Orientation tuning of curvature adaptation reveals both curvature-polarity-selective and non-selective mechanisms

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We have used a curvature after-effect, or CAE, to explore whether curvature detectors are tuned for the overall orientation of a curve. CAEs were measured for half-cycle cosine-shaped contours as a function of adaptor contour orientation for a fixed test contour orientation. CAEs (i) were greatest when the adaptor and test contours had the same orientation, (ii) decreased rapidly as the orientation of the adapting contours rotated away from the test, the data being well fit by a Gaussian function with a standard deviation of 16°, (iii) increased again to a secondary peak when the adapting contours were rotated 180° relative to the test. Control experiments showed that the shape of the curvature-orientation tuning function could not be explained by local orientation adaptation, and that instead curvature encoding mechanisms are tuned for orientation. The secondary peak in the CAE at 180° is argued to be inconsistent with curvature opponency and instead a result of the combination of polarity-selective and polarity-non-selective curvature mechanisms. The results are discussed in relation to recent psychophysical and physiological models of form processing and the possible significance of the findings with regard to symmetry processing.

Keywords: contour, curvature, orientation, adaptation, shape

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Introduction

An important step in understanding how objects are recognized is to identify the local features that are salient for recognition and furthermore to determine how they are encoded. It has been suggested that local curvature is important for recognizing objects from their outline shapes (Attneave, 1954; Biederman, 1987) and for detecting deviations from circularity in radial frequency (RF) contours (Bell & Badcock, 2008; Bell, Badcock, Wilson, & Wilkinson, 2007; Bell, Dickinson, & Badcock, 2008; Habak, Wilkinson, & Wilson, 2006; Habak, Wilkinson, Zakher, & Wilson, 2004; Loffler, Wilson, & Wilkinson, 2003; Poirier & Wilson, 2007). Recent models of global shape perception propose that local curvature is an important intermediate step in object shape representation (Cadieu et al., 2007; Pasupathy & Connor, 2002; Poirier & Wilson, 2006). The current study contributes toward our understanding of curvature encoding mechanisms by investigating whether those mechanisms are tuned for the orientation of a curve.

Evidence for curvature detectors comes from both neurophysiology and psychophysics. A subset of neurons in macaque area V4 is selective for curvature (Connor, 2004; Pasupathy & Connor, 1999, 2001), and some of these neurons are tuned for the orientation, position, and curvature of a curve. Pasupathy and Connor (2002) and Cadieu et al. (2007) have utilized these curvature tuning characteristics to develop models of shape coding, in which the positions and curvatures of the parts of an outline shape are projected onto a two-dimensional (2D) plane and encoded in an object-centric space.

Psychophysical studies of curvature (Arguin & Saumier, 2000; Gheorghiu & Kingdom, 2007b, 2008, 2009; Hancock & Peirce, 2008; Treisman & Gormican, 1988; Watt, 1984; Watt & Andrews, 1982; Wilson & Richards, 1989) are consistent with the idea of specialized detectors for curvature, but the most direct evidence comes from the finding that curvature is an adaptable stimulus feature (Gheorghiu & Kingdom, 2007b, 2008, 2009; Hancock & Peirce, 2008). For example a sinusoidal-shaped contour can appear distorted in either shape amplitude or shape frequency following adaptation (Gheorghiu & Kingdom, 2006, 2007a, 2007b, 2008), and

the evidence points to both effects being mediated by mechanisms sensitive to local curvature, rather than to local orientation, average curvature, periodicity, or shape frequency (Gheorghiu & Kingdom, 2007b, 2009). Hancock and Peirce (2008) showed that the induced angle between a pair of collinear elements following adaptation to an opposite-angled pair is not solely a manifestation of the tilt after-effect but involves a genuine after-effect of curvature.

The aforementioned studies by Gheorghiu and Kingdom have revealed several properties of curvature encoding mechanisms, such as selectivity for luminance-contrast polarity, luminance spatial frequency, color direction, curvature polarity, and the two dimensions of a curve—sag and cord. What has not been revealed by these, or any other appearance-based study of curvature processing, is whether human curvature detectors are tuned for the orientation of the curve, as has been shown to be the case for curvature-sensitive neurons in macaque V4 (Pasupathy & Connor, 1999, 2001).

To test whether curvature encoding mechanisms are tuned for the orientation of a curve, we used an analogue of the shape amplitude after-affect, or SAAE, found with sinusoidalshaped contours (Gheorghiu & Kingdom, 2006, 2007b, 2008). The adapting and test stimuli each comprised a single curve, specifically a half-cycle rather than a full sine-wave contour, and we term the associated after-effect the curvature after-effect, or CAE. We measured the CAE as a function of the orientation difference between the adapting pattern and test pattern. Subsequently, we fitted a Gaussian function to the data to provide an estimate of orientation tuning bandwidth. We also measured the size and direction of the CAE for opposite polarity (180° orientation difference) adaptor and test curves to determine if there are populations of neurons in the visual system that are not selective for the sign of curvature.

General methods

Participants

Three experienced psychophysical observers participated in this study. Two were authors (JB and EG) while the third observer was naive with regards to the experimental aims. All observers had normal or corrected-to-normal visual acuity.

Apparatus and stimuli

Stimuli were created using Matlab, version 7.6, and loaded into the frame store of a Cambridge Research Systems (CRS) ViSaGe video-graphics system. Stimuli were presented on a Sony Trinitron G400 monitor with a screen resolution of 768×1024 pixels and a refresh rate of 100 Hz. The luminance of the monitor was calibrated



Figure 1. Examples of the stimuli used throughout the study. To experience the CAE for yourself, simply stare at the fixation cross on the left-hand side of the figure (A) for approximately 30 s. Now shift your gaze to the fixation cross on the right (B) where you should experience the curves above the fixation cross as lower in curvature compared to those below the fixation cross. This exemplifies the CAE for adapting and test curves of the same orientation (0°). The bottom row illustrates the appearance of curves at orientations other than 0° (horizontal plane).

using an Optical OP200-E (Head Model # 265). The mean luminance of the monitor was 50.4 cd/m^2 .

Sample test stimuli are shown in Figure 1. Each curve constituted a half-cycle of sinusoidal modulation. A contrast smoothing function was applied to each end of the contour to minimize orientation cues at the ends. Each curve was defined by its "cord" and "sag," corresponding to the shape frequency and shape amplitude of the sinusoidal shape from which the curve was derived. The crosssectional luminance profile of each contour was a Gaussian with sigma of 0.085°. Unless otherwise stated, adaptation and test stimuli consisted of a set of four curves in each visual field. The multi-curve stimulus configuration was designed specifically for another study; however, a control condition is described later that demonstrates that a singlecurve version of the stimulus produces a similar pattern of results. The bottom row of Figure 1 shows examples of individual curves at other orientations tested.

Procedure

A staircase procedure was employed to measure the curvature after-effect, or CAE. The procedure was the same as that used by Gheorghiu and Kingdom (2006, 2007b, 2008) for measuring the shape-frequency and shape-amplitude after-effects. The procedure used to measure the tilt after-effect, or TAE, was the same as that used by Bell and Kingdom (2009).

Dual adaptor method, CAE (Experiment 1): The initial adaptation period lasted 1 min, during which the spatial location of each set of curves was horizontally jittered (up to $\pm 45'$, randomly drawn from a rectangular distribution) every 500 ms. The shape frequency of the adapting and test curves was set to 0.65 c/°, giving a cord length of 0.77°. Unless otherwise stated, the shape amplitudes of the adapting curves were 0.12° and 0.36° , which are also the sag lengths, giving a geometric mean amplitude/sag of 0.2° (see Figures 1A and 1B). Each cycle of the test period began with a 400-ms blank screen, followed by the test pair for 500 ms (signaled by a tone), then a blank screen of 100 ms and finally 2.5 s top-up adaptation. The test stimuli were presented simultaneously 3° above and 3° below the fixation cross (fixation point to the center of the stimuli). Adaptation and test stimuli were independently jittered horizontally on each trial (every 500 ms for the adaptor). The location of the fixation cross was not jittered across trials. The observer was instructed to select whether the upper or lower test stimuli appeared to be the higher in amplitude, or the more curved. Responses were made during the adaptation top-up phase. The commencement of each trial was automatic, i.e., not dependent upon the observer making a response. The amplitude ratio of the test patterns on the first test trial was set to a random number between 0.5 and 1.5 (upper divided by lower) but with the geometric mean amplitude fixed at 0.2° (Figure 1B). Following each response (a key press) the computer adjusted the ratio of amplitudes in a direction opposite to that of the response, i. e., toward the point of subjective equality (PSE). For the first 5 trials, the ratio was adjusted by a factor of 1.12, and thereafter by a factor of 1.06. Each run was terminated after 25 trials and the PSE was calculated as the geometric mean ratio of test pattern amplitudes over the last 20 trials, which on average contained 6-10 reversals. Typically, six PSEs were measured for each condition. In half of the sessions, the high amplitude adapting pattern was in the upper visual field whereas in the other half the lower amplitude adapting pattern was in the upper visual field. In addition, we measured the PSE in sessions containing no adaptation stimuli; these served as baselines with which to compare the size of the CAE with adaptation. The size of the after-effect calculated for each session was given by the log ratio of test amplitudes (corresponding to the lower and higher adapting amplitudes) at the PSE minus the same PSE value without adaptation. The mean and SE of these values across sessions are the points shown in the graphs.

Dual adaptor method: TAE (Experiment 2): The adaptation procedure for these conditions was the same as the dual adaptor method described above, but now the adapting stimuli consisted of a single curve in the upper and lower visual fields, respectively, rather than a set of four. All other attributes of the adapting stimuli were the same. The test stimuli consisted of a pair of line elements, presented in the upper and lower fields respectively. Line elements had a Gaussian profile with sigma set to give them the same cross-sectional width as that of the test curves. On each test trial (signaled by a tone) the observer was instructed to indicate which of the two line elements was rotated furthest from vertical. Following the observer's response, the staircase procedure adjusted the orientation of the upper and lower test lines toward the PSE. For the first 5 trials, 1° was added to or subtracted from the orientation of each test line: thereafter 0.5° steps were used. The change in the orientation of the upper and lower test lines was symmetrical, with the same angular change added to one being subtracted from the other. Rather than recording the ratio of the two, in these conditions the angular difference between elements was measured. The angular difference over the last 20 trials was used to calculate the mean difference and standard error at the PSE in each condition. We also ran trials involving no adaptation, in order to measure the average angular difference between elements in these cases (baseline). The data shown plot the average angular difference between elements following adaptation, minus the baseline measurement.

Single adaptor method, CAE (Experiment 3): In order to determine if the CAE for opposite polarity adaptor/test curves was unidirectional (i.e. all adaptors caused opposite polarity tests to appear only higher, or only lower in amplitude) or bi-directional (i.e. low amplitude adaptors caused higher amplitude opposite polarity tests to appear higher, whereas higher amplitude adaptors caused lower amplitude opposite polarity tests to appear lower), we used a single adaptor method. In each session, a single adapting stimulus was presented, either in the upper or lower field (equal numbers of both and in random order). The test pattern was presented in the same retinal location as the adapting pattern, while a comparison pattern was shown in the opposite hemi-field. The test was fixed in amplitude $(0.1^{\circ}, 0.2^{\circ}, \text{ or } 0.3^{\circ} \text{ in separate conditions})$ while the comparison amplitude was adjusted using the same staircase procedure. All other aspects of procedure were the same as for the dual adaptor method.

Experiments

Experiment 1: Are curvature detectors tuned for orientation?

The first experiment tests whether curvature detectors in the human visual system are tuned for the orientation of the curve. The orientation of the adapting curves was rotated away from that of the test curve in Log 2 steps (0° , 6.125°, 11.25°, 22.5°, 45°, 90°, and 180°; see bottom row of Figure 1 for examples). These conditions included those where the adaptor and test shared the same relative orientation (0° difference) and those where they had opposite curvature polarity (180° difference). Orientation tuning functions were measured for test curves at orientations of 0° (horizontal plane) and 45° (oblique), with the same range of adaptor test relative orientation differences employed for both.

Figure 2 shows the CAE as a function of adaptor orientation for test orientations of 0° (left panels) and 45° (right panels). CAEs are largest when the adaptor and test are of the same orientation and rapidly decrease as the orientation of the adapting curve is rotated away from that of the test curve. The strong tuning for curvature orientation is evident in all three observers and for each test orientation. As a control experiment to determine if local interactions between neighboring curves might contribute to the shape of this function, two observers (JB and EG) re-measured the CAE at several orientations using a single curve in each hemi-field (gray outlined data points in the left panels of Figure 2). Similar magnitudes and orientation tuning of the after-effect was obtained with the single-curve stimuli, indicating that local interactions between curves did not contribute to the shape of the data reported in Figure 2. The similarity in the size of the CAE for single- and multicurve stimuli also implies that the CAE to reach its maximum with only a single curve. The CAEs are similar in size to those measured using sine-wave-shaped contours (Gheorghiu & Kingdom, 2007b) where curvature aftereffects peaked for a single half-cycle of sine-wave modulation.

A notable feature of Figure 2 is that observers obtained significant CAEs when the orientation of the adapting curve was rotated 180° relative to the test, i.e., was of opposite curvature polarity. The after-effect for opposite curvature polarity is in the same direction as that for same curvature polarity. That is the adaptors in both cases caused a lower-in-amplitude test to look even lower in amplitude and/or a higher-in-amplitude test to look even higher in amplitude. The magnitude of the opposite curvature-polarity after-effect however is approximately half that of the same curvature-polarity after-effect. We will return to the significance of these findings with opposite curvature-polarity stimuli later.

Next we sought to estimate the orientation tuning bandwidth of our data. The lower right panel in Figure 2 combines the data across observers after normalizing each observer's data to the CAE at 0° orientation difference. Error bars are standard errors across different observers. The combined data are well fit by a Gaussian function with a standard deviation of 16.76°, or a half-width of 17.9° at half-height (full width 35.8°). The data for the opposite curvature-polarity CAEs (180° orientation difference) are not included in this fit.

Although the results of Experiment 1 suggest that curvature detectors are strongly tuned for orientation, it is possible that the shape of the tuning function in Figure 2 is a result of orientation not curvature adaptation, i.e., a manifestation of the tilt after-effect, or TAE (e.g., see Blakemore & Over, 1974 and Timney & MacDonald, 1978). Experiment 2 tests this idea.

Experiment 2: Assessing the role of orientation adaptation

Previously two of us showed that the shape-frequency and shape-amplitude after-effects obtained with sinewave-shaped contours were not caused by the TAE (Gheorghiu & Kingdom, 2007b). However, this does not preclude the possibility that TAEs (Gibson & Radner, 1937; Magnussen & Kurtenbach, 1979; Ware & Mitchell, 1974) contribute to the shape of the curvature orientation tuning function obtained in Experiment 1, although it seems on a priori grounds to be unlikely because we used a rectangular distribution to randomly jitter the horizontal position of each adapting curve every 500 ms, and of each test curve on each trial. In other words, there was no modal horizontal position for adaptor or test and therefore no systematic relationship between the orientation and position information of the adaptors and tests.

In order to investigate the possible role of local orientation adaptation, we measured TAEs in straight-line test contours following adaptation to curves of various orientations (0° , 22.5°, or 90°). The adaptation procedure and the arrangement of adapting curves was the same as used in Experiment 1 for the 0° test curve condition. We measured TAEs at two different test orientations, orientations that are tangents in the 0° test curve used in Experiment 1. The test orientations were the tangents to the curve at the d.c. (the DC TAE condition) and the tangents to the curve at the point mid-way between the d.c. and the apex of the curve (the Mid TAE condition; see inset of Figure 3 for an illustration of the line elements and of where they are tangents in the original curve). The length of the test lines was half of the cord length of the adapting curve. We can compare TAEs and CAEs by considering the size of CAEs in terms of the angular difference between the upper and lower curves at the PSE, rather than the difference in amplitude/sag. The d.c. crossings of the test curves are the points where the orientation at the tangent to the curves differs maximally between different amplitudes. In the data below, we compare the difference in tangent orientation at the PSE to the magnitude of the tilt aftereffect produced by adapting to curves under the same conditions.

Figure 3 shows CAEs and TAEs for two observers. The horizontal axes indicate the orientation of the adapting curves and the vertical axes show the direction and magnitude of the after-effect. Black square points in each panel re-plot CAEs from Experiment 1 (0° test curve) expressed as an angular difference. Gray squares and unfilled gray circles show TAEs measured at orientations corresponding to the DC TAE



Figure 2. CAEs for three observers as a function of the orientation difference between the adapting and test curves. Vertical axes describe the size of the after-effect on a log scale. Horizontal axes describe the orientation of the adapting curves. Panels on the left-hand side show data for a test curve at 0° orientation. Gray outline squares for JB and EG show data when the adapting and test stimuli were comprised of a single curve in each hemi-field, rather than the set of curves shown in Figure 1. Central and upper panels on the right-hand side show data for two observers using a test curve at 45° orientation (oblique). Error bars on each data point show ± 1 standard error. The lower right panel shows the combined data from all observers and from both test orientations. Data are plotted as a ratio of the after-effect when the adaptor and test shared the same orientation. Data were fit with a Gaussian function and the standard deviation of this fit is given in text ± 1 *SE*.



Figure 3. The stimulus figure at the top shows the appearance of individual line elements in relation to the standard test curve. Relevant arrows beside each line indicate the point within the curve at which the orientation of each test line corresponds to. *Note*: Line elements have been nudged in position in order to make it easier to view them and their designated origin. Data panels for each observer show two different types of TAE (DC TAE [gray squares] and Mid TAE [open circles]) and a subset of conditions replotted from Figure 2 (CAE data [black squares]). Vertical axes show, in degrees, the direction (attractive "+" or repulsive "-") and magnitude of the difference between the upper and lower test patterns at the PSE. Horizontal axes indicate the orientation of the adapting curve.

and Mid TAE angle, respectively. Plotted as an angular difference, we see that CAEs are strong and "repulsive" when the adaptor and test share the same orientation and then decrease as the adapting curve is rotated away from the test curve, culminating in no CAEs when the adaptor is rotated 90° relative to the test. DC TAEs also decrease as the adapting curve is rotated away, however for oblique (22.5°) and orthogonal (90°) adapting conditions, DC TAEs

are not "attractive" after-effects, meaning they are *not* in opposition to the "repulsive" CAEs and are therefore unlikely to be playing a significant role in the reduction of the CAE at these orientations. Mid TAEs are consistently repulsive, irrespective of the orientation of the adapting curve; if they were to have an impact they would produce a constant magnitude CAE as a function of adaptor orientation, which is not what we find.



Figure 4. Opposite curvature polarity CAEs measured as a function of the amplitude of the adapting curve. Each panel shows a different amplitude test curve. Vertical axes describe the size and direction of the after-effect on a log scale. Positive values indicate that the test curve appeared higher in curvature amplitude. Negative values indicated that the test curve appeared lower in curvature amplitude. Horizontal axes show the amplitude of the adapting curve (single adaptor method). Vertical dashed lines indicate the amplitude of the test curve in each panel. Horizontal dashed lines indicate no CAE.

While our data suggest that TAEs cannot explain the results of Experiment 1, it must be born in mind that there are many tangent orientations in a curved arc. Thus although it seems unlikely, we cannot rule out the possibility that other tangent orientations could have produced TAEs, and hence implicating a significant role for orientation adaptation in the CAE orientation tuning data of Experiment 1.

Having provided evidence that the pattern of CAEs is not due to the TAE, we now consider further the finding of an opposite curvature-polarity CAE. The presence of a small but significant CAE for opposite curvature-polarity adaptor/test curves is not consistent with opposite curvature-polarity curves being processed independently, but nor is it consistent with opposite curvature-polarity curves being processed by a single mechanism, since this would have produced the same sized CAE for same and opposite curvature-polarity conditions. The results are perhaps best explained by the combined operation of selective and non-selective curvature-polarity mechanisms and this possibility is explored in Experiment 3.

Experiment 3: Evidence for curvature-polarity non-selective mechanisms

Experiment 1 showed that CAEs can be induced between opposite curvature-polarity adapting and test curves differing in curvature amplitude. These CAEs were consistently smaller than those found for same curvaturepolarity adaptor and test curves. If there is a population of curvature detectors that are not tuned for curvature polarity, one would expect opposite curvature-polarity CAEs to be found across a range of curvature amplitudes. On the other hand, if opposite curvature-polarity CAEs are only found for one particular stimulus configuration, then it would suggest that the opposite curvature-polarity CAEs reported in Figure 2, and by Gheorghiu and Kingdom (2008) using strings of sine-wave contours of similar amplitudes, may simply be an artifact of local orientation and positional adaptation. Experiment 3 measured amplitude tuning functions for opposite curvature-polarity adaptor/test combinations at three test amplitudes (0.1°, 0.2° , and 0.3°). To measure the direction and magnitude of the CAE, the single adaptor method was used (see the Procedure section).

Figure 4 shows CAEs as a function of adaptor amplitude (i.e., amplitude tuning functions) for three different test amplitudes (0.1° upper; 0.2° central; 0.3° lower panels, respectively). The vertical dashed line in each figure indicates the amplitude of the test pattern. The horizontal dashed line indicates no CAE. Figure 4 shows a bi-directional amplitude tuning function for all three test amplitudes, i.e., an adapting curve causes a higher amplitude test of opposite curvature polarity to appear even higher in amplitude and a lower amplitude test of opposite curvature polarity to appear even lower in amplitude. On average, the tuning functions at each test amplitude pass through zero (no CAE) when adaptor and test are equal in amplitude. The slopes of these amplitude tuning functions become shallower as the amplitude of the test pattern is increased, showing that the opposite curvature-polarity after-effect decreases somewhat with amplitude. Overall, the data show that CAEs for opposite curvature-polarity adaptors and tests are tuned for pattern amplitude. Amplitude tuning has been shown for shapeamplitude after-effects involving full sinusoidal contours (Gheorghiu & Kingdom, 2007b) but had not been shown for opposite curvature-polarity adapting curves and test curves. The findings here are consistent with the existence of a subpopulation of curvature detectors that are tuned for pattern amplitude, or "sag," but that are not selective for the polarity of a curve.

General discussion

The current study reveals new information about the mechanisms responsible for encoding curved contours. Several properties of curvature encoding mechanisms have already been revealed by Gheorghiu and Kingdom's (2006, 2007a, 2007b, 2008) studies of curvature after-effects using sine-wave-shaped contours. Here we have employed a single half-cycle of a sine-wave shape to measure a curvature after-effect. Our evidence has revealed an additional dimension to the encoding of contour curvature, namely the orientation of a curve (Figure 2) and the presence of a subpopulation of curvature detectors that are tuned for the amplitude but *not* curvature polarity of a curve (Figures 2 and 4).

Our finding that curvature detectors are tuned for the orientation of a curve is consistent with research on curved grating detection (Timney & Macdonald, 1978) and with reports from recent physiological studies of curvature processing in monkeys. Pasupathy and Connor (1999, 2001, 2002) recorded from macaque area V4 and found neurons that were not only selective for curved contours but in some cases selective for their curvature, position, and orientation (Pasupathy & Connor, 1999, 2001). These findings have led some neurophysiologists to propose that these curvature-selective neurons, as a population, could accurately code the major features of the outline contours of an object (Cadieu et al., 2007; Connor, 2004; Muller, Wilke, & Leopold, 2009; Pasupathy & Connor, 2002). The current study presents psychophysical evidence that curvature orientation is likely to be an important dimension of such a population code.

The second important finding from the current study is the evidence for curvature mechanisms that are tuned for the sag, or amplitude of a curve but not for curvature polarity (Figures 2 and 4). While CAEs (curvature after-effects) were absent for intermediate-sized adaptor-test orientation differ-

ences (45° and 90°), they were robust for 180° orientation differences. Although Gheorghiu and Kingdom (2008) previously found a degree of cross adaptation between opposite polarity curves, the measurements made here across the full range of adaptor-test orientation differences have revealed that the opposite polarity condition is a "special case." This conclusion is reinforced by the finding that the opposite polarity after-effects fell to zero only when the amplitudes/sags were approximately the same (Figure 4). Such tuning for amplitude/sag is hard to explain in terms of extraneous factors such as local orientation adaptation and is compelling evidence for the presence of a subpopulation of curvature detectors that are selective for amplitude/sag but non-selective for curvature polarity. To our knowledge, no neurons have been found that respond selectively to a curve and its mirror opposite, so we hope that the results of this study will act as a stimulus to search for just such neurons.

The findings with opposite curvature-polarity curves are not consistent with the idea that opposite polarity curvature detectors are organized in an opponent manner (Poirier & Wilson, 2006), as two of us have also previously concluded (Gheorghiu & Kingdom, 2008), though our findings do not rule out the possibility that some detectors might be organized in such a way. It is also unlikely that opposite polarity curves are processed only by non-selective curvature-polarity mechanisms, since this would predict similar sized CAEs for same and opposite curvaturepolarity conditions, rather than the approximately halfmagnitude CAEs obtained in the opposite curvature-polarity conditions. Rather, we suggest that opposite curvaturepolarity CAEs are mediated by both curvature-polarity selective and non-selective mechanisms. This idea has yet to be incorporated into models of the receptive-field structure of curvature detectors (Gheorghiu & Kingdom, 2009).

What might be the functional role of detectors that are sensitive to both polarities of curvature? One obvious candidate is symmetry detection (Wagemans, 1995). Humans are highly sensitive to symmetry (Dakin & Hess, 1997; Dakin & Watt, 1994; Rainville & Kingdom, 2000; Van der Zwan, Badcock, & Parkin, 1999; Wilson & Wilkinson, 2002) and while it has yet to be established whether curvature per se is a salient feature in symmetry perception, studies with multi-element symmetric textures have shown that symmetry perception is served by a wide range of orientations (Rainville & Kingdom, 2000). The sagselective but curvature-polarity-non-selective mechanism revealed here might give a strong response to two mirroropposite curves placed next to one another. Gheorghiu and Kingdom (2008), using adaptors composed of mirroropposite curve pairs and tests composed of single curves, found that the curvature after-effect showed a local maximum when the apexes of the two adaptor curves were just touching, i.e., forming a "seat" configuration, with smaller after-effects when the curves either overlapped or were separated. In the experiments reported here the positions of the adaptors were jittered such that on a proportion of stimulus presentations a mechanism with a "seat" receptive field structure would be stimulated by an adaptor curve as well as an opposite polarity test curve. If indeed the opposite curvature polarity mechanism revealed here is sensitive to mirror symmetry, the inputs to it from each curve would have to be combined in a way other than by pure multiplication in order to allow an effective response to a single curve. We are currently investigating the role of curvature when judging the symmetry of curved contour shapes.

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