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# Aftereffect of adaptation to Glass patterns

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#### Abstract

Our visual systems constantly adapt their representation of the environment to match the prevailing input. Adaptation phenomena provide striking examples of perceptual plasticity and offer valuable insight into the mechanisms of sensory coding. Here, we describe an aftereffect of adaptation to a spatially structured image whereby an unstructured test stimulus takes on illusory structure locally perpendicular to that of the adaptor. Objective measurement of the strength of the aftereffect for different patterns suggests a neural locus of adaptation prior to the extraction of complex form in the visual processing hierarchy, probably at the level of primary visual cortex. This view is supported by further experiments showing that the aftereffect exhibits partial interocular transfer but complete transfer across opposite contrast polarities. However, the aftereffect does show weak position invariance, suggesting that adaptation at higher levels of the visual system may also contribute to the effect. © 2005 Elsevier Ltd. All rights reserved.

Keywords: Spatial vision; Visual cortex; Psychophysics; Sensory coding; Orientation; Global form

## 1. Introduction

We studied adaptation to spatial image structure using a stimulus, the Glass pattern (Glass, 1969), whose perception involves pooling orientation information across significant distances of visual space (Wilson & Wilkinson, 1998; Wilson, Wilkinson, & Asaad, 1997). Each Glass pattern consists of a large number of pairs of dots, and is constructed as follows. One dot in each pair is positioned randomly within the stimulus according to a probability distribution uniform over area. The second dot of each pair is then positioned at a fixed distance from its partner in a direction defined by the particular pattern being generated. For example, if the direction of displacement is directly away from the centre of the image then a radial "sunburst" pattern is generated (Fig. 1A). If the displacement is perpendicular to the position vector relative to the centre then the pattern is concentric (Fig. 1B).

The spatial structure in Glass patterns has been termed static flow (Kovacs & Julesz, 1992) by analogy with optic flow, the pattern of retinal motion generated by self-motion. This seems an appropriate analogy because the static Glass pattern stimulus can be considered as the superimposition of successive frames of a random dot kinematogram (although in optic flow stimuli dot displacement between successive frames typically scales with eccentricity whereas in Glass patterns the distance between the two dots in a pair is independent of position within the pattern). Indeed, it has been argued that the mechanisms responsive to the complex spatial structure in Glass patterns are not so much concerned with the perception of complex form per se but rather with the analysis of the spatial image structure or "motion streaks" that result from the temporal integration of images undergoing global motion (Barlow & Olshausen, 2004).

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Fig. 1. Aftereffect of adaptation to Glass patterns. (A) Radial and (B) concentric Glass patterns of 100% coherence used as adapting stimuli. (C) Incoherent (0%) pattern composed of randomly oriented dot dipoles. Illustration of the appearance of the incoherent pattern after adaptation to a coherent (D) radial or (E) concentric stimulus. Adaptation causes the test to take on the opposite appearance to the adaptor with an apparent coherence of around 35%.

In studies of optic flow perception, it is common to vary the coherence of stimuli in order to control their visibility (Newsome & Paré, 1988). The coherence of a stimulus is the percentage of elements in the stimulus conforming to the global pattern. It is straightforward to extend the idea of varying stimulus coherence to studies of the perception of static flow in Glass patterns (Maloney, Mitchison, & Barlow, 1987). Following adaptation to a coherently moving dot pattern, a compelling motion aftereffect (MAE) can be observed by testing with a pattern in which all dots move at the same speed as the adaptor but in random directions: a dynamic test stimulus with 0% coherence (Blake & Hiris, 1993; Hiris & Blake, 1992). The directionally ambiguous test is perceived as drifting in the direction opposite to the adapting motion. In the spatial domain, the analogous situation is to adapt to a coherent Glass pattern and then test with a stimulus composed of randomly oriented dot dipoles of the same intra-dipole dot separation (Fig. 1C). When this is done, the test stimulus appears to take on a spatial structure locally perpendicular to that of the adaptor. For example, adaptation to a radial pattern causes an incoherent test to appear to contain concentric structure (Fig. 1D) while adaptation to a concentric pattern produces a radial aftereffect (Fig. 1E). The coherence level of the patterns in Fig. 1D and E used to illustrated the aftereffect (35%) is based on objective measurements of its magnitude, described below.

The aftereffect can be experienced by viewing the movie at the following web address: http://www.psych.

usyd.edu.au/staff/colinc/HTML/glass\_adapt.htm. On each cycle of the movie, a brief presentation of the same incoherent test pattern is presented on either side of the central fixation point, followed by several seconds of the adapting stimuli. The adapting stimuli to the left and right of fixation are coherent radial and concentric patterns, respectively. This format was chosen for demonstration purposes to facilitate comparison of the effects of adaptation to the two opposite patterns. Over the course of several cycles, the salience of the adapting patterns decreases while the illusion of structure in the test stimuli becomes stronger. The same effects are evident whether the test stimuli are composed of randomly oriented dipoles or of unpaired random dots.

One means of measuring the MAE has been to adapt observers to a constantly moving dot pattern of 100% coherence and then present them with moving test stimuli at varying levels of coherence (Blake & Hiris, 1993; Hiris & Blake, 1992). For example, if the adapting stimulus was moving downwards (+100% coherence) then test stimuli would range from coherent upwards motion (-100% coherence) through random motion (0% coherence) to coherent downwards motion (+100% coherence). Observers would then be required to report whether the test stimulus appeared to be moving upwards or downwards. The stimulus coherence at which observers were equally likely to respond in either direction provides a measure of the point of subjective stationarity: the coherence at which no consistent direction of motion is seen. The difference in the point of subjective stationarity before and after adaptation then serves as a measure of the magnitude of the MAE. Here, we used an analogous method to investigate the effects of adaptation to Glass patterns on the subsequent perception of spatial image structure.

## 2. Methods

A total of six experiments were conducted. Three or four subjects were tested in each: one or both of the authors, CC and EW, and one or two volunteer observers naïve to the purposes of the study. Stimuli were generated using Matlab software to drive a VSG 2/5 graphics card (Cambridge Research Systems) and displayed on a gamma-corrected 21" Sony Trinitron GM 520 monitor ( $1024 \times 768$  resolution; 120 Hz refresh rate).

Experiment 1 investigated the effects of adaptation to radial or concentric spatial structure on the subsequent perception of Glass patterns ranging in coherence from -70% (concentric) through 0% to +70% (radial). Observers were required to report whether they perceived radial or concentric structure in each test pattern. In addition to a central fixation marker, each stimulus consisted of 4000 dots in a circular annulus with outer and inner diameters of 14.0° and 0.3°. Each dot was  $0.04^{\circ} \times 0.04^{\circ}$  in size, giving a density of 4.2%. Dot pairs were randomly assigned to be 100% contrast increments or decrements from the  $62.8 \text{ cd/m}^2$  background, such that the two dots in each pair always had the same luminance. Intra-pair dot spacing was 0.18°. False matches between dots from different dipoles create ambiguous local orientation information, such that even in the 100% coherent Glass patterns there were on average 2.6 dots closer to any given dot than its partner.

The initial adaptation duration was 30 s, with 5 s topup adaptation before each subsequent test. The adapting stimulus was updated with a new random instantiation of the same pattern of static flow once per second to avoid adaptation at the retinal level. At rapid rates of update, Glass patterns give rise to a compelling percept of motion (Ross, Badcock, & Hayes, 2000). However, the percept of motion is much weaker with the 1 Hz update rate used here, and updating is not essential to generate the aftereffect of Glass pattern adaptation. The test stimulus was presented for 500 ms within a raised-cosine temporal envelope (333 ms at full contrast; 83 ms each ramping on and off) following a 833 ms blank screen at the mean luminance of the stimulus.

Experiment 2 used identical methods except that the adapting stimuli were translational (vertical or horizontal) Glass patterns and the test patterns varied in coherence between -70% (vertical) and +70% (horizontal).

Experiment 3 measured the interocular transfer of the aftereffect of adaptation to concentric Glass patterns. The two eyes' stimuli were each surrounded by a circular

fusion lock in different regions of a single monitor and viewed using a mirror stereoscope. The left eye was adapted to a concentric Glass pattern while the right eye saw a uniform field at the mean luminance of the adapting stimulus. Presentation of the test stimulus was also monocular in either the same or opposite eye. Due to the limited field of view available, the spatial parameters of the stimuli were chosen to be different from those in the other experiments. Each stimulus consisted of 3000 dots in a circular annulus with outer and inner diameters of 7.0° and 0.3°. Each dot was again  $0.04^{\circ} \times 0.04^{\circ}$ , giving a density of 12.5%. Intra-pair dot spacing was 0.09°. False matches again created ambiguous local orientation information, such that there were on average 2.0 dots closer to any given dot than its partner in the 100% coherent patterns.

Experiment 4 investigated the polarity specificity of Glass pattern adaptation. All dots within any given stimulus had the same contrast polarity. Each stimulus consisted of 3000 dots in a circular annulus with outer and inner diameters of  $14.0^{\circ}$  and  $0.3^{\circ}$ . Each dot was  $0.04^{\circ} \times 0.04^{\circ}$  in size, giving a density of 3.1%. Intra-pair dot spacing was  $0.18^{\circ}$ . Due to false matches, there were on average 2.0 dots closer to any given dot than its partner in the 100% coherent patterns.

Experiment 5 investigated whether the effect of Glass pattern adaptation is restricted to the region of the visual field in which the adapting stimulus is presented. Each stimulus consisted of 1500 dots presented in two opposite quadrants of a circular annulus with outer and inner diameters of 14.0° and 0.3°. The remaining two quadrants were a uniform grey at the mean luminance of the stimulus. Each dot was  $0.04^{\circ} \times 0.04^{\circ}$  in size, giving a density of 3.1%. Intra-pair dot spacing was  $0.18^{\circ}$ . Due to false matches, there were on average 2.0 dots closer to any given dot than its partner in the 100% coherent patterns. On separate runs, the concentric adapting stimulus was presented either in the top and bottom or in the left and right quadrants. The test stimulus was presented either in the same quadrants ("concrete" condition) or in the two previously blank quadrants ("phantom" condition).

Experiment 6 used identical methods to Experiment 5 except that the stimuli were translational (vertical or horizontal) Glass patterns.

## 3. Results

Experiment 1 measured the effects of adaptation to radial and concentric Glass patterns. Fig. 2 shows the proportion of trials in which the stimulus was reported as radial rather than concentric for three subjects in three conditions. The point of subjective incoherence (PSI) in each condition was taken to be the coherence value at which the fitted logistic function crossed 50%:



Fig. 2. Proportion of times the test stimulus was perceived as being radial as opposed to concentric. Data are shown for three observers as a function of test coherence (negative values denote concentric structure) for (A) unadapted, (B) adapt radial and (C) adapt concentric conditions. Adaptation can be seen to shift the psychometric functions laterally towards the coherence of the adapting stimulus such that an incoherent test tends to appear structured opposite to the adaptor.

the point at which no consistent structure was seen. In Experiment 1, the average PSI across three subjects in the unadapted state was found to be  $3.9 \pm 1.6\%$ , revealing a slight bias to see concentric rather than radial structure (Fig. 2A). This is consistent with a previous report that sensitivity is slightly higher to concentric than radial Glass patterns (Wilson & Wilkinson, 1998). After adaptation to radial or concentric structure, judgments were biased away from the adapting pattern by  $34.2 \pm 1.8\%$  coherence (Fig. 2B and C). The magnitude of the shift in PSI between unadapted and adapted conditions is a measure of the strength of the perceptual aftereffect. The PSIs for the three subjects, summarized in Fig. 3A, provide clear evidence of a negative aftereffect of perceived spatial image structure.

In Experiment 2, the same three subjects were tested with translational Glass patterns. The magnitude of the aftereffect was found to be  $29.3 \pm 3.9\%$  (Fig. 3B), similar to that for complex patterns.

Experiment 3 measured the interocular transfer of the aftereffect of adaptation to concentric Glass patterns (Fig. 4). Four subjects were tested monocularly in each eye before and after adaptation to a stimulus presented only in the left eye. The degree of interocular transfer (IOT) was calculated for each subject as the change in PSI for right eye testing as a percentage of the change in PSI for left eye testing:



Fig. 3. Objective measures of the aftereffect for three observers. Point of subjective incoherence (PSI) at which responses are at chance level for (left) complex (right) translational Glass patterns. (Left) Black, grey and white bars denote adaptation to radial, unadapted, and adapted to concentric, respectively. (Right) Black, grey and white bars denote adaptation to horizontal, unadapted, and adapted to vertical.



Fig. 4. Interocular transfer of adaptation to concentric Glass patterns for four observers. Adaptation was always in the left eye. Black bars show adapted PSIs, white bars unadapted. Percentage interocular transfer for each observer is shown in the top right of the respective panels.

$$IOT = \frac{A_{opp} - U_{opp}}{A_{same} - U_{same}} \times 100\%$$

where A and U denote the adapted and unadapted PSI and the subscript indicates testing in the same (left) or opposite (right) eye as the adaptor. An IOT of 100% would signify complete transfer of the aftereffect between eyes, whereas an IOT of 0% would indicate that the aftereffect was entirely monocular. The IOTs for the four subjects were 22% (EW), 51% (JW), 54% (CC) and 84% (SR): mean 53%; standard deviation 25%.

Experiment 4 measured the extent to which the aftereffect of adaptation to concentric Glass patterns transfers between dot patterns of opposite contrast polarity (Fig. 5). The degree of transfer across contrast polarity (CPT) was calculated for each subject as the change in PSI for the opposite polarity adapt/test conditions expressed as a percentage of the change in PSI for the same polarity adapt/test conditions:

$$CPT = \frac{(B_{w} - U_{w}) + (W_{b} - U_{b})}{(W_{w} - U_{w}) + (B_{b} - U_{b})} \times 100\%$$

where B, W and U denote the adaptation condition (adaptation to black, adaptation to white, or unadapted) and the subscript indicates the contrast polarity (black or white) of the test pattern. A CPT of 100% would signify complete transfer of the aftereffect across contrast polarity, whereas a CPT of 0% would indicate that the aftereffect was entirely polarity specific. The



Fig. 5. Transfer across contrast polarity of adaptation to concentric Glass patterns for three observers. Black, grey and white bars denote adaptation to black, unadapted, and adaptation to white, respectively. Percentage transfer across polarity for each observer is shown in the top right of the respective panels.

CPTs for the three subjects were 72% (CC), 84% (EW) and 123% (CM): mean 93%; standard deviation 27%.

Experiment 5 investigated the extent to which adaptation to concentric Glass patterns presented in two opposite quadrants of a circular aperture transfers to the remaining two quadrants (Fig. 6). The degree of position invariance (PI) was calculated for each subject as the change in PSI for the conditions in which adaptor and test were presented in different locations expressed as a percentage of the change in PSI for the conditions in which adaptor and test were presented in the same location:

$$PI = \frac{(TB_{lr} - U_{lr}) + (LR_{tb} - U_{tb})}{(LR_{lr} - U_{lr}) + (TB_{tb} - U_{tb})} \times 100\%$$

where TB, LR and U denote the adaptation condition (adaptation in top and bottom quadrants, adaptation in left and right quadrants, or unadapted) and the subscript indicates the location (top and bottom or left and right) of the test pattern. A PI of 100% would signify complete transfer of the aftereffect across positions, whereas a CPT of 0% would indicate that the aftereffect was entirely specific to position. The PIs for the three subjects were 7% (CC), 22% (EW) and 43% (SD): mean 24%; standard deviation 18%.

Experiment 6 measured the position invariance of adaptation to vertical Glass patterns for the same three subjects in an analogous manner. The PIs for the three subjects were 5% (EW), 18% (CC) and 22% (SD): mean 15%; standard deviation 9%.

#### 4. Discussion

We observed that adaptation to Glass patterns generates an aftereffect whereby an unstructured test stimulus takes on illusory structure locally perpendicular to that of the adaptor. Where in the visual hierarchy might the aftereffect of Glass pattern adaptation be mediated? Specifically, at what level(s) in the visual system is neuronal adaptation occurring? It has previously been shown that the coherence necessary for detection of complex (radial or concentric) Glass patterns is lower than that for translational (horizontal or vertical) patterns, demonstrating the existence of complex form detectors in human vision (Wilson & Wilkinson, 1998, 2003; Wilson et al., 1997; although see Dakin & Bex, 2002, 2003). Wilson et al. (1997) proposed a filter-rectify-filter model of the neural extraction of global form from Glass patterns. An initial stage of oriented linear filtering identified with local processing in V1 is followed by full-wave rectification prior to a second stage of filtering. The responses of these second stages filters are then pooled spatially at a level identified with processing in area V4. The stages of local and global processing in



Fig. 6. Position invariance of adaptation to (left) concentric (right) vertical Glass patterns for three observers. Black, grey and white bars denote adaptation in top and bottom quadrants, unadapted, and adaptation in left and right quadrants, respectively. Percentage transfer across position for each observer is shown in the top right of the respective panels.

the extraction of concentric and radial Glass patterns are illustrated schematically in Fig. 7.

Only two previous studies have employed adaptation to Glass patterns. In the first, De Valois and Switkes (1980) investigated the effect on contrast detection thresholds for grating stimuli rather than testing with spatially structured suprathreshold stimuli and thus found only an orientation-dependent elevation in thresholds similar to that found following grating adaptation (Gilinsky, 1968), consistent with adaptation at an early stage of local oriented filtering. More recently, McGraw, Badcock, and Khuu (2004) reported the qualitative observation that steady viewing of a Glass pattern results in dissipation of the perceived structure. They suggested that this effect was due to adaptation at the level of global integration mechanisms.

In the motion domain, adaptation to complex optic flow patterns produces stronger aftereffects than adaptation to translational motion (Bex, Metha, & Makous, 1999) consistent with the involvement of neurons selective for complex patterns of motion (Morrone, Burr, & Vaina, 1995; Saito et al., 1986). We find that, as in the motion domain, the aftereffect of adaptation to complex Glass patterns appears subjectively more compelling than with translational patterns. This apparent difference in strength is consistent with mediation by neuronal adaptation at the level of complex form detection rather than at the level of local orientation coding. In this case, an objective measure of aftereffect strength in terms of stimulus coherence should show a stronger effect for complex than translational patterns.



Fig. 7. Schematic representation of the stages of local and global processing in the extraction of concentric and radial Glass patterns according to the model of Wilson et al. (1997). The aftereffect of adaptation to Glass patterns could in principle be mediated by neuronal adaptation at either or both of the local and global processing stages. Bold arrows indicate possible inhibitory interactions between oppositely tuned detectors within a given level of processing. One possible mechanism underlying the aftereffect of adaptation to Glass patterns is release from inhibition. Under such a mechanism, adaptation of neurons tuned to the adapting stimulus structure would reduce inhibition to neurons representing the opposite spatial structure. An unstructured test stimulus would then be perceived as containing spatial structure locally perpendicular to that of the adaptor.

However, it is important to note that if the aftereffect were mediated by neuronal adaptation early in the visual hierarchy, prior to the spatial pooling of local orientation signals, then its subjective strength might simply reflect the sensitivity of global mechanisms subsequent to the site of adaptation. Thus, it could be that the subjectively weaker aftereffect for translational Glass patterns is due to lower sensitivity for translational than complex structure, rather than to weaker adaptation. In this case, an objective measure of aftereffect strength in terms of stimulus coherence would reflect the properties of the early orientation-selective mechanisms rather than depending on the global form of the pattern, so no difference should be evident between the objective strengths of adaptation to complex and translational Glass patterns.

Indeed, when the magnitude of the aftereffect to translational Glass patterns was quantified in terms of coherence (Experiment 2) it was found to be similar to that for complex patterns (Experiment 1): translational  $29.3 \pm 3.9\%$ ; complex  $34.2 \pm 1.8\%$ . That this objective measure of aftereffect magnitude is independent of the global pattern rather than reflecting the greater sensitivity of the human visual system to complex than translational Glass patterns (Wilson & Wilkinson, 1998) suggests that the aftereffect is mediated by neuronal adaptation prior to the spatial pooling of local orientation information by global form detectors.

If the aftereffect is indeed underpinned by neuronal adaptation at the level of local rather than global processing then certain predictions can be made that are testable psychophysically in terms of the interocular transfer, contrast polarity specificity and position invariance of Glass pattern adaptation. Physiological evidence suggests that the local orientation information between dots within a pair is first processed in V1 (Smith, Bair, & Movshon, 2002), while selectivity for more complex, global patterns does not emerge until extrastriate regions (V2: Hegdé & Van Essen, 2000, 2003; V4: Gallant, Braun, & Van Essen, 1993; Gallant, Shoup, & Mazer, 2000). V1 contains neurons with a range of ocular dominance properties, from purely monocular to completely binocular, while extrastriate regions are almost entirely binocular (Hubel & Wiesel, 1962). Consequently, when adapting and test stimuli are each presented monocularly to opposite eyes, aftereffects mediated by neuronal adaptation in V1 should show only partial interocular transfer while aftereffects with higher-level substrates would be expected to transfer completely (Blake, Overton, & Lema-Stern, 1981). Indeed, the repulsive tilt aftereffect, which has been argued to be mediated by largely neuronal adaptation in V1 (e.g. Wenderoth & Johnstone, 1987), shows interocular transfer of around 50% (Paradiso, Shimojo, & Nakayama, 1989). Conversely, adaptation to complex motion shows almost total interocular transfer (Steiner, Blake, & Rose, 1994), consistent

with the observation that neurons selective for complex patterns of motion are not found prior to the extrastriate MT/MST complex in the motion processing hierarchy (Saito et al., 1986).

Here, in Experiment 3, we found that the aftereffect of Glass pattern adaptation transfers partially between the eyes (mean of four subjects 53%, range 22–84%). Despite clear inter-subject variability, this range of values is remarkably similar to that reported for interocular transfer of the repulsive tilt aftereffect (Paradiso et al., 1989: mean of three subjects 46%, range 23–82%). Such partial interocular transfer has been argued to be characteristic of neuronal adaptation at the level of V1 (Moulden, 1980), though involvement of higher visual areas cannot be excluded.

In Experiment 4 we investigated the extent to which the aftereffect of Glass pattern adaptation transfers between adapting and test patterns of opposite polarities. Previous studies have found that the tilt aftereffect exhibits complete transfer across contrast polarity (Magnussen & Kurtenbach, 1979; O'Shea, Wilson, & Duckett, 1993). Thus, if adaptation to Glass patterns were mediated at the level of local oriented filtering of the visual image as might be occurring in area V1 then this aftereffect would also be expected to show complete interocular transfer.

At the level of complex form detection, simultaneous masking studies have shown that randomly oriented dot pairs of one contrast polarity do not interfere with the detection of a Glass pattern if it is of the other polarity (Badcock, Clifford, & Khuu, 2005; Wilson, Switkes, & De Valois, 2004) suggesting that the visual system contains global form detectors sensitive to contrast polarity. These recent studies are inconsistent with the idea that full-wave rectification precedes global pooling in Glass pattern detection (Wilson et al., 1997). However, they do support the notion of an intermediate role for concentric form detectors in the perception of faces (Rentschler, Treutwein, & Landis, 1994) since our perception of faces is known to be strongly impaired by contrast reversal (Galper, 1970). If global form detectors are indeed selective for contrast polarity then neuronal adaptation at this stage of processing should not transfer across contrast polarities.

The results of Experiment 4 show that the aftereffect transfers almost completely across contrast polarities. Expressed as a percentage of the aftereffect magnitude for same polarity adaptor and test, the strength of the cross-polarity effect was 93% (mean for three subjects; standard deviation 27%). Thus, the results of Experiment 4 are again consistent with neuronal adaptation at the level of V1.

A further qualitative observation also supports the idea that adaptation is occurring at an early level of processing in the visual hierarchy. The reader will observe from the demonstration movie that the strength of the aftereffect of Glass pattern adaptation appears to build up slowly over the course of several 5-s presentations of the adapting stimulus. Even in 100% coherent Glass patterns, false matches between dots from different dipoles create ambiguous local orientation information and pooling of information from a wide area of the stimulus is required to extract the global form (Wilson & Wilkinson, 1998; Wilson et al., 1997). Given that the receptive fields of orientation-selective neurons in primary visual cortex (V1) sample only a small region of the stimulus, it is perhaps not surprising that even V1 neurons strongly selective for the orientation of grating stimuli show only weak selectivity for the spatial structure contained in Glass patterns (Smith et al., 2002). While V1 neurons adapt rapidly to oriented gratings (Müller, Metha, Krauskopf, & Lennie, 1999), they might be expected to adapt more slowly when stimulated only weakly by the ambiguous orientation information present locally in Glass patterns. Thus, the slow build-up of adaptation to Glass patterns again seems consistent with mediation prior to the spatial pooling of local orientation signals.

The previous experiments have provided evidence that the aftereffect of adaptation to Glass patterns involves neuronal adaptation at an early stage of processing prior to the extraction of global form. However, they do not necessarily rule out an additional contribution from neuronal adaptation of global form detectors. In Experiments 5 and 6 we actively sought evidence for neuronal adaptation at this later stage of processing.

Neurons in V1 sensitive to local image structure are known to have small, well-localized receptive fields (Hubel & Wiesel, 1962). As we proceed up the visual hierarchy, not only does the complexity of the properties to which neurons are tuned increase, so too does the size of their receptive fields (Desimone & Schein, 1987). Borrowing from a previous study of "phantom" aftereffects in global motion processing (Snowden & Milne, 1997), we reasoned that to isolate the effects of neuronal adaptation at the level of global form we could present adapting and test stimuli to non-overlapping regions of the visual field. At the level of V1, the test stimulus would not impinge upon the receptive fields of the adapted neurons, so any aftereffect observed would not be attributable to neuronal adaptation at that level. However, the adapting and test stimuli should both fall within the larger receptive fields of global form detectors later in the processing hierarchy. Thus, neuronal adaptation at the level of global form detection would be expected to affect the processing and hence the perception of the test stimulus.

In Experiment 5 we found that adaptation to two quadrants of concentric Glass patterns generated "phantom" aftereffects in the other two quadrants that were on average 24% of the corresponding "concrete" aftereffects obtained by adapting and testing in the same two quadrants. This degree of position invariance was somewhat lower than the average of 37% found by Snowden and Milne (1997) for adaptation to complex motion, but it does indicate at least some adaptation beyond the level of local orientation detection. Small phantom aftereffects averaging 15% were also found in Experiment 6 after adapting to vertical Glass patterns, again rather lower than the average of 55% for adaptation to translational motion reported by Snowden and Milne (1997). The existence of albeit quite weak phantom aftereffects for Glass patterns indicates that they cannot be explained entirely on the basis of adaptation at the stage of local oriented filtering by V1 neurons. However, it is not clear from our results whether adaptation at the level of global form processing proper is involved or simply adaptation at an intermediate level of processing by neurons with receptive fields large enough to sample both adapting and test regions.

## 5. Conclusion

We have reported what we believe to be a novel aftereffect of adaptation to Glass patterns. Adaptation causes an unstructured test stimulus to appear to take on illusory structure locally perpendicular in orientation to that of the adaptor. Several lines of evidence indicate that this effect is mediated predominantly at the level of local oriented filtering of the image, as thought to be carried out by neurons located in primary visual cortex. Firstly, the objectively measured magnitude of the aftereffect appears essentially independent of the global structure of the adaptor. Secondly, the aftereffect transfers only partially between the two eyes. Thirdly, the aftereffect transfers almost completely across contrast polarities. However, the generation of small but systematic "phantom" aftereffects in unadapted regions of the visual field indicates that adaptation is also occurring at a more global level of form analysis, presumably involving neurons in extrastriate visual areas. Thus, it appears that the aftereffect of adaptation to Glass patterns is mediated by neuronal adaptation at multiple levels of the cortical visual processing hierarchy.

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