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

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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. The circle-polygon illusion produces polygonal percepts during adaptation when a static dark outline circle is pulsed at 2 Hz alternating with a gradient luminance circle. 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 size on the retina. We show the following: (1) Scale invariance 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 also demonstrates that the curvature coding occurs in the early visual system. (2) We want to quantify the relationship parametrically between cortical size and polygon order. 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 and we extracted the slope that provides a metric for how well the polygon order reported fits the size and eccentricity of the stimulus, with its size adjusted to its retinal or cortical coordinates.

Keywords: shape adaptation, cortical adaptation

Introduction

Why is curvature perception important? Coding of curvature through the 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. The research

objective is to answer the following questions: (a) Is curvature coded on a low level retinal plane or is it a product of a higher order cortical process? (b) Is the coding stimuli-scale variant or invariant: Does the size of the stimuli change the number of sides of the polygon seen in the percept after adaptation? (c) Does the polygon order (shape) change with size and eccentricity? Can we quantify the relationship between the shape seen during in-place adaptation and the independent variables, size and eccentricity, at which the stimuli is presented?

Circle Polygon Illusion We adopt 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. The circle-polygon illusion demonstrates that polygons are produced after prolonged adaptation to flashing circles. Although (Khuu, 2002; Sakurai, 2014; Sakurai & Beaudot, 2015) only report hexagon as the emergent shape, Ito in (Ito, 2012) presents an array of shapes (triangle,square,pentagon,hexagon,heptagon and circle) as the independent variable response type with several responses that are not hexagons. (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.

Lower level or higher level? The early visual system is defined by the retina, and controlled through the receptive fields of regions V1 through V2 (Hubel & Wiesel, 1959; Hubel, Wiesel, & Stryker, 1978; Hegdé & Van Essen, 2000). The higher mid-level V4 neurons, with larger receptive fields, while showing preference for certain angles, show scale-invariance to different sized arc boundaries that subtend the same angle at the stimulus's center (Pasupathy & Connor, 2001, 2002; El-Shamayleh & Pasupathy, 2016a). We probe systematically across eccentricity and size to see if this scaling phenomenon holds and if not, can we deduce a relationship that explains the scaling. Ito (Ito, 2012) assert that the circle-polygon phenomenon is cortical because interocular transfers result in users reporting circles whereas each eye under monoptical conditions, when shown the same circular stimuli would produce a polygon. Sakurai in (Sakurai & Beaudot, 2015), build on Khuu's circle-appearing-as-polygon illusion and also cite a cortical process is responsible given that the adaptation occurs almost instantly when the stimuli pulsation is varied between 0.5 Hz to 8 Hz. Beyond the plausible observation that it is cortical, can we quantitatively state that polygons produced are determinant of the size and eccentricity as a known function? If the polygonal response to curvature was coded on the retinal plane or lower levels V1 and V2, it would be influenced by the neuronal responses to the shape as it appears on the retina. However, if it was coded higher up in the cortex, it might show more complex representations such as scale invariance with respect to size (Pasupathy & Connor, 2001, 2002; El-Shamayleh & Pasupathy, 2016a).

Scale invariance is a well known property of the higher human visual system, beyond V4 (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). 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. Neurons are selective for certain views and broadly tolerant to transformations such as rotation and scaling that is centered around the primary view (Logothetis et al., 1995).

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? The presence of regularization itself suggests that retinal bleaching or retinal adaptation (Spillmann, 1994; Schrauf, Lingelbach, & Wist, 1997) is an unfavourable hypothesis since bleaching produces disappearances in features or production of new ones (opposite coloured fault lines) when intensity rods are fatigued (Spillmann, 1994; Schrauf et al., 1997). The disappearance occurs peripheral to fixation where fatiguing is pronounced and lacks the deliberate production of symmetry which could only be produced if rods or neurons were aligned in a corresponding symmetrical pattern. We test if a cortical process operating in the lower regions such as V1 utilizes long range connections in the production of polygonal shapes. In this paper, we compare a retinal and a competing cortical model to see which better explains the adapted polygon and if we can quantitatively define a relationship. 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.

Parametric cortical equation 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). 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 (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.

Rovamo and Virsu in (Rovamo & Virsu, 1979) estimate M, for the principal meridians of the visual field in equation 1 and the accompanying table for coefficients. Here, M_o is $7.99mm/^\circ$, 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	$0 \leq E \leq 60\,\mathrm{deg}$

If we integrate M, we obtain the distance on the cortex as a function of eccentricity. Our skeletal algorithm, see Algorithm 1, computes the integral on the cortex and is explained in the Methods section.

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

In order to explain if the polygons observed above can be explained quantitatively by a retinal model or a higher level cortical model, we apply linear regression. 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. 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 shall hereby call the retinal circumference size, retinal length, and the cortical circumference size, cortical length. See Figure 12 (a,b,d).

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 can be replaced by other magnification factors that perform hierarchical sampling, such as when the cortical representation in V4 is represented by how the region in V1 is sampled (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. Harvey and Dumoulin (Harvey & Dumoulin, 2011) show that the cortical magnification factor in area V4 is smaller than those in V2 and V3 which was in turn is less than V1. The cortical magnification factor for fields such as V2,V3 and V4 that sample from V1 is independently constructed. We, therefore, use V4's cortical magnification factor when considering if polygon order reported could be a function of cortical scaling in region V4, which is known for curvature representation.

In Algorithm 1, we approximate the cortical length formed by sampling the retinal stimuli's circumference at a fixed number of points and projecting that sampled length onto the cortex. The length formed on the cortex is scaled by the magnification factor, M, to give the cortical length.

We use boot strapping and use the coefficient of determination, R^2 to estimate the goodness of fit when fitting a linear regression function, polygon order as a function of the retinal and cortical length.

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. The experimental data and source code are stored at the Open Science Framework at the following link `https://osf.io/x8n3p/`.

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.

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 Quadro K2200 graphics card and a DELL P2715Q LCD screen. The stimuli were presented on the same machine in the lab. A chin rest was used to ensure stable head position. The monitor resolution was 3840 pixels by 2160 pixels with a refresh rate of 60 Hz. The distance of the observer from the center of the monitor screen was 60 cm. The background was white. The mean luminance of the monitor was 26 cd/m^2.

Psychtoolbox's *Screen* function was used to create stimuli. The distance of the observer from the center of the screen and the size of the screen, both in centimeters, were used to compute the angle in degrees subtended at the user's eye. Using the monitor's resolution in pixels, the pixel per degree was computed. The *Screen* function was used to draw the appropriate stimuli using the pixel per degree information.

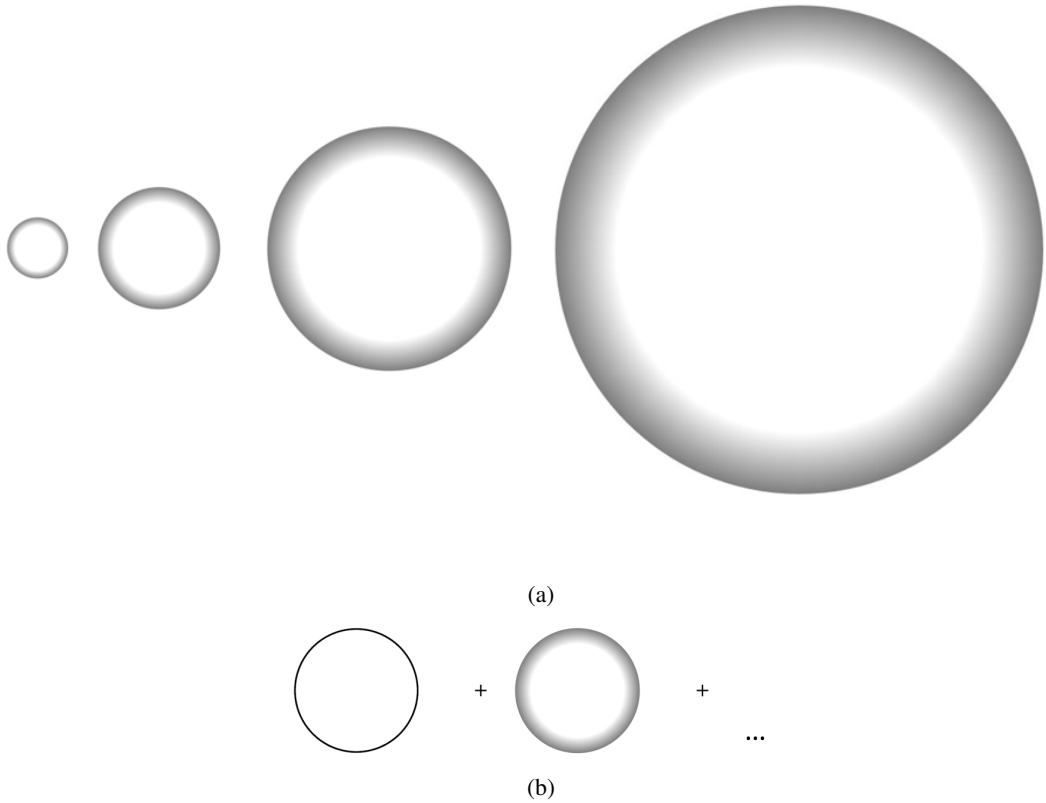


Figure 1: (a) Stimuli size: Circles,with inward gradation, whose size (diameter) subtends 2,4,8 and 16 degrees of visual angle respectively on the user's eye. The pictures are for illustration only and show the relative sizes of the stimuli. Stimuli do not subtend the exact degree on the reader's eye. (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.

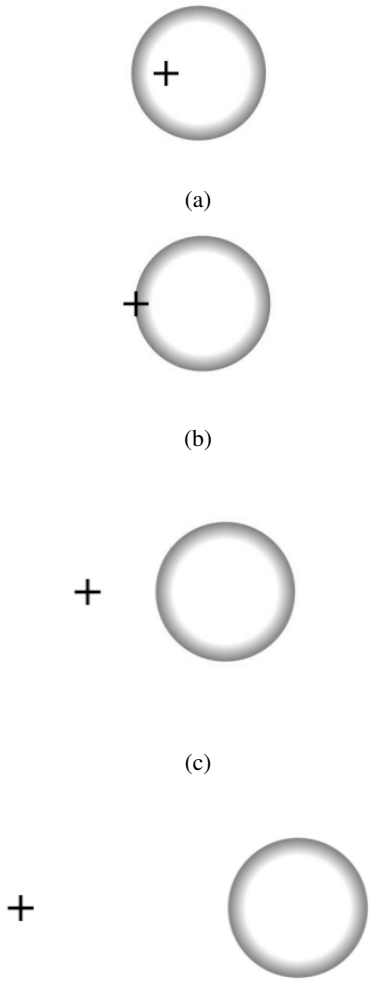


Figure 2: Presentation eccentricity: Circles,with inward gradation, presented at eccentricities of 1,2,4 and 8 degrees of visual angle respectively on the user's eye. The circle's size (diameter) is 4 degrees.

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 randomly. Verbal feedback was provided to the user as they navigated the trials. The participants were read the instructions, outlined below, before starting the practice trials.

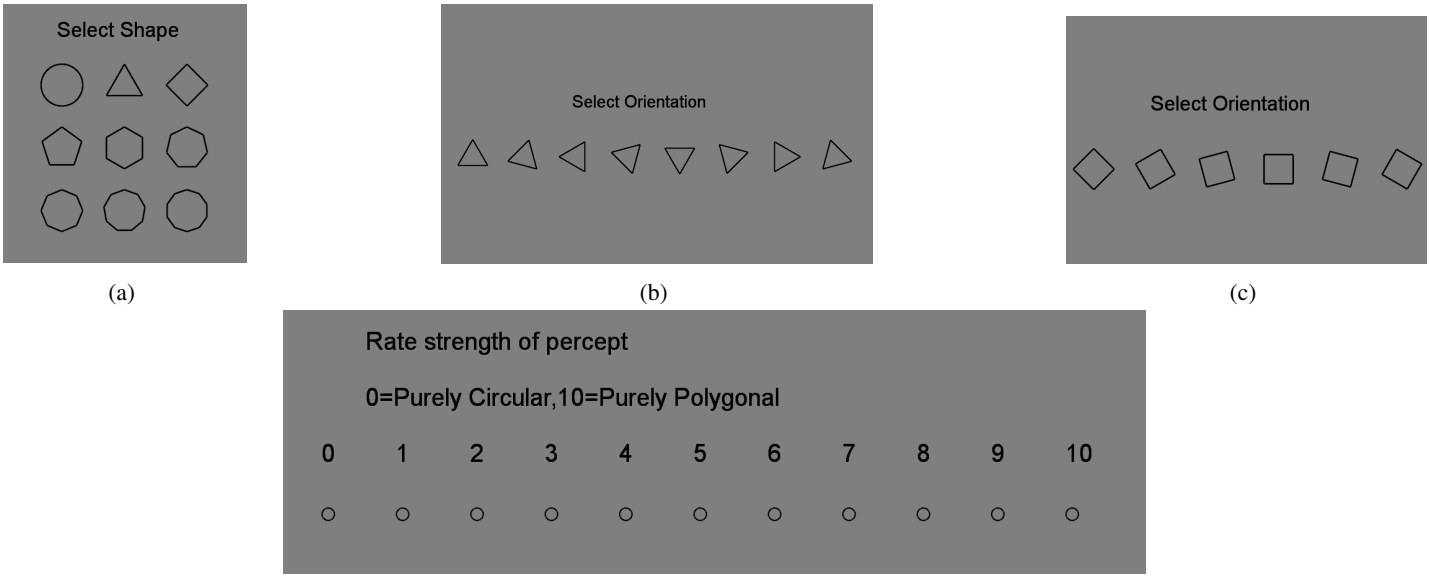
"Please maintain fixation on the central cross - do not move your eyes during this first phase of the trial. A flashing shape will appear for several seconds. It will have a circular appearance but may gradually appear slightly polygonal as well. After this first phase of the trial, a menu of shapes 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. There were 10 blocks, each block randomly selecting and presenting the set of 16 stimuli once. 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.

The frames presenting the stimulus had a white background and the response stages were performed on grey background frames. Therefore, the induced adaptation would not bias test shapes and the time gap between the response stage and the subsequent presentation stage was long enough that adaptation would not transfer influence different stages. .



(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.

Measurement Techniques

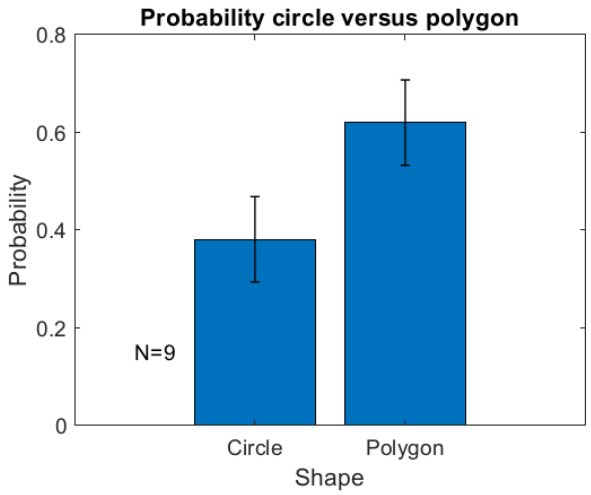
The testing took place in a darkened room. Observers used a standard mouse with a middle mouse button and a left button. The participants indicated the polygon to which they adapted, the polygon's orientation and its strength. Once the participant recorded a response, they pressed the middle mouse button 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.

Results

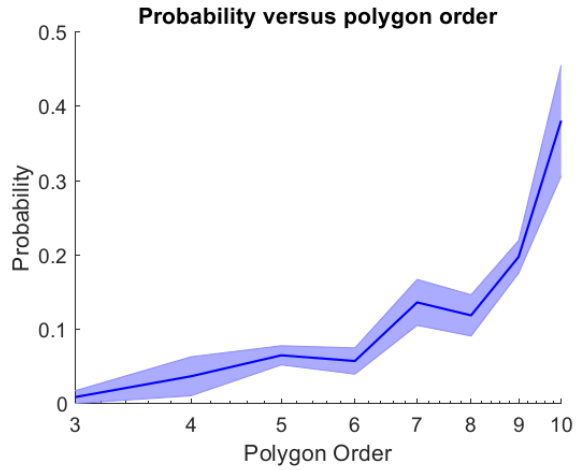
The results from the nine observers is shown in Figure 4. On average, most observers report more polygons than circles during the entire experiment. Polygons are reported 61.9 % of the time versus circles that are reported 38% of the time. This means that the formation of polygonal percepts is a phenomenon that occurs in the sampled population. A Student's 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) to rule any effect of anisotropy in peripheral vision, asymmetric foveal confluence influencing shape formation and in the difference between the left and right visual field (Schwartz et al., 1983; Schira, Tyler, Breakspear, & Spehar, 2009).

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



(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. The means are reported across participants. (mean +- standard error of mean) (b) Probability distribution of the different polygon orders across all participants. (polygon order +- standard error of mean).

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.

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.

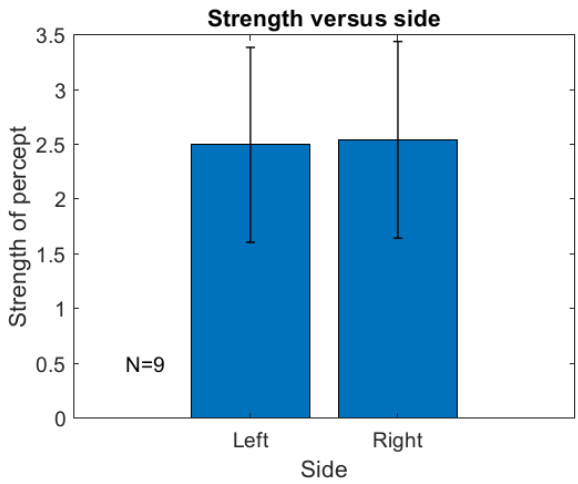
Eccentricity

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

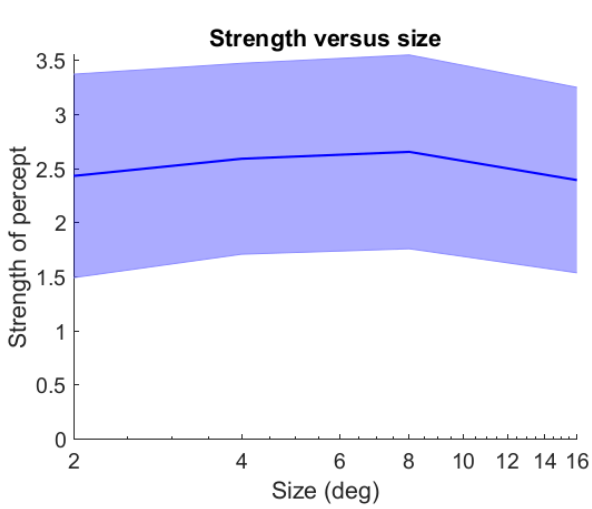
We compare observer responses to a uniform distribution of 15 angle increments starting from 0 to the first axis of symmetry for the polygon in question. For most polygon orders, a uniform distribution is observed across all orientations of the polygon. The triangle showed a relatively high KL divergence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

Preference for contour orientation, where the contour is pointing in a particular angle and direction, is a known phenomenon in

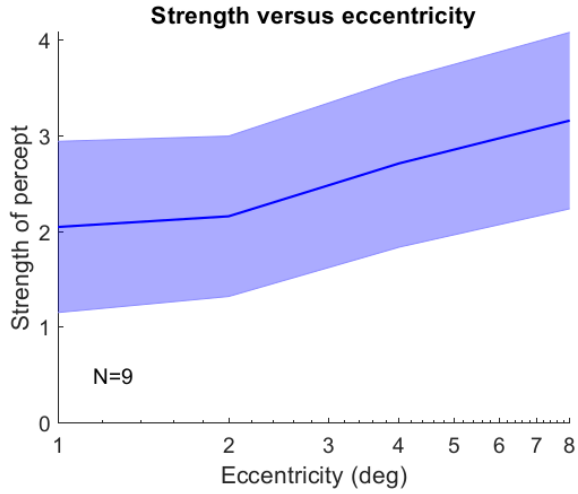


(a)

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. (Strength +- standard error of mean).

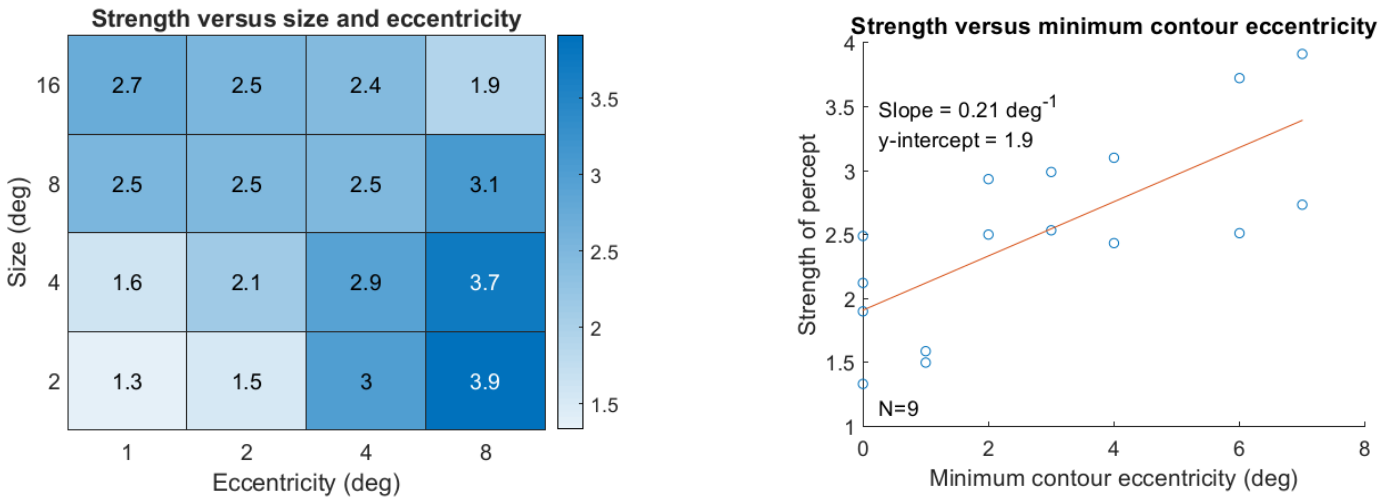


(a)



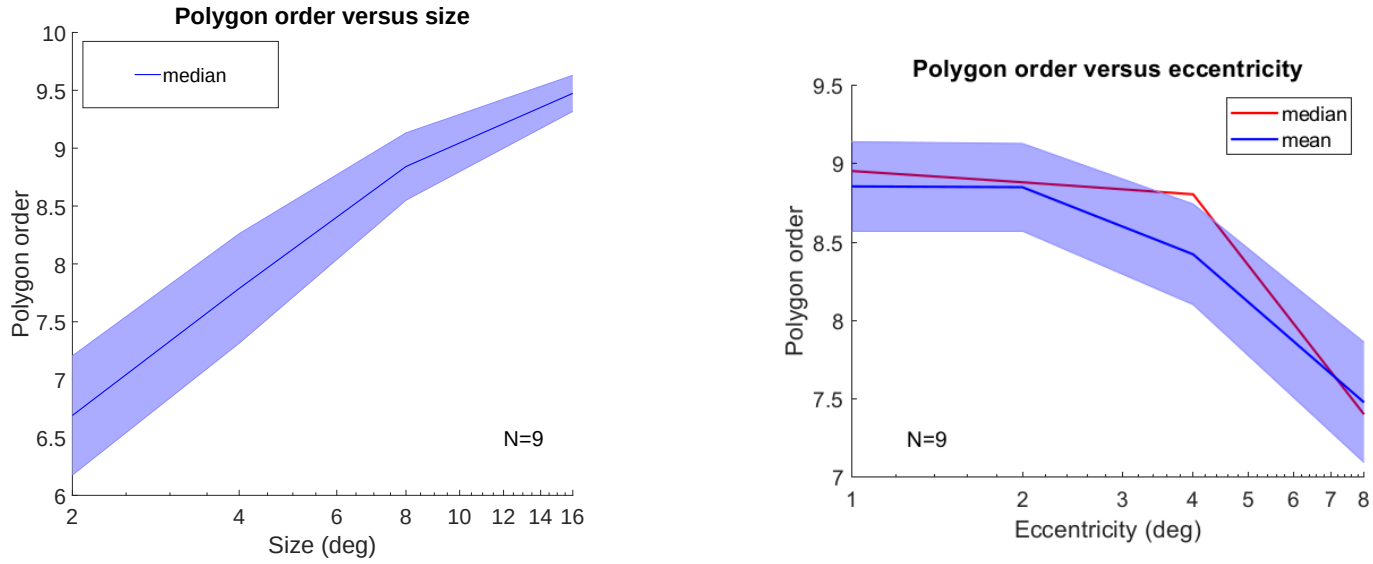
(b)

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. The mean is reported across participants (mean +- standard error of mean).



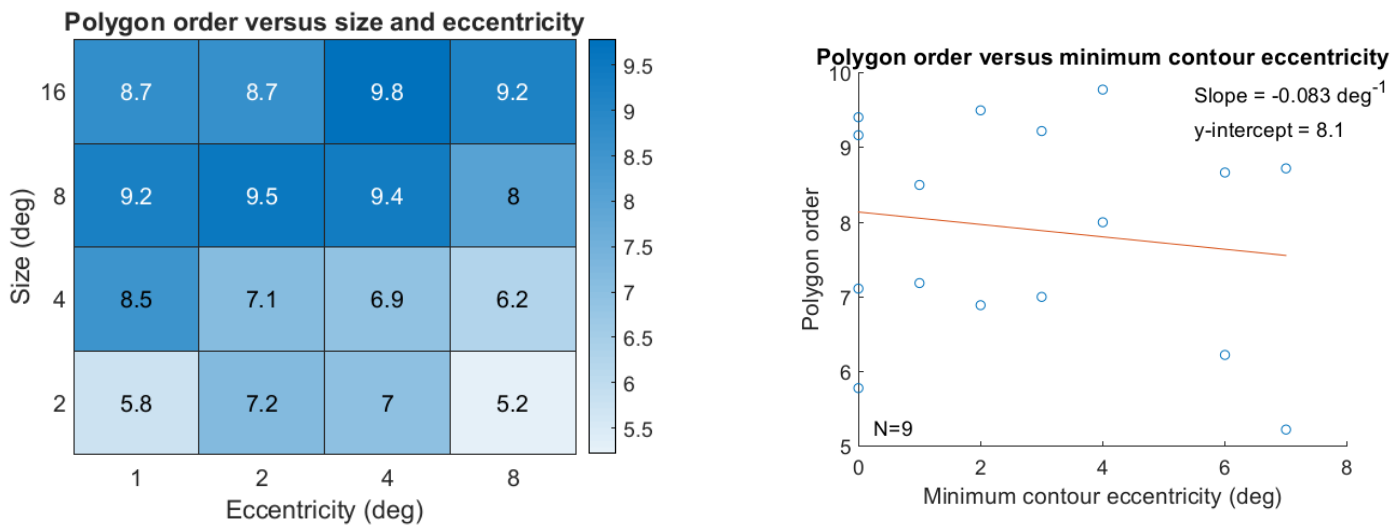
(a) (b)

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. Strength values are means across all participants.



(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. All values reported are means across all participants. The median and mean are shown for eccentricity only since they are not as closely overlapping and show slight user differences.



(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. Means are over all participants.

mid-level vision, specifically in region V4 (Pasupathy & Connor, 1999a, 2001, 2002). However, the responses recorded do not see any emergent internal polygon angle, after fatiguing of the circular contour, that is angled or oriented as part of its constituent contour shape as shown in (Pasupathy & Connor, 1999a, 2001, 2002). Pasupathy and Connor (Pasupathy & Connor, 1999b) show that there is a neural preference for angles oriented in the 135 ° to 180 ° direction.

Model that explains the polygon order observed

Using regression, 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

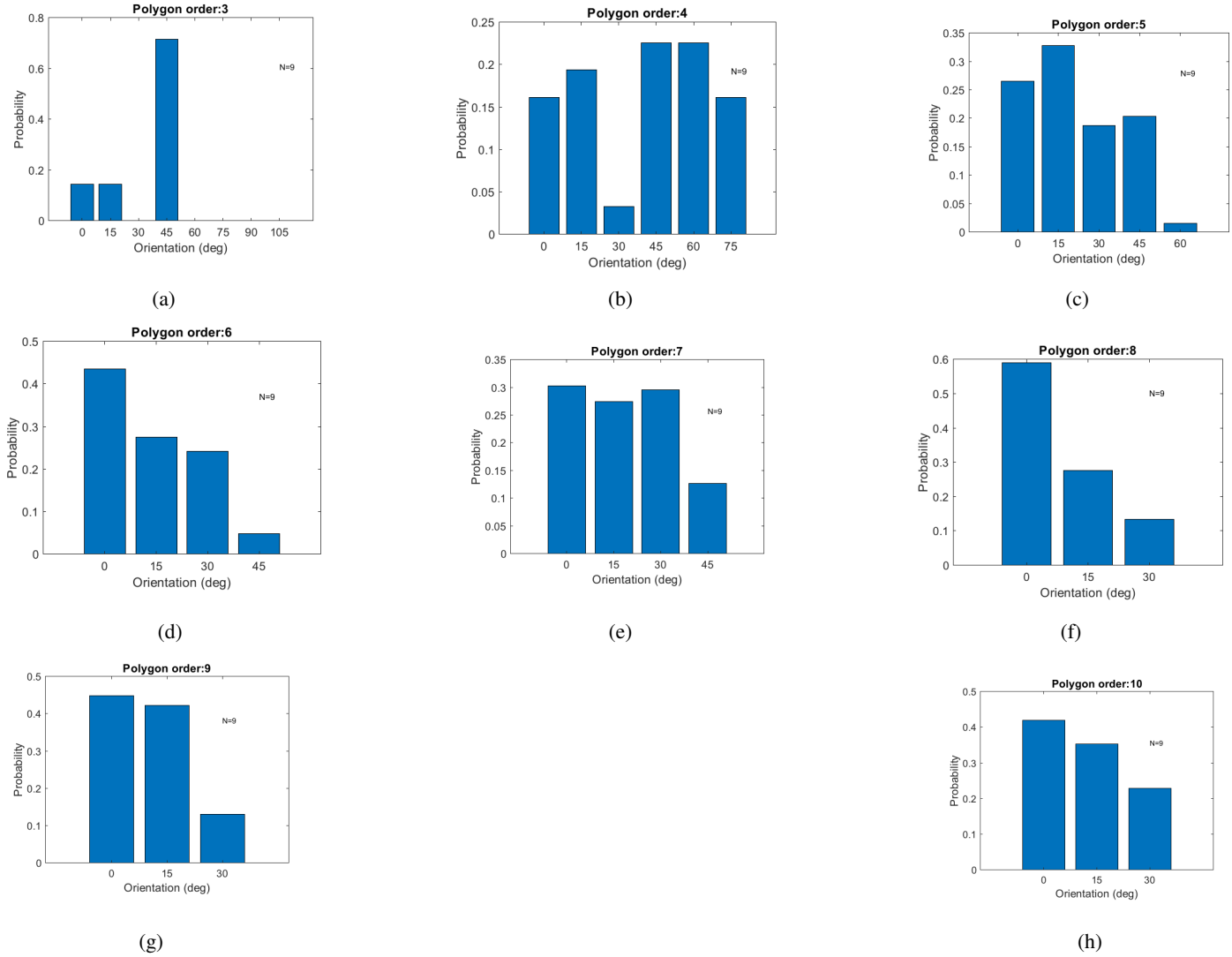


Figure 10: Probability versus orientation : For each polygon that was selected by the user, we show the distribution of the orientations selected. The canonical form (0 deg orientation) is when the polygon is centered with its apex at the 12 o'clock position. The responses are computed over all users, shown as a probability of selecting that orientation over all the orientations selected per polygon. In Figure 3(b,c), the first shape in the orientation array is the canonical representation of the triangle and square respectively.

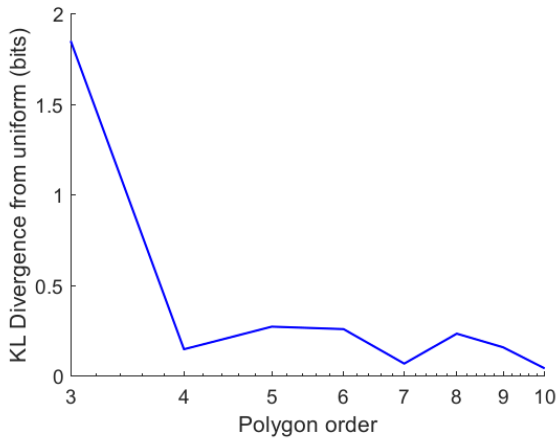


Figure 11: KL divergence: KL divergence shows how much the orientation differs from a uniform distribution of orientations. When observers select a triangle as the in-place adaptation polygon, they mostly select the 45 degree orientations. Other shapes show a more uniform spread in the orientations selected.

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.

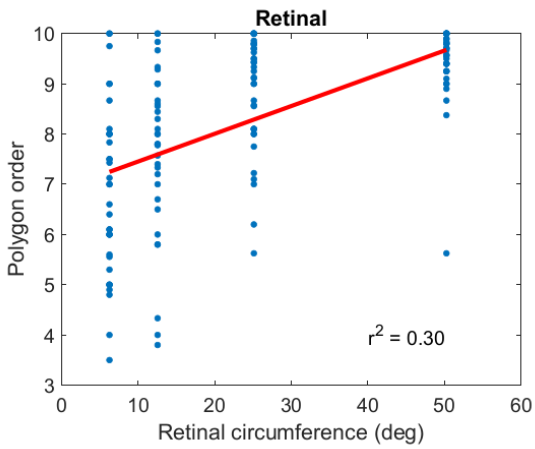
As evident from regression, a better summary of the relationship between the polygon order seen during adaptation is provided by a cortical function than a retinal function in the brain's region V1 using Rovamo and Virsu's magnification factors. The cortical magnification factors used from lower level 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

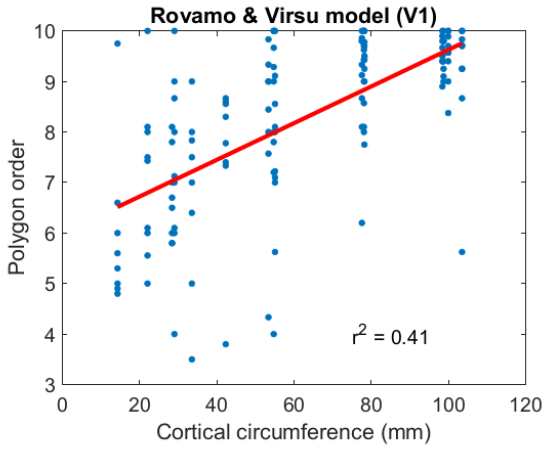
Several studies have attempted to understand how the curve is mechanistically coded. Curvature built by a neural population is widely favoured because curvature appearance is explained by neurons tuned to different curvatures (Ben-Shahar & Zucker, 2004; Gheorghiu & Kingdom, 2017). Neural populations 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 early cortical computation. The simplest mechanistic model that describes the polygon is defined by the equation given by the regression equation,

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

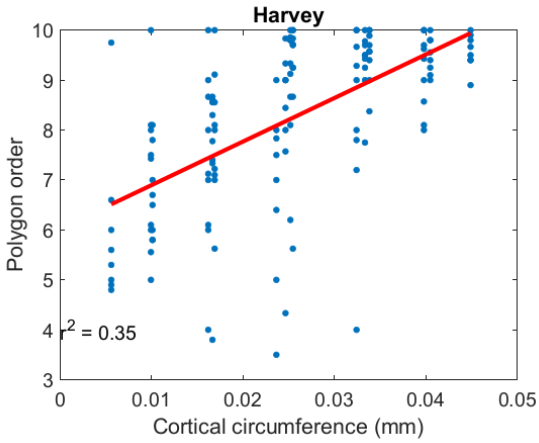
We make an important observation about scale invariance in this paper. As polygon order changes with changing size, it shows that scale invariance, a distinct property of the visual system, is not obeyed. Scale invariance is a feature of the higher order visual system. A low-level account explains an 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



(a)

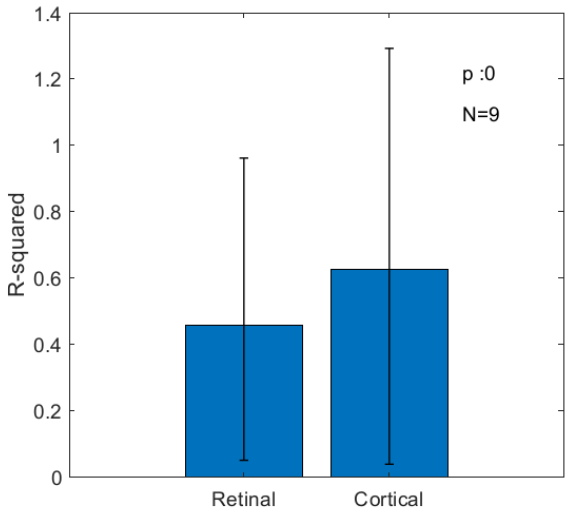


(b)



(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 cortical magnification factor (CMF) for region V1. (c) Harvey cortical model: Polygon order regressed over cortical circumference using Harvey's Cortical Magnification Factor for V4.



(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 .

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, 2016b) 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.

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