Global shape aftereffects have a local substrate: A tilt aftereffect field

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Adaptation to prevailing stimuli is a ubiquitous property of the visual system that optimizes its dynamic range. The perceived difference in orientation of successively presented lines of similar orientation is exaggerated and the perceived shape of an object is influenced by previously experienced shapes. Change in perceived shape is assumed to arise through the adaptation of shape detectors. Here we consider an alternative: adaptation within a substrate of local oriented line detectors resulting in enhanced shape contrast in similar shapes. We show that the perceived shapes of a spatially coincident circle and Cartesian grid can be manipulated independently by adaptation to geometrically transformed copies of themselves. The same transformation was applied to the circle and the grid to create the adaptors; therefore, the specificity of the effects of adaptation demonstrates that the visual system adapts to the shape of objects rather than applying transformations to the reference frame of the visual field. The tilt aftereffect predicts local changes in perceived orientation, and fields of such local effects can often account for the global change in perceived shape of complex objects, including faces.

Keywords: object recognition, face recognition, perceptual organization, plasticity, shape and contour


Introduction

The visual system constructs a model of an observer’s environment from a retinal image. Objects in the model, which frequently subtend large angles at the observer, are assembled from local samples of the scene by a hierarchy of cortical regions (Felleman & Van Essen, 1991), the neurons of which encode progressively larger and more complex features (Loffler, 2008). Simple cells in the primary visual cortex (V1) are selective for local orientation (Hubel & Wiesel, 1974; Reid & Alonso, 1995, 1996) and there are excitatory lateral connections between neurons of V1 with similar orientation preference. These connections enhance the salience of collinear line segments (Li & Gilbert, 2002) and paths with gradual orientation change (Field, Hayes, & Hess, 1995). The influence of these lateral connections extends beyond the region of the scene to which the individual neurons respond in what has been referred to as a contextual interaction (Schwartz, Hsu, & Dayan, 2007; Schwartz, Sejnowski, & Dayan, 2009). Orientation context also affects perceived local orientation. The perceived orientation of a line or grating enclosed by a modestly different orientation surround is repelled from the orientation of the surround, an effect known as the direct tilt illusion (Westheimer, 1990). For the tilt illusion, the context is spatial but the same effect on orientation is observed for a temporal orientation context (Gibson & Radner, 1937; Kohler & Wallach, 1944; Mitchell & Muir, 1976). This effect is known as the tilt aftereffect (TAE). Neuronal models have been proposed to explain the mechanism or mechanisms by which the tilt illusion and TAE are produced (Schwartz et al., 2007), but this is not the concern of this study. Here we consider the potential utility of the TAE, an apparent orientation misperception, in object perception.

The lateral occipital complex (LOC) plays a critical role in object recognition (James, Culham, Humphrey, Milner, & Goodale, 2003), responding to complete objects more strongly than unstructured texture (Malach et al., 1995), or their disassociated parts (Kourtzi & Kanwisher, 2000).
Moreover, LOC appears to treat line drawings of objects and grayscale photographs of those objects as equivalent (Kourtzi & Kanwisher, 2000), indicating that the redundancy in the image associated with its surface properties has been removed (Attneave, 1954) and that orientation information is sparse. This result may help explain the representational efficacy of line-drawing cartoons, but it also validates the use of simple closed paths in experiments investigating the component shapes of object perception. One particular versatile stimulus used to represent shapes is the radial frequency (RF) pattern, created by sinusoidally modulating the radius of a circle (Loffler, Wilson, & Wilkinson, 2003; Wilkinson, Wilson, & Habak, 1998; for an example, see Figure 1A). Experiments investigating sensitivity to RF modulation when doing so (Anderson, Habak, Wilkinson, & Wilson, 2007; Dickinson, Han, Bell, & Badcock, 2010; e.g., adaptation to Figure 1A results in the percept of an inverted, lowest amplitude, version of Figure 1A). The aftereffect, however, is bidirectional in the sense that it can exaggerate the difference of the test pattern from an adaptor with an arbitrary amplitude of deformation (Bell & Kingdom, 2009). After adaptation to a particular amplitude adaptor, subsequently presented RF patterns of the same phase but higher amplitude appear of greater amplitude still. The perceived pattern shape, therefore, exists and is modified along a continuum. Local orientation differences between the adaptor and the test patterns are exaggerated under all circumstances, and consequently, the local orientation changes due to what is perceived as a global shape aftereffect and the local TAE are in the same direction. Systematic application of local tilt aftereffects (TAEs) in what might be called a TAE field would serve to enhance ability to discriminate between shapes by enhancing the shape contrast, effectively decorrelating the responses of detectors for similar shapes (Barlow & Foldiak, 1989).

We propose that the TAE contributes substantially to the perceptual effects of adaptation to the shape of objects and serves to enhance ability to notice differences in shape by making the perceived shapes of successively presented patterns more distinct. Because the TAE is maximal for small differences in local orientation, and similar shapes will have small differences in local orientation, subsequently presented shapes that are similar to the adapting shape will be subject to a TAE field that is smoothly and continuously varying. TAEs have been shown to develop very rapidly (Sekuler & Littlejohn, 1974) and local orientation tuning functions are sufficiently narrow as to be independent (Thomas & Gille, 1979); therefore, it is possible that adaptation to different orientations could coexist locally. Subsequently experienced stimuli would then be subject to stimulus-specific TAE fields strongly weighted toward the effects of similar adaptors. This would result in a system, with specificity with regard to shape adaptation and considerable generality across shapes, which could retain the effects of adaptation to multiple objects or the same object in many places. In Experiment 1, we tested and confirmed this hypothesis by adapting to specific patterns and examining the perceived...

Figure 1. Sample visual stimuli: (A) and (B) show adapting stimuli. (A) An RF3 pattern created by modulating the radius of a circle sinusoidally with an amplitude of 0.1 times the radius of the circle and a frequency of 3 cycles of modulation in 2π radians. Unmodulated circle radius was 90’ of subtended visual angle. (B) A Cartesian grid that has been deformed using the same sinusoidal modulation of distance from the center of the pattern to every point in the pattern. Line separation in the unmodulated grid was 24’ of visual angle. (C) and (D) show test patterns used to measure the aftereffect of adapting to the test patterns. Again the modulation of each pattern conformed to the transformation $r'(\theta) = r \times (1 + A \sin(\omega \theta))$, where $r'$ is the modulated distance from the center of the pattern, $r$ is the unmodulated distance, $A$ is the amplitude of modulation, $\theta$ is the polar angle, and $\omega$ is the frequency of modulation. Pattern (C) (pattern D) approximates the pattern required to null the aftereffect of adaptation to the pattern in (A) (pattern (B)).
deformation of superimposed similar and dissimilar patterns. Experiment 2 showed that face aftereffects can also be accounted for by TAE fields.

**Methods**

**Apparatus**

Stimuli were created using Matlab (Mathworks, Natick, MA, USA) on a PC and presented from the frame buffer of a Cambridge Research Systems visual stimulus generator (a VSG2/5 for Experiment 1 and a VSG for Experiment 2) to a CRT monitor (a Hitachi Accuvue HK-4821-D for Experiment 1 and a Sony Trinitron CPD G-520 for Experiment 2). Luminance calibration was performed using an Optical OP200-E photometer (head model number 265). Screen refresh rate was 100 Hz. The screen was viewed in a darkened room with an ambient luminance of <1 cd/m². Observers made responses to the stimuli using a button box (CB3 for Experiment 1 and CB6 for Experiment 2).

**Observers**

Five experienced psychophysical observers participated in the experiments. ED, JB, and RA are authors; VB and RO were naive to the purposes of the experiments. All observers had normal or corrected-to-normal visual acuity.

**Stimuli**

The stimuli used in Experiment 1 were geometric patterns. Two patterns, a circle and Cartesian grid, provided the base patterns from which all of the test and adapting patterns were derived. The circle had an unmodulated radius of 90’ of visual angle (one screen pixel equated to 1’ of visual angle from a viewing distance of 139 cm) and the lines of the grid were separated by 24’ of visual angle. The luminance contrast profile of the lines was Gaussian in section with a full width at half-contrast of 2.35’ of visual angle. Maximum luminance of the lines was 90 cd/m² and background luminance was 45 cd/m². Distorted versions of the base patterns were created by modulating the distance from the center of the pattern to each point in the pattern sinusoidally, with three or five cycles of modulation around the full 2π radians (for a circle, this produces an RF3 or RF5 pattern, respectively). The distance from the center to a specific point in the modulated pattern, r’, is given by

\[ r'(\theta) = r \times (1 + \text{Asin}(\omega \theta)) \tag{1} \]

where A is the maximum modulation amplitude expressed as a proportion of the distance from the center of the unmodulated pattern, r. The angle \( \theta \) is the conventional polar angle and \( \omega \) is the frequency of modulation (3 or 5 cycles in 2π radians). Test patterns were composite patterns, comprising a modulated target pattern and an unmodulated version of the other geometric pattern superimposed, or RF patterns alone.

The adapting and target patterns of Experiment 2 were distorted versions of the same face. The distortion was the same sinusoidal modulation as that applied to the geometric patterns, but there was no superimposition of modulated and unmodulated stimuli in the test patterns of this experiment. The faces subtended an angle of ~20° at the viewing distance of 70 cm.

**Experimental procedure**

The method of constant stimuli (MOCS) was employed to measure the size of the aftereffect for every condition of each experiment. The trials of each of the conditions were blocked. For the composite test patterns of Experiment 1, the observer was made aware of which of the two superimposed patterns was the target pattern in each particular block. Only the target pattern of each test stimulus was modulated. The adapting pattern remained the same within each block but varied across blocks. No fixation point was used, but the observers were requested to fixate the center of the screen throughout each block of trials. Nine amplitudes of modulation for the target pattern were used. For each condition, sixty responses were collected for each of the nine amplitudes of modulation of the target pattern across three blocks of trials, a total of 540 trials for each psychometric function. For each condition in which an adapting stimulus was used, the adapting stimulus was presented initially for 20 s and then for 2 s between each test stimulus presentation. Test stimuli were presented in a randomized order with each successive trial triggered by the response to the previous trial. Observers were required to report whether the perceived modulation of the target pattern (an RF pattern, a grid, or a face) within the test stimulus was either in phase zero (the same pattern of modulation as the adaptor) or phase π radians (the opposite phase) with respect to the unmodulated stimulus, a single-interval forced-choice (SIFIC) task. The probability of responding that the pattern was in the opposite phase to the adaptor was collected for each of the amplitudes of modulation of the target stimulus. A cumulative normal distribution was fitted to the data, using non-linear regression, the mean yielding the amplitude at which the observer would be equally likely to select either response alternative, the point of subjective equality (PSE). This PSE is the amplitude of modulation of the target required to null the aftereffect. Data analysis was performed using GraphPad (GraphPad Prism version 5.00 for Windows, GraphPad Software, San Diego, CA, USA, www.graphpad.com).
Results

Experiment 1: Independent adaptation of superimposed shapes; a TAE field account

For this experiment, we chose a circle and a Cartesian grid as comparison stimuli. The circle contains all orientations in equal measure, and the grid contains only vertical and horizontal orientations. The two adapting patterns used in the first part of Experiment 1 are shown in Figures 1A and 1B. Both adapting patterns had a modulation amplitude of 0.1 (A in Equation 1). Test stimuli were composite patterns that comprised either a grid and a target RF3 pattern (Figure 1C) or a circle and a target modulated grid (Figure 1D).

Results for the six conditions tested in the first part of Experiment 1 are presented in Figure 2. The first two conditions (RF3 or Grid unadapted) are the results for test stimuli without prior adaptation and show that there is no bias in perceived phase of modulation of the target patterns prior to adaptation (at zero modulation amplitude, there is equal probability of reporting either phase). In four further conditions, observers adapted to the RF pattern or modulated grid pattern and were then required to report the perceived phase of modulation of the target pattern, either an RF pattern or a modulated grid pattern.

Figure 2 shows that when the adapting and target patterns were similar (blue) a large bias in perceived modulation amplitude was observed, implying a significant adaptation effect. However, when the adapting and target patterns were dissimilar (red) no such bias was observed. Figure 1C is a sample test stimulus with an RF3 target that would be approximately at the PSE (perceived as circular) for the three observers after adaptation to the RF3 pattern shown in Figure 1A. Figure 1D is the equivalent for adaptation to the modulated grid shown in Figure 1B. Movies 1 and 2 are hypothetical trials of Figure 2.
Movie 1 illustrates adaptation to an RF3 pattern, and Movie 2 illustrates an RF3 modulated grid. The TAE exaggerates the difference in orientation of successively presented line segments. The effect is largest for lines with similar but not identical orientation. If patterns whose local orientation differences were small but varied systematically were subject locally to the TAE across the whole pattern, then the difference in their perceived shapes would be exaggerated. Figure 3A illustrates the TAE over the whole range of orientation difference between adapting and test gratings (the data were taken from Clifford, Wenderoth, & Spehar, 2000). The colored bar next to the y-axis is a scale bar used in Figure 3 to color code the TAE predicted at any point in a pattern for particular adaptor–target pairs, a TAE field. The fields are illustrated as extending from the center of the pattern to the edge of each panel. This is of course a simplification. The grid occupies the whole area of the stimulus, but the path describing the RF pattern is constrained to a narrow range of radii. However, the tilt illusion and TAE have been shown to have similar functions describing their size with respect to the difference in orientation between test and inducer (Magnussen & Kurtenbach, 1980), which suggests that the two effects might be closely related and perhaps even spatial and temporal effects of the same mechanism. If this is the case, it might be expected that the TAE will also be experienced in neurons that are not directly stimulated by the adaptor and therefore that a point in the visual field experiences adaptation to a range of orientations present locally. This would allow the TAE field to extend over a range of radii imparting a degree of size invariance to the aftereffect induced in a circle after adapting to an RF pattern. Some evidence exists for such size invariance (Anderson et al., 2007; Bell, Dickinson, & Badcock, 2008), but we have chosen not to impose what would be an ill-defined and therefore somewhat arbitrary limit to the effect on the TAE field. Locally more complex stimuli would suffer averaging of aftereffects, which might, nonetheless, be predictable if the function describing how the influence of the local orientation on a point in the visual field falls off with distance were known accurately.

The patterns in the upper group in Figures 3B–3E represent the cases where the target patterns are similar to the adaptors. The local difference in orientation between adaptor and target is simply the orientation change introduced at a point by the transformation of the adaptor. For the circle, this can be derived from the first derivative of the modulating function, a cosine function with maximum amplitude of 0.3. The maximum gradient equates to an orientation relative to the circle of almost 17 degrees. For the modulated grid, the first derivative

Movie 1. A sample trial from Experiment 1: An RF3 adaptor is presented for 2 s. The test stimulus follows an inter-stimulus interval of 0.5 s and is presented for 150 ms. In this example, the test stimulus comprises a circle and a Cartesian grid superimposed. The circle is perceived as being modulated in opposite phase to the adaptor.

Movie 2. Another sample trial from Experiment 1: In this case, the adaptor is a modulated grid. The grid of the test pattern is seen as having the opposite phase of modulation. The circle is not systematically distorted toward one phase of modulation or the other.
must be multiplied by $|\cos(\theta)|$ to give the gradient relative to the vertical lines and $|\sin(\theta)|$ for the horizontal lines (the orientation change in a line parallel to the sheer introduced by the transformation is zero). The local orientation difference between the vertical adaptor and target patterns, $\Delta \text{Orientation}$, is converted into a TAE field using the function fitted to the data in Figure 3A and then the target pattern is transformed by this TAE field to yield the final percept. The TAE at any point, due to the local difference in orientation between adaptor and target, is illustrated using color in Figure 3B onward. The pattern shown in blue in Figure 3B is produced by starting the line at the point $(r, \theta)$ in polar coordinates, where $r$ is the radius of 90 minutes of visual angle and theta is zero, and propagating the line anti-clockwise as though it were tracing a circle but incorporating the effect of the TAE field as the line moves around the pattern. The equivalent aftereffect for the grid pattern must be composed by treating the horizontal and vertical lines independently as they experience different TAE fields, an outcome that is easily accommodated by the visual system as orientations 90° apart are coded by independent channels (De Valois, Yund, & Hepler, 1982). The pattern in Figure 3C was produced by propagating the horizontal lines from the $y$-axis left and right, respecting the appropriate TAE field. The vertical lines were treated analogously. The TAEs experienced by the vertical lines due to the modulated horizontal lines are negligible, and vice versa (see Figure 3A). The blue shapes in Figures 3B and 3E (predicted perceived shape) closely resemble the target stimuli in Figures 1C and 1D (the modulation required to null the aftereffect) but are in opposite phase. Figures 3B and 3E illustrate the predicted aftereffect, and Figures 1C and 1D illustrate the modulation required to null the effect. When the adapting and target patterns are dissimilar, however, the local differences in orientations are much more disparate. Figures 3F–3H show that the TAE fields experienced by the circle due to the modulated horizontal (Figure 3F) and vertical (Figure 3G) lines produce a pattern that is not systematically distorted toward one phase or the other of the RF3 modulation. Similarly, Figures 3I–3K predict the perceived distortion of the target grid after adaptation to an RF3 pattern. The horizontal and vertical lines are again treated separately as they experience different TAE fields. For example, the TAE induced at a position adjacent to the bottom apex of the RF3 pattern affects the horizontal lines but not the vertical lines, while the horizontal region at the top of the RF3 pattern has no effect on the perception of the horizontal lines because they are parallel to it and no effect on the vertical lines because they are

![Figure 3. The tilt aftereffect (TAE) and TAE field predictions.](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/933482/)

(A) The TAE after exposure to lines of a different orientation. Data are taken from a study that considers a broad range of aftereffects attributed to cortical processing and are typical of data describing the TAE (Clifford et al., 2000). A D1 (first derivative of a Gaussian) has been fitted to the data to allow prediction of the TAE for the full range of local orientation differences between target and adaptor. The bar along the $y$-axis relates the magnitude and direction of the TAE to a color. Yellow represents a 5° positive (anti-clockwise) TAE, induced when the local orientation of the target is anti-clockwise of the adaptor. Red represents the opposite. The remaining panels show predicted perceived shapes of circle and Cartesian grid stimuli for differing conditions of adaptor and target stimuli. (B, E) The predicted shapes after adaptation to similar patterns and (H, K) dissimilar patterns. The color of the background shows the local TAE applied to the target stimuli due to the difference in orientation of target and adaptor. (C, D) The predicted distortion of the horizontal and vertical lines of the grid after adaptation to the distorted grid. The two sets of lines experience independent TAE fields. Panel (E) reassembles the grid. (F, G) The TAE fields experienced by the circle due to the horizontal and vertical lines of the modulated grid, respectively. The circle experiences both of these fields, but it is evident that only one has an effect at any point in space. The fields have been summed in (H). (I, J) The predicted distortion of the horizontal and vertical lines of the grid after adaptation to a circle. The patterns in (B) and (E) appear modulated in the opposite phase to the adaptors, but the patterns in (H) and (K) do not.
perpendicular. The resultant pattern in Figure 3K is slightly distorted but has no systematic distortion toward the phase zero or phase π radians modulated grids. The calculation of the TAE fields in each case is detailed in the Supplementary material.

The modeling shows that a field of local TAEs can account for the perceived modulation of the shape of the patterns due to adaptation to similar patterns. The effect is also consistent with a notional global enhancement of shape contrast. However, the function describing the TAE vs. ΔOrientation (Figure 3A) has a distinctive shape. The TAE increases rapidly to a maximum and then declines more gently with increasing orientation difference. Evidence that the magnitude of the RF aftereffect had a similar relationship with modulation amplitude of the adaptor might be construed as supporting a TAE field explanation. Figure 4 shows the TAE fields and predictions for the perceived shape of a circle after adaptation to RF patterns (top row) and grids (bottom row) with increasing amplitudes of RF5 modulation (A = 0.05, 0.1, 0.15, 0.2, and 0.3). An RF5 adaptor was used in this case because the local gradient of the sinusoid increases more rapidly than an RF3 pattern with amplitude of modulation. Local differences in orientation that are greater than that at the maximum of the TAE vs. ΔOrientation function are, therefore, achieved at lower amplitudes of modulation. The figure shows that, as the amplitude of modulation of the RF5 adaptor pattern increases, the predicted perceived modulation of the circle target stimulus initially increases to and then decreases from a maximum. This is because the local differences in orientation of the adaptor relative to the circle, around the point of inflection of the modulating sine function, at first increase toward the peak in the TAE vs. ΔOrientation function (Figure 3A) but then continue beyond it (the maximum orientation difference of the RF path from a circle for each modulation amplitude is 14°, 26°, 36°, 45°, and 56°, respectively).

The modulation amplitudes of target RF5 patterns required to null the aftereffect were measured using the procedures described previously. The results are presented in Figure 5. The aftereffects experienced by the two observers are compared with the maximum amplitudes of the predictions shown in Figure 4.

The shape of the function describing the magnitude of the aftereffect vs. modulation amplitude of the adaptor is similar to that of the TAE vs. ΔOrientation function shown in Figure 3A and conforms to the prediction of the TAE field. This result provides strong evidence that a TAE field is responsible for the aftereffect.

**Experiment 2: Adaptation to radial frequency modulated faces induces an opposite phase of modulation aftereffect consistent with the influence of a TAE field**

The application of a TAE field can account for the pattern-specific adaptation effects demonstrated experimentally in the results of Experiment 1. The local nature of the field renders the mechanism utterly general and the global shape aftereffects would be most pronounced for
shapes that are similar, the very patterns that would be most difficult to discriminate. Lennie (1998) has argued, on the basis of comparison of neuronal populations across areas of the visual cortex, that the primary visual cortex probably has a broader responsibility in form processing than simply the encoding of local orientation and spatial frequency. If the dynamic range of mechanisms responsible for perception of objects were managed at the level in the visual processing hierarchy that is responsible for perception of orientation, significant economies in representation later in the hierarchy would result. Adaptation to orientation in cortical area V1 results in decorrelation of signal in populations of neurons responding to successively presented stimuli of similar but not identical orientation (Barlow & Foldiak, 1989; Muller, Metha, Krauskopf, & Lennie, 1999). Of course, this mechanism relies on the adapting and target stimuli being presented to approximately the same region of the retina and it has previously been reported that higher level spatial aftereffects show more complex spatial relationships. For example, spatiotopic aftereffects, aftereffects in the same spatial location but different retinal location, have been reported for tilt, shape (Melcher, 2005), and face stimuli (Leopold, O’Toole, Vetter, & Blanz, 2001; Melcher, 2005) and position invariant aftereffects have been reported for shape (Suzuki & Cavanagh, 1998). More recently, however, it has been claimed that the reference frame of the tilt aftereffect is retinotopic (Knapen, Rolfs, Wexler, & Cavanagh, 2010), and a recent study (Afraz & Cavanagh, 2009) has shown that a large proportion of the gender-specific face aftereffect is retinotopically based. The substrate for these retinotopic face aftereffects could also be a TAE field. Figure 6B is an image of the renowned Yorkshire and England fast bowler Darren Gough. Figure 6A is the same image transformed in exactly the same way as the circle and grid adaptors in the first part of Experiment 1 (Figures 1A and 1B).

One author, ED, and two naive observers, VB and RO, performed an experiment analogous to the experiments with similar adaptor and target patterns described earlier but using faces as stimuli. In the images, the faces were approximately life sized, and from a viewing distance of 70 cm, the face subtended a visual angle of ~20°. Although a fixation point was not used, observers were asked to fixate the center of the screen throughout the experiment. Prior to the experiment, the observers were familiarized with the unmodulated face. During the experimental trials, they were required to report whether they thought the test face had a phase zero (e.g., Figure 6C) or phase π radians (Figure 6D) modulation from the veridical face.

When no adaptor was presented, the group of observers showed no distortion of perception of the face from the veridical case (perceived modulation amplitude: 0.0016 ± 0.0053 (SD) for the group), but when adapted to the face modulated with an amplitude of 0.1 (Figure 6A), the PSE, the amplitude at which the observers believed they perceived the veridical face, was displaced significantly (0.039 ± 0.001, 39% of the adapting amplitude) toward the adapting face implying an opposite phase aftereffect. The size of the aftereffect due to a 2 s adaptation period is large but equates almost exactly to the maximum gradient, 0.039, of the TAE vs. Orientation fitted curve (Figure 3A) around its point of inflection. That is to say that, when expressed as a proportion, small orientation differences are exaggerated the most. Figure 6C is the image perceived as neutral, and Figure 6D is the implied aftereffect post adaptation. Movie 3 illustrates the aftereffect of adaptation in the form of a hypothetical trial.

The results clearly show that adaptation to a face with an arbitrary geometrical transformation applied results in a phase-specific aftereffect in an untransformed face. In order to demonstrate that the aftereffect is consistent with the application of a TAE field, the magnitude of the aftereffect was measured over a range of adapting face amplitudes. The logic is the same as that applied in Experiment 1 to the aftereffects of adapting to RF5 patterns, and RF5 modulated faces were used. Amplitudes of RF5 modulation for the adaptor of 0.5, 0.1, 1.5, 0.2, and 0.3 were again used. The adapting faces were all modulated in phase π radians. Figure 7 shows the results.

The functions describing the face aftereffect vs. face adaptor modulation amplitude in Figure 7 and RF aftereffect vs. RF adaptor amplitude in Figure 5 are of a similar
form and closely approximate the TAE vs. $\Delta$Orientation function shown in Figure 3A. This demonstrates that the aftereffects of adaptation to transformed faces and to RF patterns are consistent with the application of TAE fields.

**Discussion**

The results of the two experiments are consistent and together demonstrate that the application of local TAEs in a TAE field can account for aftereffects in RF patterns and faces that are perceived as systematic distortions of the stimuli over large areas of the visual field. The transformations used in this study are, of course, entirely arbitrary with respect to faces. However, small local differences in orientation between faces might be expected to encode identity. The application of a TAE field, therefore, would enhance identity contrast in this case. Other arbitrary transformations such as the folded face illusion (Benton, 2009) have been shown to result in specific changes in perceived emotional state. The folding of the face results in systematic rotation of local edges (particularly those close to horizontal) in the face that principally serve to impart a smile or frown. Adaptation to a folded face would result in TAEs causing the unmodified face to appear to have the opposite demeanor. Such demonstrations have presumably been arrived at by chance but imply that a local orientation field can encode emotion on a continuum and therefore indicate the potential for a TAE field to enhance the contrast in perceived emotional state. The TAE is, of course, only one of a number of local contextual effects that can result in a systematic distortion of a figure with a large spatial extent. The distance between two contours displayed simultaneously, for instance, can be exaggerated (Badcock & Westheimer, 1985; Hess & Badcock, 1995). Distortions in figures that are contrary to the expected local effects have often been used as arguments for adaptation of global mechanisms. Yamashita, Hardy, De Valois, and Webster (2005), for example, showed that adaptation to a face whose features had been pinched along the midline caused the features of a subsequently presented neutral face to appear extended along the midline. This was true even if the distorted adapting face was enlarged to such an extent that the pinched features had a greater vertical extent than those of the neutral test face. Because this result is contrary to the local repulsion effect, they concluded that the aftereffect was due to adaptation of mechanisms associated with the analysis of the global configuration of faces. The pinching of the adapting stimulus, however, introduces significant local differences in orientation of features across the pinched and neutral faces and simple inspection of the faces reveals that the appearance of the aftereffect is predicted by a TAE field. Given this explanation, this result, therefore, might be considered to demonstrate the primacy of the TAE over local repulsion. This experiment also demonstrates a certain degree of tolerance in position of the features of the adapting and test faces. The tilt illusion demonstrates
that an illusory tilt can be induced in a test stimulus by a tilted stimulus outside of the classical receptive field of the unit processing the test stimulus. Moreover, the size of the tilt illusion and tilt aftereffect have been shown to vary as the same function of angular difference between the inducing and test stimuli, which suggests that the effects might be manifestations of the same mechanism in operation (Magnussen & Kurtenbach, 1980). This result has important implications for the TAE field. A face is an extremely complex stimulus, and unknown and variable parameters such as the degree of eye movement while adapting, the spatial range over which TAEs are experienced, the rate of dissipation and competition of the local aftereffects, etc., make it very hard to model a general TAE field for patterns as complex as faces. The work in this study concentrates on effects that are approximately retinotopic. Such effects have recently been shown to be large in comparison with effects that are position invariant (Afraz & Cavanagh, 2009). However, assuming TAE fields can coexist, as implied by the results of Experiment 1, we can speculate on the nature of position and size invariant aftereffects. Multiple fixations at different retinal locations and from different distances might result in largely independent TAE fields that produce aftereffects that are retinotopic but give the impression of being position and size invariant. However, multiple fixations would also inevitably lead to local TAEs that are locally complementary or competitive. The TAE fields due to adaptation to multiple stimuli would be complex, but, given that faces are conglomerations of features, we can make predictions of the effects of homogenous TAE fields on simplifications of such features. A mouth, for example, could be thin or rounded. Blakemore and Over (1974) showed that after adaptation to a curved line a straight line was perceived as curved in the opposite sense and attributed this effect to a systematic application of a compound TAE. However, movement of the point of fixation during adaptation affected the aftereffects in ways that were specific to the orientations experienced across the visual field. Movement of the position of fixation along a chord of the curve during adaptation removed the effect, but movement perpendicular to the chord did not. Movement of fixation along the chord results in adaptation to a spectrum of orientations that is symmetrical about the orientation of the test line, while movement perpendicular to the chord does not. This illustrates that the TAEs generated in opposing directions counteract. If we assume that an area of the visual field, rather than a line through it, can become adapted uniformly to a straight, horizontal line, either through eye movement or over smaller areas via contextual interactions, we can make the prediction that a subsequently presented circle would be perceived as elongated vertically. Adaptation to a thin mouth would result in a wide mouth appearing wider still. Eye movement while adapting to a face or faces showing no emotion might result in an exaggeration in the emotion in a face interpreted as startled due to an open mouth, potentially wherever it fell in the visual field. The application of TAE fields, then, could lead to the simultaneous enhancement in contrast of two successively experienced faces along more than one dimension of interest, happy male vs. sad female for instance.

Having advocated the TAE field explanation of numerous aftereffects that have been previously attributed to adaptation of mechanisms for high-level attributes of shapes and faces, it has to be conceded that some studies have shown effects that do not yield to it. For shapes, the example that illustrates this best are the aspect ratio aftereffect observed after adaptation to rectangles (Regan & Hamstra, 1992). After adaptation to a tall rectangle, a square appears to be extended in the horizontal dimension. Because all the lines across the adapting and test figures are either parallel or perpendicular, no TAE would be expected at any point on the test stimulus. The TAE field would be everywhere zero. Watson and Clifford (2003) investigated adaptation to faces using a transformation that manipulated the width of the central region of a face while introducing only minor changes to the orientations of other features of the face. Aftereffects were demonstrated for adaptor–test face pairs that were either upright or inverted but also for pairs with one face upright and one inverted. The effects were larger for the pairs with similar arrangement, and the excess might be attributed to TAE fields, but substantial residual effect must be due to adaptation to distances or ratios of distances that define the configuration of the elements of the face. A comprehensive account of adaptation effects would need to examine these contributions as well as the TAE field. Our demonstration here serves to reinforce the variety of effects on shape that can occur through the operation of such a TAE field.

A multidimensional encoding of faces has been proposed, representing each face as a vector from the norm. Increasing the magnitude of such a vector to create a caricature results in the face being more recognizable (Rhodes, Brennan, & Carey, 1987). The fact that perceptual caricatures can be experienced by adapting to anti-faces, faces having the opposite characteristics to the test face with respect to the norm, has been used as an argument that adaptation occurs in the face processing mechanisms (Leopold et al., 2001). However, configural aftereffects produced by adapting to the anti-face are similar for upright and inverted pairs of adapting and test faces. This might be considered surprising given that face recognition is easier for upright faces, but it is entirely consistent with the application of a field of local TAEs. After adaptation to the anti-face, any face presented subsequently would be subject to a TAE field that would cause the face to be perceived as a caricature. The deficit in recognizability of inverted faces can be attributed to higher order face processing mechanisms that prefer upright faces.
Conclusions

We propose that TAE fields serve to enhance shape contrast efficiently and contribute to a broad range of retinotopic shape aftereffects that may previously have been solely attributed to higher level mechanisms. Multiple coexisting TAE fields might also explain aftereffects considered position or size invariant. These results do not preclude the existence of aftereffects due to adaptation of global mechanisms responsible for holistic shape processing but advise caution in the use of aftereffects to probe such global mechanisms.

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