminance-defined, it is not clear what role such mechanisms could have played. Certainly, it is worth noting that spatially remote adaptation conditions did introduce a contrast-defined orientation signal at the edges of the zero-contrast annulus. However, since this applies equally to remote Cartesian and remote concentric/radial stimuli, it is clear that the edges of the annulus could not have been the critical factor producing the observed tilt aftereffects.

Although perception of orientation is generally thought to be driven by the pattern of neuronal activation in early visual cortex (Haynes & Rees, 2005; Kamitani & Tong, 2005), orientation-selective neurons with relatively large receptive fields are known to exist at intermediate levels of the ventral stream such as in areas V3 and V4 (Desimone & Schein, 1987; Felleman & Van Essen, 1987). The results of recent functional neuroimaging studies further demonstrate that responses in these areas exhibit orientation-specific adaptation (Boynton & Finney, 2003; Fang, Murray, Kersten, & He, 2005; Larsson, Landy, & Heeger, 2006; Montaser-Kouhsari, Landy, Heeger, & Larsson, 2007). Assuming that these adaptation effects (i) are not simply inherited from lower levels and (ii) are sufficient to distort orientation perception, it is possible in principle that spatially remote tilt aftereffects could result from changes in the response of neurons with receptive fields that are sufficiently large to encompass both the test site and neighboring regions of the adapting stimulus. An attractive feature of this explanation is that it predicts that tilt aftereffects driven by adaptation at higher levels should be less selective for spatial frequency due to the broader tuning characteristics of neurons in these areas relative to early visual cortex (Desimone & Schein, 1987). However, this explanation is difficult to reconcile with our finding that spatially remote tilt aftereffects are not induced by adaptation to Cartesian patterns. Given the identical spatial layout of the Cartesian, radial and concentric adapting stimuli, and

Figure 5. Simple schematic model, demonstrating how feedback from global form mechanisms could produce spatially remote, spatial frequency-insensitive distortions of perceived orientation. (A) Local orientation filtering of adapting stimulus results in orientation specific suppression in active V1 neurons, the basis for traditional tilt aftereffects that are specific to the adapted location and tuned for spatial frequency. (B) Active global form detectors inhibit the set of local orientation filter over which they pool via reciprocal feedback connections. This additional source of orientation specific suppression extends to inactive input filters, whose receptive field position and/or spatial frequency tuning dictate that they are relatively unresponsive to the adapting stimulus.
the similarity of local orientation information adjacent to the test site in each case, adaptation of orientation-selective neurons with large receptive fields would produce comparable spatially remote tilt aftereffects in each case.

A final possibility worth considering is the potential influence of adaptation to higher-order contour or shape representations. Perceptual aftereffects have been demonstrated for a range of spatial form properties, including convexity (Suzuki, 2001), contour curvature (Gheorghiu & Kingdom, 2006, 2007), polar form (Clifford & Weston, 2005), and deviations from circularity (Anderson, Habak, Wilkinson, & Wilson, 2007). Importantly, these effects are not readily explained by adaptation of local orientation encoding mechanisms alone. In line with these previous studies, it is feasible to propose that our stimuli might have adapted neurons in extrastriate cortex that respond to certain higher-order form characteristics. However, a critical difference in the present study is that the test stimuli contained in the adapting stimulus. Figure 5 shows a simplified schematic of local orientation filtering and global pooling of responses to a concentric pattern, coupled with feedback mechanisms. During adaptation, responses of filters activated by the pattern are suppressed, generating traditional spatially specific tilt aftereffects for subsequently viewed stimuli. In addition, active global form detectors suppress the responses of their complete set of local orientation filter inputs via reciprocal feedback connections. Feedback-mediated suppression of input filters that are inactive during adaptation has the potential to produce spatially remote, spatial frequency-insensitive TAEs that are subjectively equivalent to their traditional counterparts.

Although neural processes that distort veridical perception might appear maladaptive, it is likely that visual adaptation plays a wider functional role outside the laboratory. Adaptation mechanisms underlying the TAE are thought to aid self-calibration and redundancy reduction in neural representations of orientation (Barlow & Foldiak, 1989; Clifford et al., 2000, 2006; Wainwright, 1999) and to facilitate discriminative accuracy (Regan & Beverley, 1985). Our results suggest for the first time that these benefits may be realized via dynamic reciprocal interactions between multiple levels of analysis in the visual cortex and raise the possibility that feedback-mediated modulation of the adapted state of neurons could be a universal feature of cortical adaptation.

**Hypothesis 3: Feedback-mediated adaptation**

Spatially remote tilt aftereffects appear to be specific to the use of adapting stimuli containing global structure that can only be encoded by pooling different orientation signals across space. However, since local orientation coding precedes the extraction of global structure in the form processing hierarchy, these results are difficult to reconcile with contemporary feedforward adaptation frameworks. Instead, we propose that spatially remote, spatial frequency-insensitive tilt aftereffects arise because global form coding mechanisms activated during adaptation inhibit the input they receive from local orientation filters in early visual cortex. The extensive network of feedback connections projecting from cortical areas implicated in global form analysis provides a likely neural substrate for this inhibitory influence (Rockland & Van Hoesen, 1994; Zeki & Shipp, 1989). Feedback connections from extrastriate cortex are known to target the same groups of neurons that provide feedforward connections to a given site (Angelucci et al., 2002; Lund, Angelucci, & Bressloff, 2003). As a result, feedback-driven inhibition would result in specific suppression of neurons with orientation preferences consistent with the global structure contained in the adapting stimulus. Figure 5 shows a simplified schematic of local orientation filtering and global pooling of responses to a concentric pattern, coupled with feedback mechanisms. During adaptation, responses of filters activated by the pattern are suppressed, generating

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