Curvature coding in early visual system revealed by scale variance during adaptation to flashing circles

Irfa Nisar
Department of Electrical Engineering and Computer Science
Center for Vision Research, York University

James H. Elder
Department of Electrical Engineering and Computer Science
Center for Vision Research, York University

How is curvature coded in the early human visual system? This question is the essence of basic shape recognition and may explain why humans are so successful in recognizing objects under difficult and varying environment conditions. We use the circle-polygon illusion (Khuu, 2002), to reveal coding mechanisms in the early visual system. The stimulus, constructed by Sakurai's method (Sakurai, 2014), is a static dark outline circle augmented with a 2 Hz pulsed luminance gradient around the inner border. Both the radius and eccentricity of the stimulus were varied in a crossed design over 1-8 deg. Observers reported a circle or the polygon order and the strength of the percept. We test a lower level account that argues for curvature opponency between neurons against a higher level account that codes for whole shapes. This higher level account supports scale invariance, a property through which we recognize objects regardless of the object's rotation (or orientation) and its size on the retina. We show the following: (1) Scale invariance, a property of the higher level visual system feature through which we recognize objects regardless of the object's rotation (or orientation) and its size on the retina, is not obeyed during adaptation. The mean order of the perceived polygon increased with stimulus size and decreased with eccentricity. It did not remain constant for a stimulus size. This demonstrates that the curvature coding occurs in the early visual system. (2) Linear regression analysis reveals that the cortical size of the stimulus is a better predictor of perceived polygon order. We computed the circumference of each stimulus in both retinal and cortical coordinates, taking cortical magnification into account.

Keywords: shape adaptation, cortical adaptation

Introduction

Why is curvature perception important? Coding of curvature in the early visual system influences how complex shapes are recognized in the world and why the human visual system is able to deduce shape under the most challenging of conditions. How is curvature

coded in the brain? Is curvature coded on a low level retinal plane or is it a product of a higher order cortical process? If curvature was coded on the retinal plane, it would be influenced by the two dimensional spatial relationships between geometric parts of the shape on the retina. However, if it was coded higher up in the cortex, it might show more complex representations such as scale invariance that is observed with position, rotation and size. We use the circle-polygon illusion that was discovered by Khuu (Khuu, 2002) and use Sakurai's technique (Sakurai, 2014; Sakurai & Beaudot, 2015) to construct the phenomenon to understand how curvature is coded in the brain.

Sakurai's illusion builds on Khuu's circle-appearing-as-polygon illusion by temporally pulsing a graded circle with its outline at 2 Hz inducing rapid adaptation in just a few seconds. Ito in (Ito, 2012) shows that adaptation to a static and a rotating circle,either filled or unfilled, generates an afterimage of a hexagon. In (Sakurai, 2014; Sakurai & Beaudot, 2015), Sakurai show that if a circle and its inward gradation are alternated, we see a polygon shape perception of the circular stimuli itself. That shape is a hexagon. Scale invariance is a well known property of the human visual system (Schwartz, Desimone, Albright, & Gross, 1983; Desimone, Albright, Gross, & Bruce, 1984; Logothetis, Pauls, & Poggio, 1995; Brincat & Connor, 2004; Liu, Agam, Madsen, & Kreiman, 2009; Rust & DiCarlo, 2010). Notable among these studies, in the context of this paper, are the studies by Schwartz et. al and Logothetis et. al. Schwartz et. al (Schwartz et al., 1983) demonstrate invariance by recording from the inferotemporal (IT) region, a region that codes for global shape, by showing that position and size invariance is observed for stimuli constructed from Fourier descriptors. Logothetis et. al show invariance in the IT by showing that neurons are selective for certain views and broadly tolerant to transformations such as rotation and scaling that is centered around the primary view.

Why is the circle-polygon illusion a cortical process? How can we measure the retina's projection on the cortex? After a coloured figure is observed for a long time, a negative coloured afterimage appears. Coloured afterimages after adaptation are explained by either lateral inhibition or recurrent self inhibition (Anstis, Rogers, & Henry, 1978). Lateral inhibition is best explained by suppression in the same colour system whereas recurrent self inhibition is best explained by reduced sensitivity of the system undergoing prolonged simulation, giving rise to negative afterimages. Neither lateral inhibition or recurrent inhibition are necessarily cortical processes. Shimojo et. al in (Shimojo, Kamitani, & Nishida, 2001) demonstrate that the afterimage is a negatively coloured perceptually enlarged filled in surface, greater in surface area, rather than a simple negative afterimage of the same size after adaptation. Surface enlargement signals the presence of cortical adaptation rather than retinal bleaching or neural adaptation in the retina. Ito's experiment (Ito, 2012), therefore, signals that cortical adaptation accounts for the shape observed in the afterimage shape. In this paper, we demonstrate that early curvature formation is indeed a cortical process by relating the adapted shape seen during the Circle-Polygon illusion with its cortical magnification.

As seen in(Sakurai, 2014; Sakurai & Beaudot, 2015), the circular stimuli, when alternated with its inward gradation, makes the cortical process adapt to the curvature and gives rise to symmetrical regular hexagons instead of an irregular organic shape.Gheorghiu and Kingdom in (Gheorghiu & Kingdom, 2007, 2009, 2017) demonstrate that population neural code affects perception of local curvature through an AND-gate multiplication mechanism. However, none of the above experiments explain the order of the polygon as a function of the stimuli size. Neurophysiological studies conducted on non-primate data in (Das & Gilbert, 1995) show that receptive

fields that fire for a similar range of orientations cluster together but long-range connections can sometimes influence the range of degree to which orientations are recognized. Why is the regularity of the afterimage, also called regular polygonalization, an important attribute in the afterimage? Could neurophysiology explain this regularization? Indeed, the presence of regularization itself suggests that retinal bleaching or adaptation is an unfavourable hypothesis and alludes that the answer might be a cortical process operating in the lower regions such as V1 where such long range connections play a role in the building of curvature. In this paper, we draw a comprehensive list of the types of the polygons seen given varying circles and compare a retinal and a competing cortical model to see which better explains the adapted polygon. The retinal model relates the retinal size of the stimulus to the order of the polygon. The second model, relies on cortical M-scaling and relates the cortical image of the stimulus to the order of the polygon.

How can one quantify the stimuli's projection on the cortex? It is known that receptive field size increase towards the retina's periphery (Rovamo & Virsu, 1979). However, the cortical representation of the receptive field remains constant due to a reciprocal relationship with the cortical magnification factor, M. M is defined as the ratio between the cortical representation of the receptive field (in mm) and its size on the retina (degrees of visual angle). In simpler terms, it is the cortical distance between two points that are 1 ° apart in the visual field. Human acuity and resolution is a constant multiplier of the estimated M (Cowey & Rolls, 1974; Drasdo, 1977; Rovamo & Virsu, 1979; Virsu, Rovamo, Laurinen, & Näsänen, 1982). Rovamo and Virsu in (Rovamo & Virsu, 1979) estimate and reduce M, for the principal meridians of the visual field in four equations. See Equation 1 and the accompanying table for coefficients. Here, M_o is $7.99mm/°$, the magnification at the fovea. *r* is the eccentricity in degrees.

$$M(r) = (1 + ar + br^3)^{-1} M_o \tag{1}$$

Area where magnification is computed	a	b	Eccentricity range
Nasal	0.33	0.00007	$0 \leq E \leq 60\,\mathrm{deg}$
Superior	0.42	0.00012	$0 \leq E \leq 45\,\mathrm{deg}$
Temporal	0.29	0.000012	$0 \leq E \leq 80\,\mathrm{deg}$
Inferior	0.42	0.000055	$0 \leq E \leq 60\,\mathrm{deg}$

In (Daniel & Whitteridge, 1961), Daniel and Whitteridge show that an increment of 1 degree visual angle measured from the central fixation point corresponds to an arc length of M mm on the theoretical visual cortex. If we integrate M, we obtain the distance on the cortex as a function of eccentricity. In this paper, we build a generic skeletal algorithm to compute that integral on the cortex. Other, coarser forms such as simply integrating over eccentricity have been suggested in (Sereno et al., 1995). We extend Sakurai's circle as the stimuli in an effort to study the cortical representation. The diameter of the circles we present as stimuli, subtend a visual angle of 2,4,8 and 16 ° on the user's eye. The eccentricity at which the circle center is presented is at 1,2,4 and 8 °.

Through adaptation, we fatigue the neurons in the higher parts of the visual system and hope to recover the coding mechanism by observing the deficit percept. We address several questions in this paper. Does the size of the stimuli change the number of sides of the polygon seen in the percept after adaptation? Does the adaptation polygon change from trial to trial? Does the eccentricity of the stimuli

change the percept seen after adaptation? Are the vertices located in the same place from trial to trial? And finally, in summary, what do all the adaptation percepts collectively tell us about the underlying cortical process?

Experiment 1

The experiment reports the polygon percept seen during adaptation as the circle radius and the eccentricity of the circle's placement varies.

Methods

Observers

Nine graduate students (6 male, 3 female) at the university participated in the experiment. Four of the graduate students had prior experience in participating in psychophysical experiments. The remaining five students had limited or no experience related to psychophysics. All the students had normal or corrected to normal vision. Each observer passed the stereoacuity test. Stereoacuity was assessed using the Randot stereoacuity test to ensure observers could detect depth from binocular disparities of at least 40 seconds of arc.

Stimuli

The stimuli consisted of a circle with a black outline that alternated with another circle of the same size but with an inward gradation pattern. The black outlines were constructed of penwidth 5 using Psychtoolbox. See 1 (b). The circles were built of different sizes. The diameter of the circle was 2,4,8 or 16 °. See Figure 1 (a). The eccentricity at which the circle was presented was 1,2,4 and 8 °. See Figure 2. Randomized trials presented every combination of the circle radius and its eccentricity. Every unique combination of eccentricity and radius was presented ten times for a total of 160 trials. The circle was placed left of the central fixation cross half the time and on the right of the fixation cross half of the time. The stimuli was presented against a white background.

Apparatus

Stimuli were generated using the Psychtoolbox (Brainard, 1997) in Matlab on a Windows machine with a NVIDIA GeForce GTX1060 graphics card and a Lenovo laptop screen. The participants participated in the experiments on their own machines. They were restricted to desktops only with a monitor of size at least 13 inches. The participants were also asked to adjust their chair and screen so that the screen was at a comfortable viewing distance with adequate room to use the keyboard and mouse. They were asked to ensure that the center of the screen directly faced their eyes.

Procedure

Observers were briefly explained the experiment at the start of the trial. They were told that they had unlimited time to record responses. Observers received 16 practice trials at the start of the experiment session that presented every combination of stimuli radius and the stimuli's eccentricity. Verbal feedback was provided to the user as they navigated the trials. The participants were read the

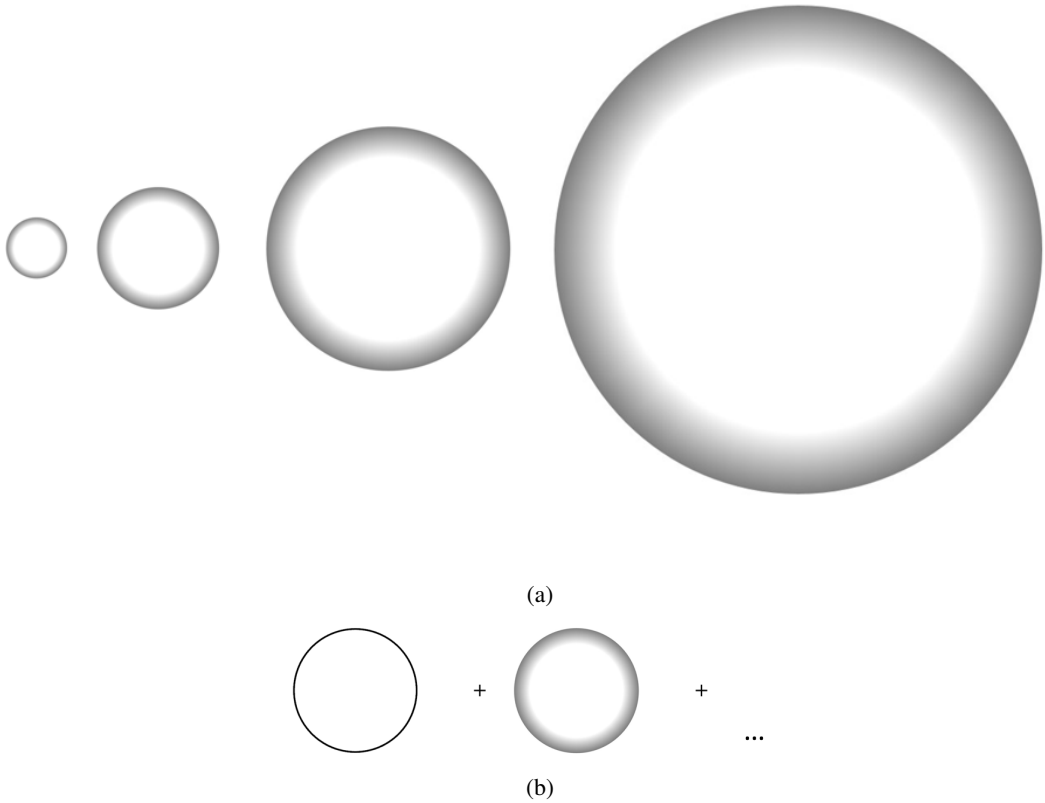


Figure 1: (a) Stimuli size: Circles,with inward gradation, whose size (diameter) subtends 2,4,8 and 16 degrees of visual angle respectively on the user's eye. The pictures are for illustration only and show the relative sizes of the stimuli. Stimuli do not subtend the exact degree on the reader's eye. (b) Flashing stimuli: Circle in a black outline and its inward luminance gradation. The outline and the inward gradation alternate at 2Hz. The circle is presented to the left of the fixation cross.

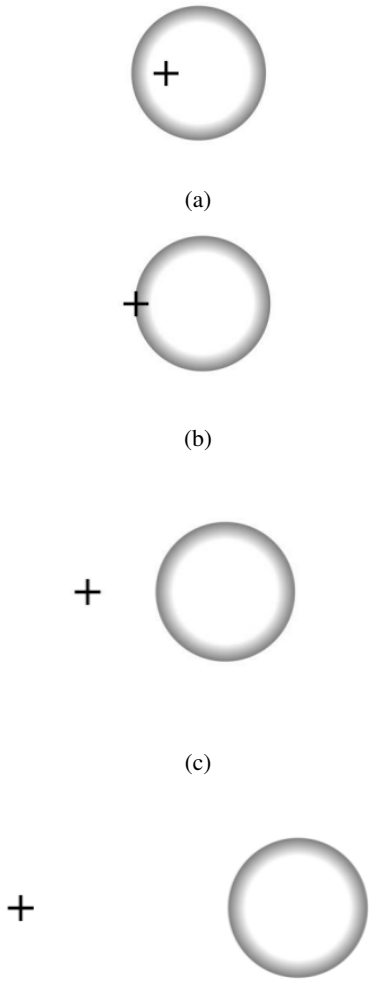


Figure 2: Presentation eccentricity: Circles,with inward gradation, presented at eccentricities of 1,2,4 and 8 degrees of visual angle respectively on the user's eye. The circle's size (diameter) is 4 degrees.

instructions, outlined below, before starting the practice trials.

"Please maintain fixation on the central cross - do not move your eyes during this first phase of the trial. A flashing shape will appear for several seconds. It will have a circular appearance but may gradually appear slightly polygonal as well. After this first phase of the trial, a menu of shapes will appear. If your percept of the flashing shape remained entirely circular, select the circular icon. However, if the flashing shape developed a slight polygonal appearance select the polygon it most resembled.If you select a polygon shape, in a third phase of the trial you will be presented with a menu of orientations for the selected polygon and asked to select the orientation that most resembled the polygon orientation perceived in the first phase of the trial. You will then rate the strength of the polygonal percept on a scale from 0 to 10, where 0 means purely circular and 10 means purely polygonal. The experiment begins with a practice session of 16 trials. Following the practice session, you will complete a full session of 160 trials. "

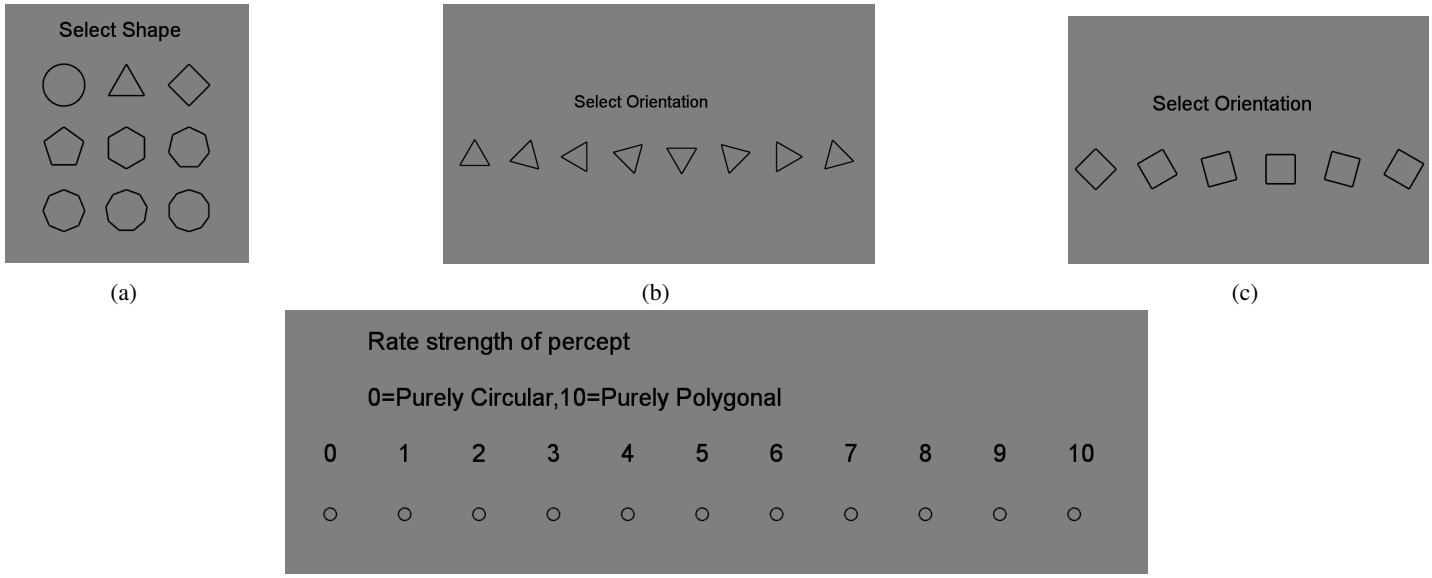
The experiment encompasses 160 trials. A fixation cross on a white background is shown for 1 second before the onset of each stimulus. There are four circles, each circle of a diameter of degree 2,4,8 and 16 ° respectively. There are four eccentricities at which the circle is presented. The eccentricities are of degree 1,2,4 and 8 ° respectively. Each circle is presented in a black outline for 0.5 seconds, after which an inward gradation pattern of the circle is presented for another 0.5 seconds. The background is white. The alternation repeats for a total of 10 seconds.

An array of polygons that the user could identify as the shape is displayed subsequently. See Figure 3 (a) . Instruction appears centrally on the screen, above the array of polygons, that informs participants to select a shape. There is no time limit imposed during the response recording. The polygon that the participant could pick as an adapted percept, could be one of a circle,a triangle,a square,a pentagon,a hexagon,a heptagon,an octagon, a nonagon or a decagon. After the shape is selected, an array of different orientations of the selected shape is presented. See Figure 3 (b,c). We have shown the triangle and square as the chosen figure for brevity. The orientations are rotated clockwise in increments of 15 degrees. The participant is cued by instructions to select an orientation of the shape.

A Likert scale from 0 to 10 is shown and is used to measure the strength of the percept. 0 means the percept was purely circular and 10 means it was purely polygonal. Participants are asked to mark a circle with the scale number that matches their strength response.

Measurement Techniques

The testing took place in a darkened room. Observers used a standard mouse with a middle mouse button and a left button. The participants indicated the polygon to which they adapted, the polygon's orientation and its strength. Once the participant recorded a response, they pressed the middle mouse button on the mouse to move to the next stimuli presentation. The experiment was run in 5 blocks. After a block of 32 stimuli, a break was awarded to the observer. They could resume the next block of trial when ready. The left mouse button was used for all response recording tasks such as selecting the shape, its orientation and the strength of the percept.



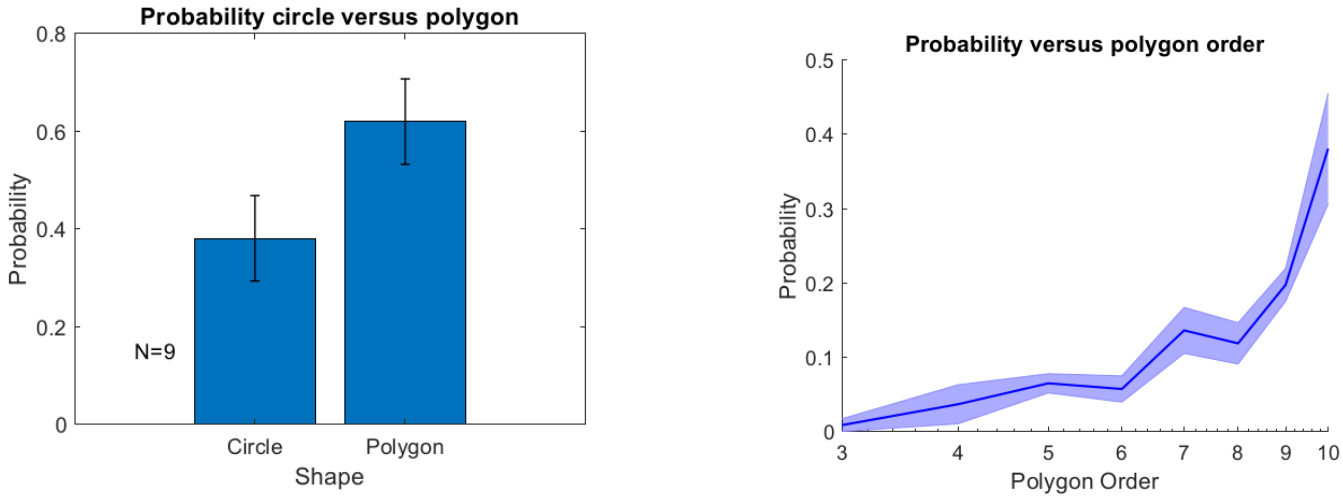
(a) (b) (c)

(d)

Figure 3: (a) Shape Selection: An array of polygons from which the observer selects the percept they saw after staring at the flashing circular stimuli for 10 seconds. (b-c) After selecting the polygon in (a), the user sees orientations of the shape and selects the one that best matches the orientation they saw. (d) The observer is asked to indicate the strength of the percept.

Results

The results from the nine observers is shown in Figure 4. On average, most observers report more polygons than circles during the entire experiment. Polygons are reported 61.9 % of the time versus circles that are reported 38% of the time. A t-test confirmed no significant difference in tendency to perceive polygons between displays shown to the right or left of observer's fixation (t(x) =T, p=.75)



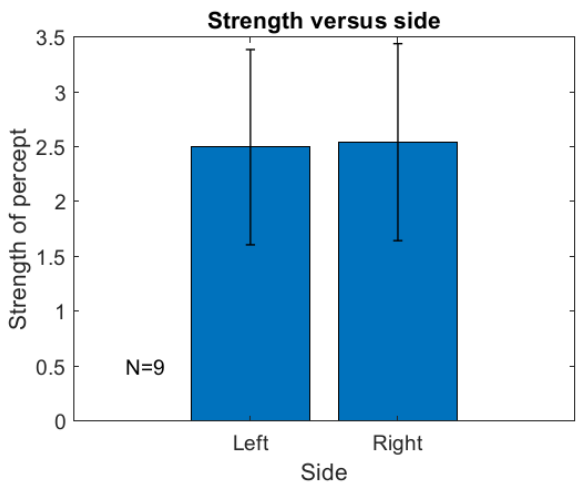
(a) (b)

Figure 4: (a) Proportion Polygon: Observers report seeing polygons after adaptation 61.94 % of the time and seeing the same circle as the stimulus 38.06% of the time across all the stimuli combinations and trials presented. (b) Probability distribution of the different polygon orders.

Strength

The experiment measured the strength of a percept on a scale from 0 to 10. 0 meant that the observer did not see a polygon percept after adaptation. The percept in this case remained the same as the circular stimuli. A 10 on the scale indicated a crisp regular polygon. Figure 5 (a) shows that observers do not report a difference between the left and right visual receptive fields when adapting to the stimuli. The strongest effect is for small objects at large eccentricities. See Figure 7 (a).

Large objects at small eccentricities and small objects at large eccentricities produce large effects. Small objects at small eccentricities and large objects at large eccentricities produce smaller effects. This is demonstrated in the co-relation matrix in Figure 7 (a). The minimum contour eccentricity measures the eccentricity of the closest part of the contour from the fovea center or the fixation cross. Figure 7(b) shows that the further the contour is from the fovea, the stronger the effect.



(a)

Figure 5: (a) Strength Versus Side: Users do not report any significant differences between the left and right visual receptive fields. The same stimuli is presented on the left and the right.

Size

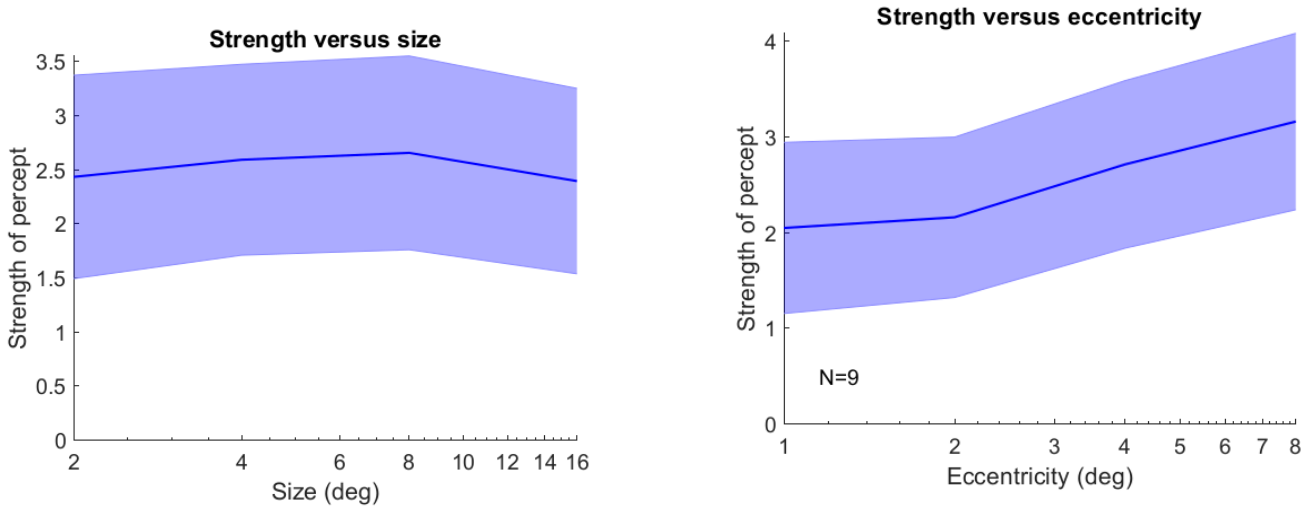
The major effect here is stimuli size. Smaller circular stimuli generally show smaller order polygons. Bigger circular stimuli show higher order polygons. This is an interesting feature that indicates that rather than creating large edges between vertices, smaller, more numerous edges are created between numerous vertices.

Eccentricity

Eccentricity has a modest effect on the polygon order reported. Proximity to the fovea shows higher order polygons. This is a smaller effect. See Figure 8(a),(b)

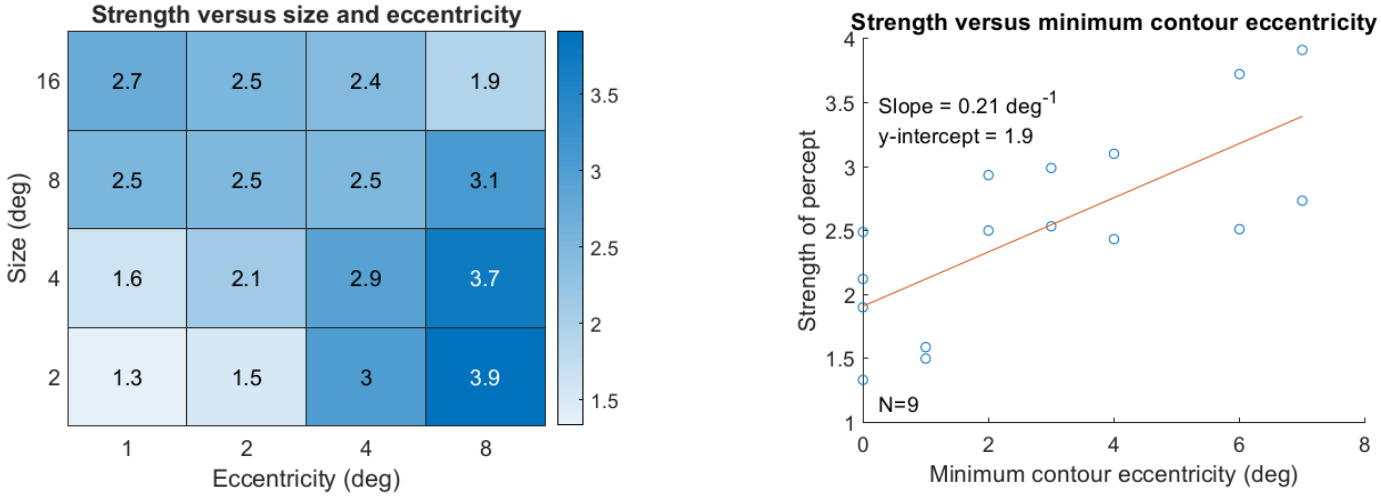
Orientation

We compare observer responses to a uniform distribution of 15 angle increments starting from 0 to the first axis of symmetry for the polygon in question. For most polygons orders, a uniform distribution is observed across all orientations of the polygon. The triangle



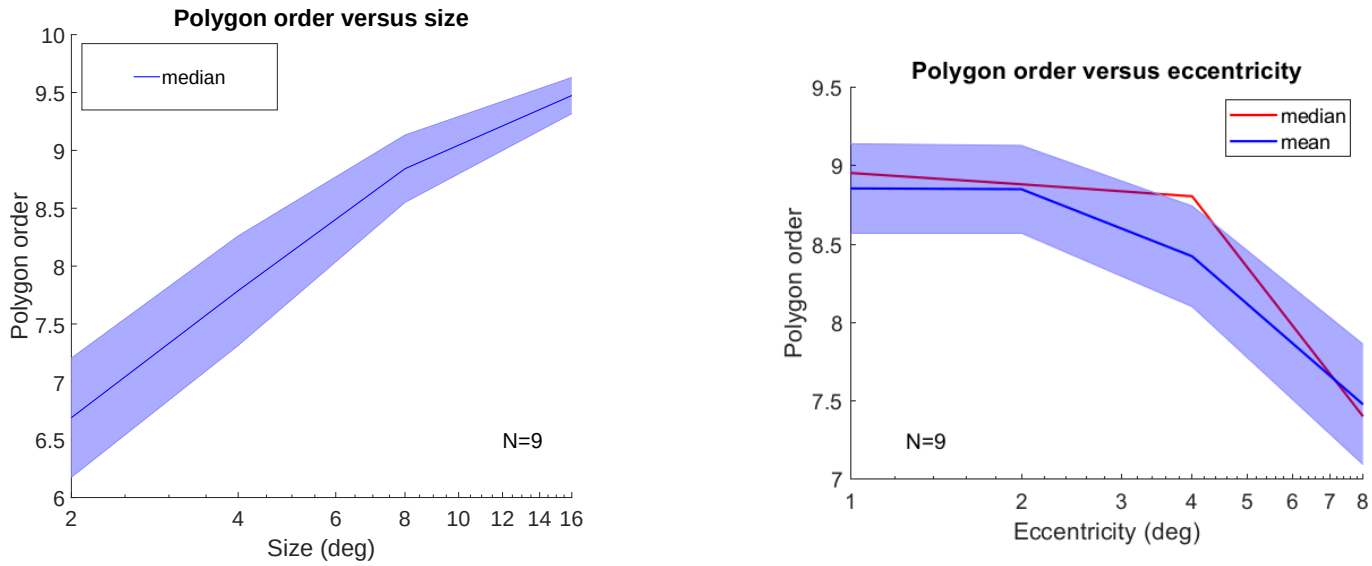
(a) (b)

Figure 6: (a) Strength versus size: Users, on average, report the sharpest perception of the polygon when the radius of the polygon subtends 4 degrees of visual angle on the user's eye. (b) Strength versus eccentricity: Users report the sharpest polygon responses when the stimuli is presented at the largest degree (8 deg) of visual angle.



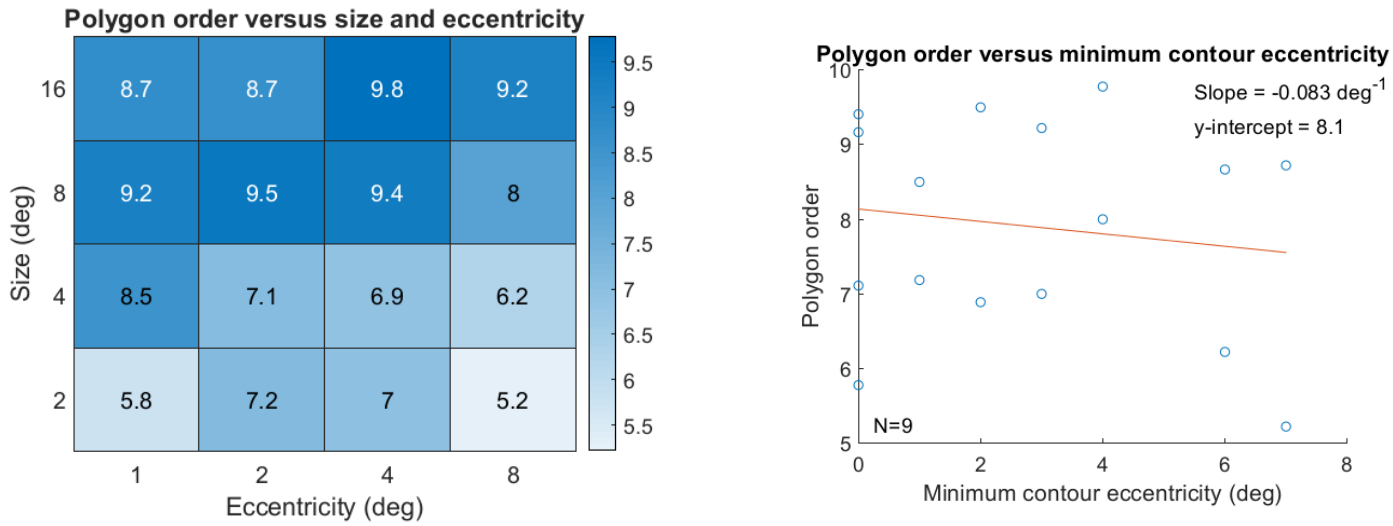
(a) (b)

Figure 7: (a) A co-relational matrix shows the strength as a function of size and eccentricity. (b) Strength versus minimum contour eccentricity: The strength of the percept strengthens as we move away from the fovea.



(a) (b)

Figure 8: (a) Polygon order versus size: Larger order polygons were reported as the radius of the stimuli increased. (b) Polygon order versus eccentricity: In general, observers report lower order polygons at higher eccentricities,larger order polygons at middle eccentricities, followed by slightly lower order polygons at smaller eccentricities. Eccentricity has a modest effect on polygon order.



(a) (b)

Figure 9: (a) Co-relation matrix showing polygon order (mean) versus size and eccentricity. (b) Polygon order versus minimum contour eccentricity. On average, the minimum contour eccentricity from the fovea only modestly effects the polygon order.

showed a relatively high KL divergence value compared to other polygons. With the triangle, observers preferred the 45 ° orientation strongly. Figure 10 shows the responses recorded and the orientation selected for the response polygon.

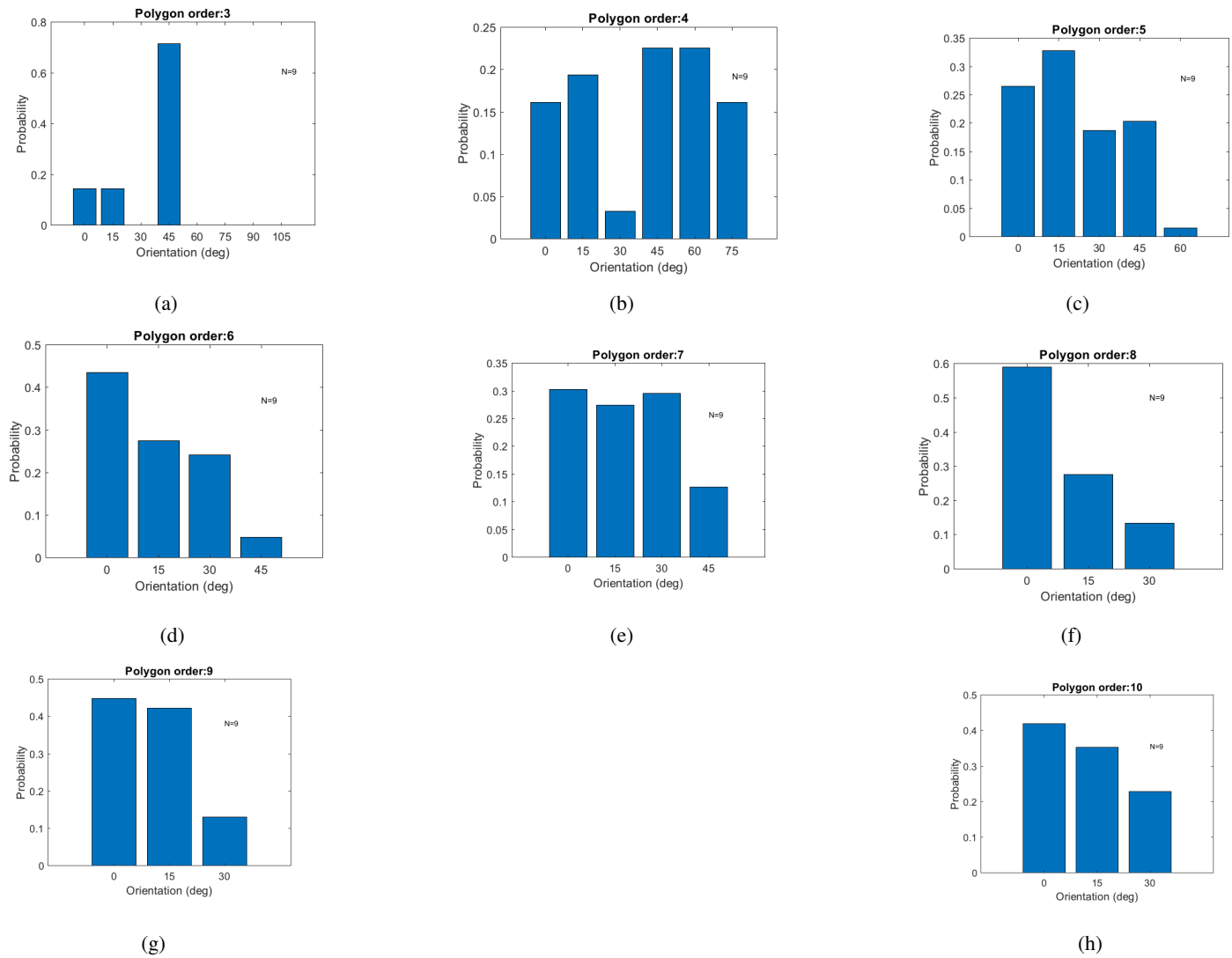


Figure 10: Probability versus orientation

Model that explains the polygon order observed

Can the polygons observed above be explained by a retinal model or a higher level cortical model? A retinal function samples the circular stimulus in 2D cartesian co-ordinates. The domain of the function is degree visual angle representing eccentricity. The cortical length can be computed from the points on the circle seen on the 2D retinal plane and applying the cortical M-scaling, that measures millimetres of cortex per degree of visual angle, as a function of eccentricity, on those sampled 2D points.

We fit a first order linear model of the polygon order as a function of retinal size and another as a function of cortical circumference size. We shall hereby call the retinal circumference size, retinal length, and the cortical circumference size, cortical length. See Figure 12 (a,b,d).

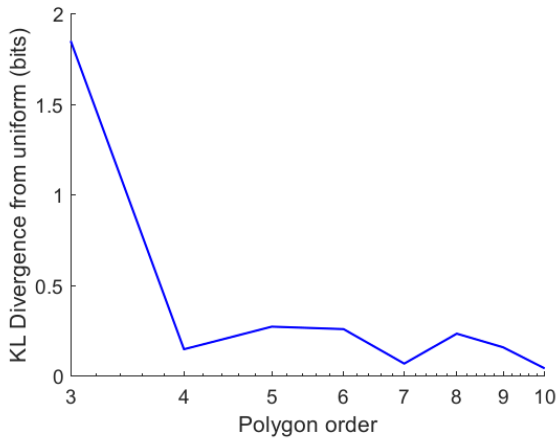


Figure 11: KL divergence: KL divergence shows how much the orientation differs from a uniform distribution of orientations. When observers select a triangle as the in-place adaptation polygon, they mostly select the 45 degree orientations. Other shapes show a more uniform spread in the orientations selected.

The M-scaling factors in the cortical function were borrowed from (Rovamo & Virsu, 1979). This is a skeletal model with Rovamo and Virsu cortical magnification factors. The cortical magnification factors are replaced by other magnification factors in other neurophysiology studies (Harvey & Dumoulin, 2011). Harvey and Dumoulin create a model that maps population receptive fields and cortical magnification factor as a function of the cortical magnification factor of the first field in the visual hierarchy, V1. Later fields such as V2,V3 and V4 must sample from V1.

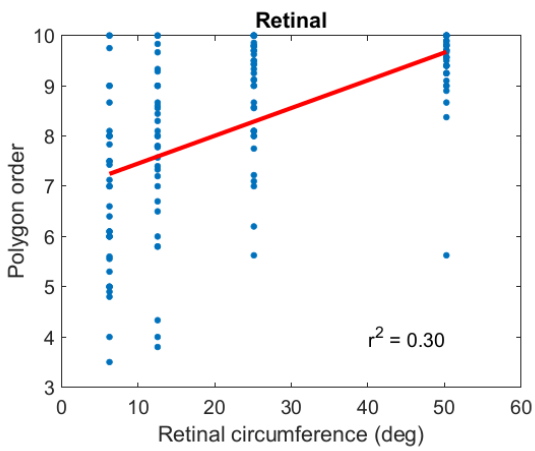
From this regression model, we build an equation for the polygon order as a function of the retinal circumference (Equation 2) and as a function of the cortical circumference (Equation 3).

$$y = 6.8995 + 0.0552x, \text{x is a point on the retinal circle} \tag{2}$$

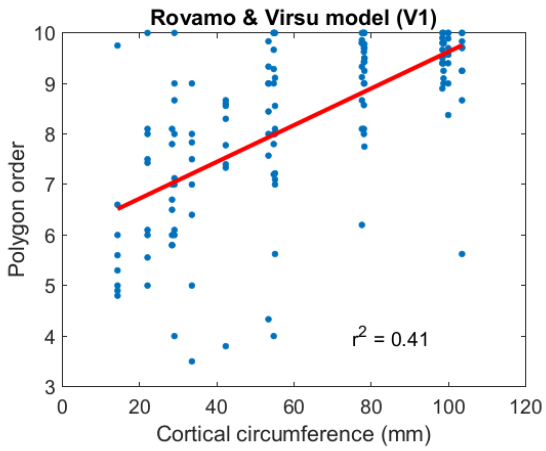
$$y = 5.9936 + 0.0364x, \text{x is a point on the cortical circle} \tag{3}$$

The R^2 value explains how well the model explains the variability in the responses based on the variability in the predictor values. The cortical length's R^2 reports higher value than the R^2 for the retinal length measurements. We used bootstrapping on the observer's responses i.e. polygon order and computed the retinal function and cortical function R^2 values. Among the models that we studied - (a) the skeletal model with Rovamo and Virsu cortical magnification factor and (b) the Harvey model - we found R^2 values are the highest with the skeletal model using the Rovamo and Virsu cortical magnification factors. This model, therefore, becomes our model of choice in explaining the type of polygon seen during adaptation. The p-value measures what proportion of times R^2 is bigger for the retinal than the cortical function. The cortical function R^2 of 1 compared favourably over a retinal function R^2 value of 0. See Figure 13. This proves that our brain samples the curve at points along the circle's circumference which is better explained by a cortical length function.

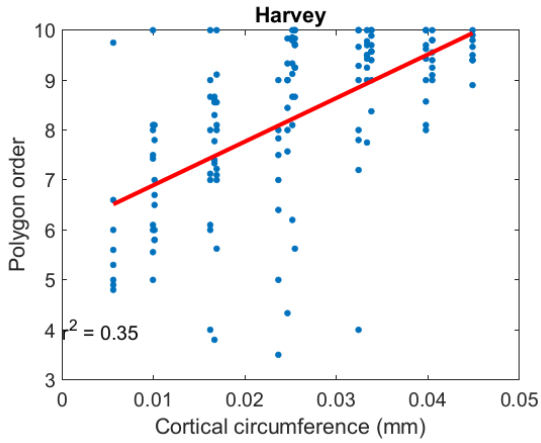
As evident from regression, a better summary of the relationship between the polygon order seen during adaptation is provided



(a)



(b)



(c)

Figure 12: (a) Retinal model: Polygon order regressed over retinal circumference. (b) Rovamo and Virsu cortical model: Polygon order regressed over retinal circumference using Rovamo and Virsu's CMF for region V1. (c) Harvey cortical model: Polygon order regressed over cortical circumference using Harvey's Cortical Magnification Factor for V4.

Algorithm 1: Cortical mapping function using a neurophysiological derived cortical magnification factor
Compute the cortical length using the M-scaling magnification factor for a circle of a given radius and presented at a particular eccentricity.

▷ radius: Radius of the circle ▷ center: Center of the circle; The center, in cartesian coordinates, represents the eccentricity at which the circle is presented on the retinal 2D plane.

procedure COMPUTE(radius,center)

Output Cortical length (in mm) as represented on the cortex region called V1.

Initialization

Set number of point samples on the circle, call it n

unit sample length = 1/n

Do:

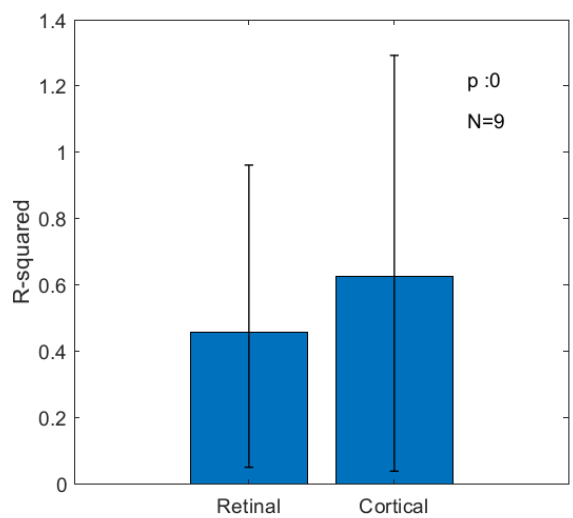
tangent=$2 * \pi * radius * (-sin(2\pi t), cos(2\pi t))$ ▷ Compute the tangent; t runs in unit sample length increments between 0 and 1

speed = $\|tangent\|$ ▷ Compute the speed on the curve using the tangent

M = (1 + 0.33 * eccentricity + 0.00007 * eccentricity^3)$^{-1} * M_o$ ▷ Cortical magnification factor for region V1. Use Rovamo and Virsu's value as an example.

Cspeed=M*speed ▷ Speed on the cortex

len=Cspeed*unit sample length ▷ Compute the cortical length by multiplying the M-scaling magnification factor with the speed over the sample length.



(a)

Figure 13: R-squared, from 10000 bootstrapped samples, for retinal circumference function and cortical circumference function. p-value measures by how much R^2 for the retinal circumference function is greater than R^2 for the cortical circumference function. Proportion times retinal is greater than cortical is 0 . Proportion times cortical is greater than retinal is 1 .

by a cortical function than a retinal function in the brain's region V1 using Rovamo and Virsu's magnification factors. The cortical magnification factors used from lower level V1 (Rovamo and Virsu model) offers a better fit than the cortical magnification factors used from higher regions from the brain such as V4 (Harvey model).

Discussion

How curvature is coded in the cortex is quite different from how it is detected and discriminated. Several studies have attempted to understand how the curve is mechanistically coded. Curvature built by a neural population is widely favoured because curvature appearance is explained by neurons tuned to different curvatures (Ben-Shahar & Zucker, 2004; Gheorghiu & Kingdom, 2017). Neural populations often define the shapes of afterimages, because it is often the aggregted inhibition responses, collectively that influence what is seen as an afterimage (Gheorghiu & Kingdom, 2017). In our experiment, we show that the unique formation of regular polygons during the adaptation process is a manifestation of the cortical computation. The simplest mechanistic model that describes the polygon is defined by the equation given by the regression equation,

$$y = 5.9936 + 0.0364x, \text{x is a point on the cortical circle} \tag{4}$$

We make an important observation about scale invariance in this paper. As polygon order changes with changing size, it shows that scale invariance, a distinct property of the visual system, is not obeyed. Scale invariance is a feature of the higher order visual system. A low-level account explains an opponency between localized curvature-tuned neurons in early visual cortex, while the higher-level account assumes an opponency between neurons in higher visual areas coding whole shapes. Because the high-level account that would predict invariance to size and position fails, the low-level account that predicts that the order of the perceived polygon will increase with the size and decrease with the eccentricity of the stimulus, due to cortical magnification, becomes a plausible theory.

Future work can explore the stimuli as gradually increasing arcs of the circle to see how much of the local curvature i.e. arc circumference is needed to code the polygon seen. El-Shamayleh et. al in (El-Shamayleh & Pasupathy, 2016) show that scale invariance can be explained by neurons that respond to normalized curvature instead of absolute curvature. Normalized curvature is described as the rate of change in tangent angle per unit of angular length. Absolute curvature is described as the rate of change in tangent angle with respect to contour length. When the shape scales up or down, the normalized curvature remains the same while the absolute curvature changes. A large set of neurons, coding for normalized curvature, maintain selectivity for the shape across size changes whereas a smaller proportion show a shift in selectivity for shape with changing size. Neurons firing for normalized curvature describe orientation that scales with size whereas neurons firing for absolute curvature describe orientation at points described by linear distances. This raises interesting questions about the lower limits of normalized curvature coding by the population neurons and the upper limit of local curvature coding by the population neurons when polygon order changes with size. These limits are exposed during adaptation when the neurons are fatigued in upcoming future work. A limitation of the current experiment is the upper limit on the polygon order offered during shape selection. This will be addressed in future work that allows large polygon order shape selection.

Acknowledgements

The authors would like to thank Bob Ho for setting up the apparatus and Nicholas Baker for graciously reading this manuscript and offering valuable editorial suggestions.

References

Anstis, S., Rogers, B., & Henry, J. (1978). Interactions between simultaneous contrast and coloured afterimages. *Vision Research*.

Ben-Shahar, O., & Zucker, S. W. (2004). Sensitivity to curvatures in orientation-based texture segmentation. *Vision Research*.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*. Available from http://doi.org/10.1163/156856897X00357

Brincat, S. L., & Connor, C. E. (2004). Underlying principles of visual shape selectivity in posterior inferotemporal cortex. *Nature Neuroscience*.

Cowey, A., & Rolls, E. T. (1974). Human cortical magnification factor and its relation to visual acuity. *Experimental Brain Research*.

Daniel, P. M., & Whitteridge, D. (1961). The representation of the visual field on the cerebral cortex in monkeys. *The Journal of Physiology*, *159*(2), 203221.

Das, A., & Gilbert, C. D. (1995). Long-range horizontal connections and their role in cortical reorganization revealed by optical recording of cat primary visual cortex. *Nature*. , doi:10.1038/375780a0

Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience*.

Drasdo, N. (1977). *The neural representation of visual space [31].*

El-Shamayleh, Y., & Pasupathy, A. (2016). Contour curvature as an invariant code for objects in visual area V4. *Journal of Neuroscience*.

Gheorghiu, E., & Kingdom, F. A. (2007). The spatial feature underlying the shape-frequency and shape-amplitude after-effects. *Vision Research*.

Gheorghiu, E., & Kingdom, F. A. (2009). Multiplication in curvature processing. *Journal of Vision*.

Gheorghiu, E., & Kingdom, F. A. (2017). Dynamics of contextual modulation of perceived shape in human vision. *Scientific Reports*.

Harvey, B. M., & Dumoulin, S. O. (2011). The relationship between cortical magnification factor and population receptive field size in human visual cortex: Constancies in cortical architecture. *Journal of Neuroscience*. Available from http://doi.org/10.1523/JNEUROSCI.2572-11.2011

Ito, H. (2012). Cortical shape adaptation transforms a circle into a hexagon: A novel afterimage illusion. *Psychological Science*, *23*(2), 126–132. Available from http://doi.org/10.1177/0956797611422236

Khuu, B., McGraw. (2002). Misperceptions in the peripheral representation of curvature. *Perception*, *31*(1_suppl), 1-190. Available from https://doi.org/10.1177/030100660203 10S101

Liu, H., Agam, Y., Madsen, J. R., & Kreiman, G. (2009). Timing, Timing, Timing: Fast Decoding of Object Information from Intracranial Field Potentials in Human Visual Cortex. *Neuron*.

Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. *Current Biology*.

Rovamo, J., & Virsu, V. (1979). An estimation and application of the human cortical magnification factor. *Experimental Brain Research*.

Rust, N. C., & DiCarlo, J. J. (2010). Selectivity and tolerance (”invariance”) both increase as visual information propagates from cortical area V4 to IT. *Journal of Neuroscience*.

Sakurai, K. (2014). Shape distortion illusion of circles without prolonged viewing. *Journal of vision*, *14 10*, 247. Available from http://doi.org/10.1167/14.10.247

Sakurai, K., & Beaudot, W. (2015). Shape distortion illusion of flashed circles can be induced by dichoptic stimulation. *Journal of Vision*. Available from http://doi.org/10.1167/15.12.528

Schwartz, E. L., Desimone, R., Albright, T. D., & Gross, C. G. (1983). Shape recognition and inferior temporal neurons. *Proceedings of the National Academy of Sciences of the United States of America*.

Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., et al. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*. Available from http://doi.org/10.1126/science.7754376

Shimojo, S., Kamitani, Y., & Nishida, S. (2001). Afterimage of perceptually filled-in surface. *Science*.

Virsu, V., Rovamo, J., Laurinen, P., & Näsänen, R. (1982). Temporal contrast sensitivity and cortical magnification. *Vision Research*.