Curvature formation in the Visual Cortex: How do we sample?

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Does the human visual system sample shapes at discrete points? During adaptation when the neurons are fatigued, one observes the underlying principles that were once less prominent than the fatigued features. Operating under deficit, these less prominent features expose the original contributions from the fatigued neurons that are now absent. An underlying lower order neural process, is thus, now revealed. In this paper, we conduct experiments using flashing circles in order to reveal the brain's sampling pattern. We find that the size and eccentricity, taken together, best explain the edge length reported by users and that size alone is the most reasonable fixed parameter. The users, as a random effect, do not influence the mean of the edge length reported when considering the best model reported (size and eccentricity together) according to loglikelihood. However, the users do influence edge length reported only when using mean eccentricity or eccentricity as the parameter influencing edge length. Arc lengths of a circle produce same or similar edge lengths. The length of the curve does not play a significant role signifying that biological neurophysiology at an eccentricity controls the edge length formation.

Keywords: shape adaptation, cortical adaptation

Introduction

Both the contour type and its angular orientation are important descriptors for shape selectivity (Pasupathy & Connor,1999,2001). In other words, the higher part of the ventral system encodes higher order contour derivatives in the form of tuning for broad curvature as well as certain sharp narrow curvature. However, there has been little study done to vigorously study the simplest convex shape, the circle, under adaptation. Adaptation is a process by which a set of population neurons are fatigued, thereby allowing other sets of neurons that encode inhibition and are not fatigued, to reveal their neural preference for structure and shape. Indirectly, it also reveals the original coding that is now absent. In an earlier experiment, we showed how different regular polygon of varying orders are observed as the in-place adaptation response when a flashing circle is alternated with its black outline.

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Why does the brain sample in that way? Is the sampling a by product of closure Wertheimer(1912,1923), (MacLeod & Ellis,1939;Wertheimer,2007) from Gestalt theory or more neuro-physiologically a mapping of the arrangement of the receptive fields (Gilbert,1992)? Is it possible that while higher-order human vision is scale and space (rotation) invariant, lower level account of human vision is not and this is revealed by adaptation? In (Nisar & H. Elder,2021) , we show that the in-place adaptation polygons observed from flashing circles are symmetrical regular polygons of varying orders based on their eccentricity and the size of the flashing stimuli. Adaptation, reveals certain closure properties induced by the activity of population neurons present at certain biological eccentricities (Nisar & H. Elder,2021).

Edge length, also defined as the gap between contours, allows the construction of closed shapes if they are small (Elder & Zucker,1993). This property is called closure. Closure is often thought to be a primitive property, separate from the ventral stream pathway that culminates in the inferotemporal region (IT) that makes inferences about global shape from earlier components. Wertheimer's earliest experiments in psychology (Wertheimer,2007) assert that the quality of the part is a function of its integration in the whole. In other words, the whole is more significant and determines the quality of the part. The paradigm of global or local shape being competing features in defining shape is a natural progression from this earlier research in Gestalt principles (Kimchi,1992). Homomorphic class differences are processed earlier and outside the ventral stream. This is revealed in several psycho-physical experiments by Chen and Palmer (Chen,1982;Palmer & Rock,1994). Chen states that connectedness, closed or open, and the number of holes are topological features that form important perceptual representations that are extracted early in the visual process (Chen,1982). Palmer in (Palmer & Rock,1994) show that uniform connectedness is a property where regions of similar lightness, colour or texture are perceived as single units even before grouping principles such as proximity and similarity begin to take effect.

From a previous study of flashing circles built of different sizes and presented at various eccentricities (Nisar & H. Elder,2021), we discovered that the strength and polygon order of the percept changed with eccentricity and size. The strength was strongest when the circle was of size 1 degree visual angle and was presented at an eccentricity 8 degree visual angle. The largest polygon order was observed when the percept was of size 8 and at eccentricity 4 degree.

In this study, we also alter the stimuli from the first study and probe if the arc length of the stimulus effects the edge length seen and reveals sampling patterns for curvature closure. We keep in mind the importance of *connectedness* and therefore use arc lengths as the probing parameter. We use edge lengths instead of polygon order as a measure of the polygon order seen.

Methods

Observers

30 observers participated in the experiment. All observers participated in the online version of the experiment, hosted on Pavlovia. Participants were recruited using Prolific, an online recruitment site. The participants were screened for being fluent in English and for having corrected-to-normal vision.

Apparatus

Stimuli were generated using the Psychtoolbox (Brainard,1997) in Matlab on a Windows Lenovo machine with a Nvidia GTX1060 graphics card. During presentation of the stimuli using Pavlovia, the viewing distance was determined from the participant. The participant measured the distance from the monitor using a tape measure. The background of the experiment was white. The mean luminance of the monitor was expected to read 26 cd/m^2. The participants were asked to scale a credit card on their screen and make it the size of a physical credit card. Pixels per degree was simply computed from the process and this value was used to draw stimuli in pixels given any size and eccentricity.

Measurement Techniques

Participants were instructed to provide their viewing distance in centimeters using a measuring tape and scale a credit card to match a physical credit card. The participants indicated the polygon to which they adapted by selecting the edge length in an array of edge lengths during the response selection phase. A standard mouse was assumed to be used to point and click on the edge length since the participants were online. Unlimited time was awarded to select an edge length. Once the edge length was selected, a Likert scale from 1 to 10 was shown to mark the strength of the percept if the participants had indicate a somewhat polygonal percept. Once the participant recorded a response, the next stimuli presentation appeared.

Experiment 1

The experiment reports the edge length of the polygon percept seen as the circle diameter and eccentricity of the circle's placement varies. We present stimuli that are circles and alternate with a circle that is its inward gradation pattern. The diameter of the circles we present as stimuli, subtend a visual angle of 2,4,8 and 16 $^\circ$ on the user's eye. The eccentricity at which the circle center is presented is at 0,1,2,4 and 8 $^\circ$. There were a total of 36 unique stimuli presentations when accounting for the size, eccentricity and the handedness of the stimuli appearance from the fixation cross (left or right). We study the adaptation produced in place, induced by the flashing stimuli, at varying eccentricities along the horizontal meridian and report the resulting polygonal percepts that form. We do not measure the polygon order directly. Instead we use edge lengths that would represent the regular polygon. Participants mark an edge length of the polygon percept they see. The url for the experiment is available at *https://run.pavlovia.org/inisar2/fragmentonline30*.

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 Figure 1(b). The circles were built of different sizes. See Figure 1(a). The eccentricity at which the circle was presented was 1,2,4 and 8 $^\circ$. 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 360 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.

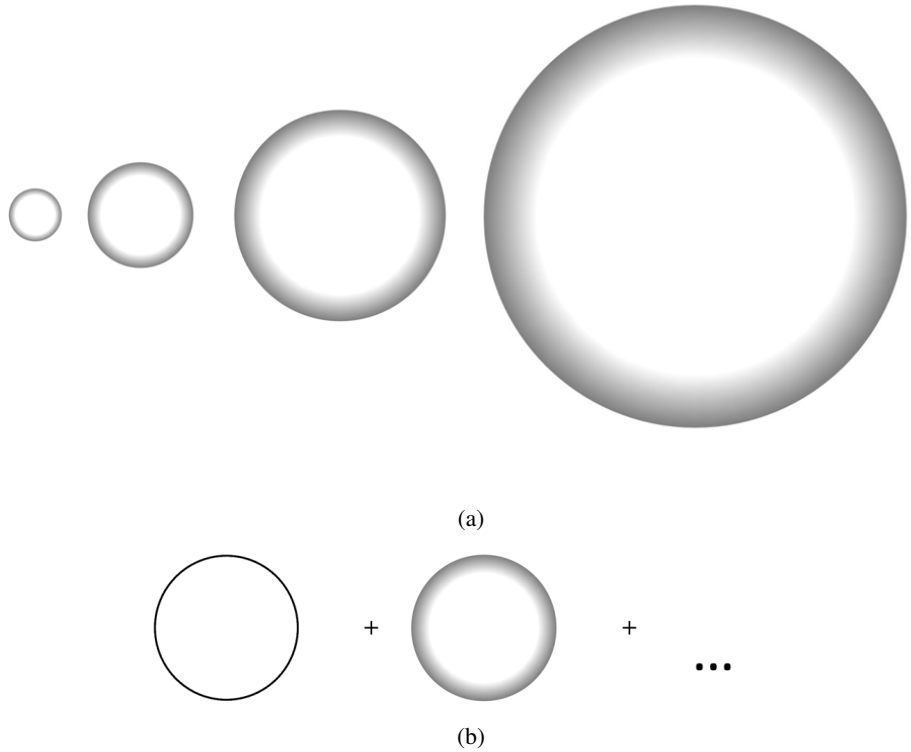


Figure 1: Experiment 1: (a) Stimuli sizes: Circles with inward gradation, whose diameter subtends 2,4,8 and 16 degrees of visual angle respectively on the user's eye. The pictures are for illustration only and show the relative sizes of the stimuli. Stimuli do not subtend the exact degree on the user's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

Experiment 2

In this experiment, we construct several circular arc lengths. The arc lengths are 1/8, 1/4, 3/8, 1/2, 5/8, 3/4, 7/8 and 1 (or whole) of a circle. The circle stimuli are of size 4 deg and 8 deg visual degree angle presented centrally. In this experiment we probe the edge length seen during adaptation using the arc length of the circle. The url for the experiment is available at *https://run.pavlovia.org/inisar2/fragmentonline29*.

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. See Figure 2. The stimuli were arc lengths of a circle. The arc lengths were 1/8,1/4,3/8,1/2,5/8,3/4,7/8 and the whole of a circle. Two stimuli sizes were used. One was a size of 4 ° and the other was a size of 8 °. There were a total of 16 unique stimuli when allowing both size and arc length. All stimuli were presented at 0 ° eccentricity. The black outlines were constructed of pen width 5 using Psychtoolbox. The renderings were hosted on Pavlovia. Randomized trials presented each stimulus 10 times. There were a total of 160 trials. Participants were allowed 16 practice trials.

(a) (b) (c) (d) (e) (f)

Figure 2: Experiment 2: (a) Arc length that is 1/8 of a circle (b) Arc length that is 1/4 of circle (c) Arc length that is 3/8 of a circle (d) Arc length that is 5/8 of a circle (e) Arc length that is 7/8 of a circle. Half and three-quarters of a circle are left out of the figures for brevity.

Procedure

Experiment 1

The eccentricity at which the circle center is presented is at 0,1,2,4 and 8 °. There were a total of 36 unique stimuli presentations when accounting for the size, eccentricity and the handedness of the stimuli appearance from the fixation cross (left or right). The circles were presented at random orientations during the trial. In each trial, the circle with the outline flashed with its graded luminance at 2Hz for 10 seconds.

20 practice trials were offered for an estimated time of 4 minutes. After the practice session, the participants were presented 220 trials in blocks of 22 stimulus for a total of 10 blocks. The entire recorded experiment took 55 minutes, discounting voluntary breaks.

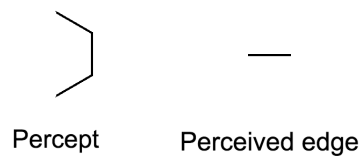
Experiment 2

There are 16 distinct stimuli presentations. Each circle has 8 different arc length configurations and the circle are of two different sizes: 4 ° and 8 °. The circles were presented at random orientations during the trial. In each trial, the circle with the outline flashed with its graded luminance at 2Hz for 10 seconds.

A complete set of 16 practice trials were offered for an estimated time of 3 minutes. After the practice session, the participants were presented 160 trials in blocks of 16 stimulus for a total of 10 blocks. The entire recorded experiment took 45 minutes, discounting voluntary breaks.

Procedure for both experiments

The participants were asked if the stimulus seen was purely circular or somewhat polygonal. If the participants indicated it was somewhat polygonal, they were then asked to judge the perceived edge length and the strength of the percept. The perceived edge lengths were displayed as a series of eighteen line segments built from the equation $log(a * b^c)$ such that $a = 1$ and $b = 0.9$. c belonged to the range $[1, 20]$ and each value of c gave rise to a unique line segment. The difference between the line lengths, when they were represented in their log formats, was uniform. The shortest line segment subtended 0.105 $^\circ$ visual angle on the eye whereas the largest line segment subtended 2.107 $^\circ$ visual angle on the user's eye.



(a) (b)

Figure 3: (a) Percept shown in the experiment brief (b) Perceived edge that the participant would have to mark was shown to the participants.

Prior to starting the experiment, the observers were briefed with the following instruction:

"After the first phase of the trial, you will be asked if you saw a perfect circle or a polygonal percept. If you perceived the shape as somewhat polygonal, you will indicate the perceived length of the polygonal edges. An example of the polygon seen and the corresponding edge length that you will mark is shown on the right. If you indicated a polygon percept, you will indicate the strength of the polygon percept on a scale from 1 (very weak) to 10 (very strong). "

The participants were asked for their viewing distance from the screen by measuring and reporting the distance (in centimeters) between the bridge of their nose and the center of the screen.

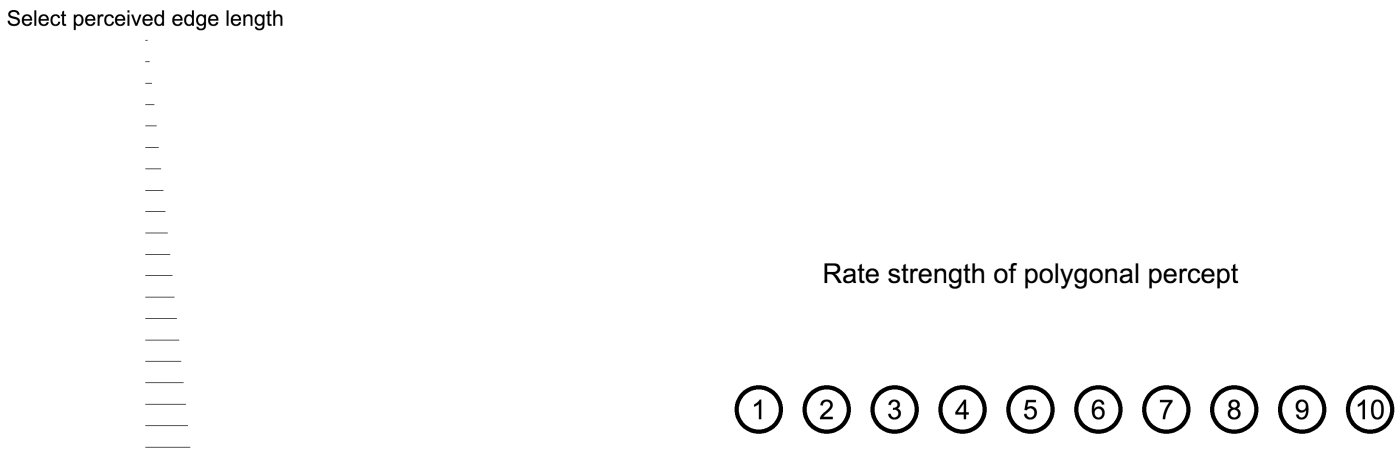
To ensure that the stimuli were the right size, the participants were asked to scale an image of a credit card displayed on the screen till it matched a physical credit card using the arrow keys. The scaling allowed the computation of pixels per degree for the participant's monitor screen and the appropriate display of the stimuli in degrees thereafter.

Results from Experiment 1

Shape

The results from the 30 observers are shown in the graphs below. Most observers reported circles than polygons.

A further breakdown by eccentricity does not reveal significant results based on the eccentricity per stimulus size.

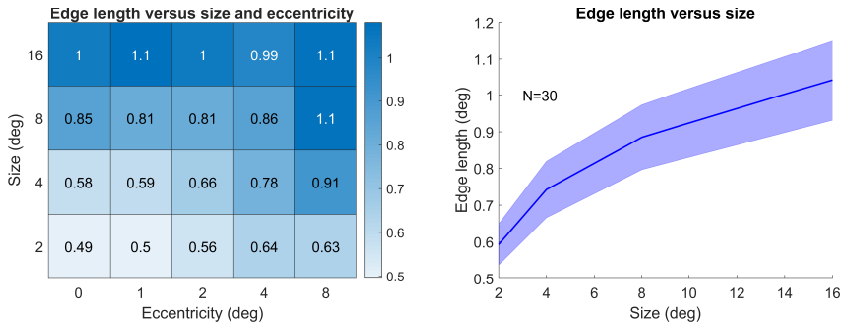


(a) (b)

Figure 4: (a) Users were asked to select the perceived edge from an array of uniformly incremented log-length lines. (b) Users were asked to rate the strength of the polygonal percept from 1-10.

Edge Length

The edge length decreases with increasing size and increases with eccentricity.



(a) (b)

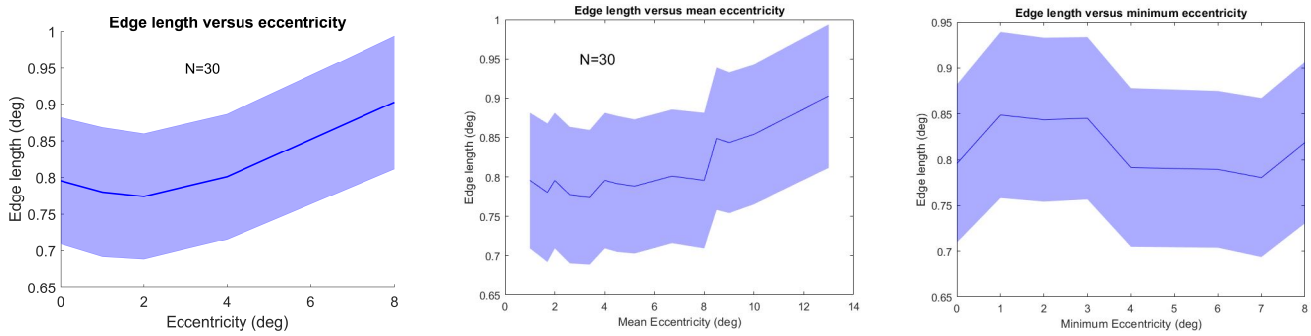
Figure 5: (a) Mean edge length (in deg) for different sizes of the circle stimuli: 2, 4, 8 and 16 , presented at different eccentricities of 0,1,2,4 and 8 degrees. (b) Edge length versus size
Edge length increases slightly with size and also with eccentricity. Size has a larger effect. Eccentricity has a more moderate effect.

Strength

The experiment measured the strength of the 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. The strongest effect is for small objects at large eccentricities. See Figure 8 (b). 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 matrix in Figure 8 (a).

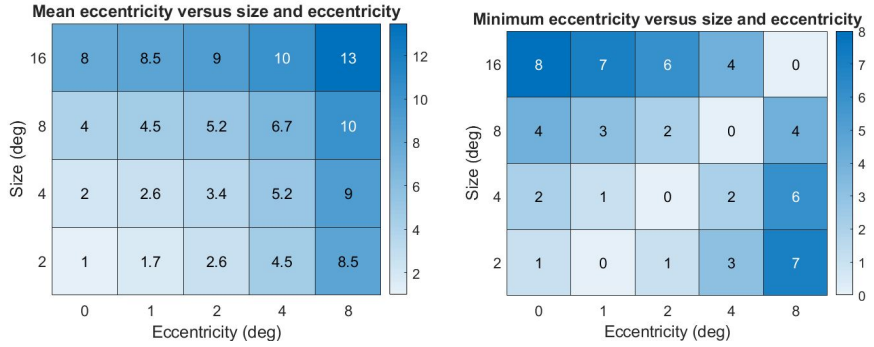
Eccentricity

Eccentricity has a modest effect on the polygon order reported. Proximity to the fovea shows higher order polygons. This is a



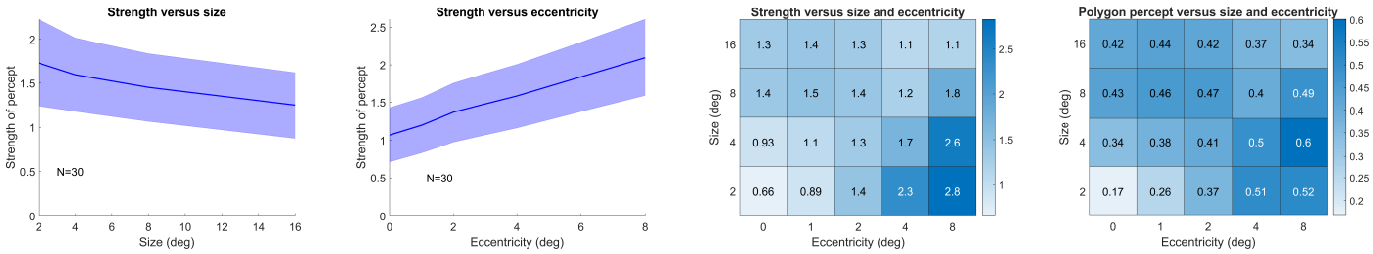
(a) (b) (c)

Figure 6: (a) Edge length versus eccentricity (b) Edge length versus mean eccentricity (c) Edge length versus minimum eccentricity Edge length increases slightly with size and also with eccentricity. Size has a larger effect. Eccentricity has a more moderate effect.



(a) (b)

Figure 7: (a) Mean eccentricity (b) Minimum eccentricity



(a) (b) (c) (d)

Figure 8: (a) Strength versus size (b) Strength versus eccentricity (c) Strength decreases with size and increases with eccentricity. Size has a larger effect. Eccentricity has a more moderate effect. (d) Probability polygon percept as a function of size and eccentricity

smaller effect. See Figure 6(b).

Model that explains the edge length observed

Can the edge length observed be explained by a retinal model or a higher level cortical model? A retinal function samples the circular stimulus in 2D eccentric cartesian coordinates. We fit a first order linear model of the edge length as a function of the retinal size and another as a function of the cortical circumference size. We shall hereby call the retinal circumference size, retinal length, and the cortical circumference size, cortical length. The functions for edge length as a function of the retinal length and the cortical length is given below in Equation 1 and Equation 2. Equation 1 describes x as a point on the retinal circle whereas 2 describes x as a point on the cortical circle.

$$y = 0.309 + 0.00198 * x \tag{1}$$

$$y = 0.296 + 0.00175 * x \tag{2}$$

The M-scaling ratio between the experimental cortex and the retinal scaling is 1.15. This is across all eccentricities. The M-scaling ratio between the experimental cortex and the retinal scaling, following Rovamo and Virsu (Rovamo & Virsu,1979), averaged over eccentricities, is 4.4, suggesting that the scaling observed during adaptation does not necessarily follow neuro-physiological ground truth values. This illustrates the fact that even though neurophysiology might predict shape formation, the mechanistic observation of curvature is subjective.

Figure 10(d) shows how the cortical magnification factor obtained from psychophysical recording differs from that measured by Rovamo and Virsu's measured neurophysiological recordings.

The cortical length can be computed from the points seen on the circle seen on the 2D retinal plane and after applying the cortical M-scaling that measures mm of cortex per degree of visual angle, as a function of eccentricity, on those sampled 2D points. The cortical mapping function can be built as follows: (a) create a tangent at sample points on the stimuli circle seen in the retinal 2D plane (b) The tangent is then used to compute the speed on the curve (c) The cortical magnification factor is multiplied by the speed and the small sample step size to get the cortical length traced on the cortex. For a detailed description, see Table 1.

The M-scaling factors were borrowed from (Rovamo & Virsu,1979) and we plot edge length versus cortical length in Figure 10(a,b). This is a skeletal model with Rovamo and Virsu cortical magnification factors. The R^2 value explains how well the model explains the variability in the response 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. edge length and computed the retinal function and cortical function R^2 values.

From this regression model, we build an equation for the edge length as a function of the retinal circumference and as a function of the cortical circumference.

Harvey and Dumoulin in (Harvey & Dumoulin,2011), create a model that maps population receptive fields and cortical magnifica-

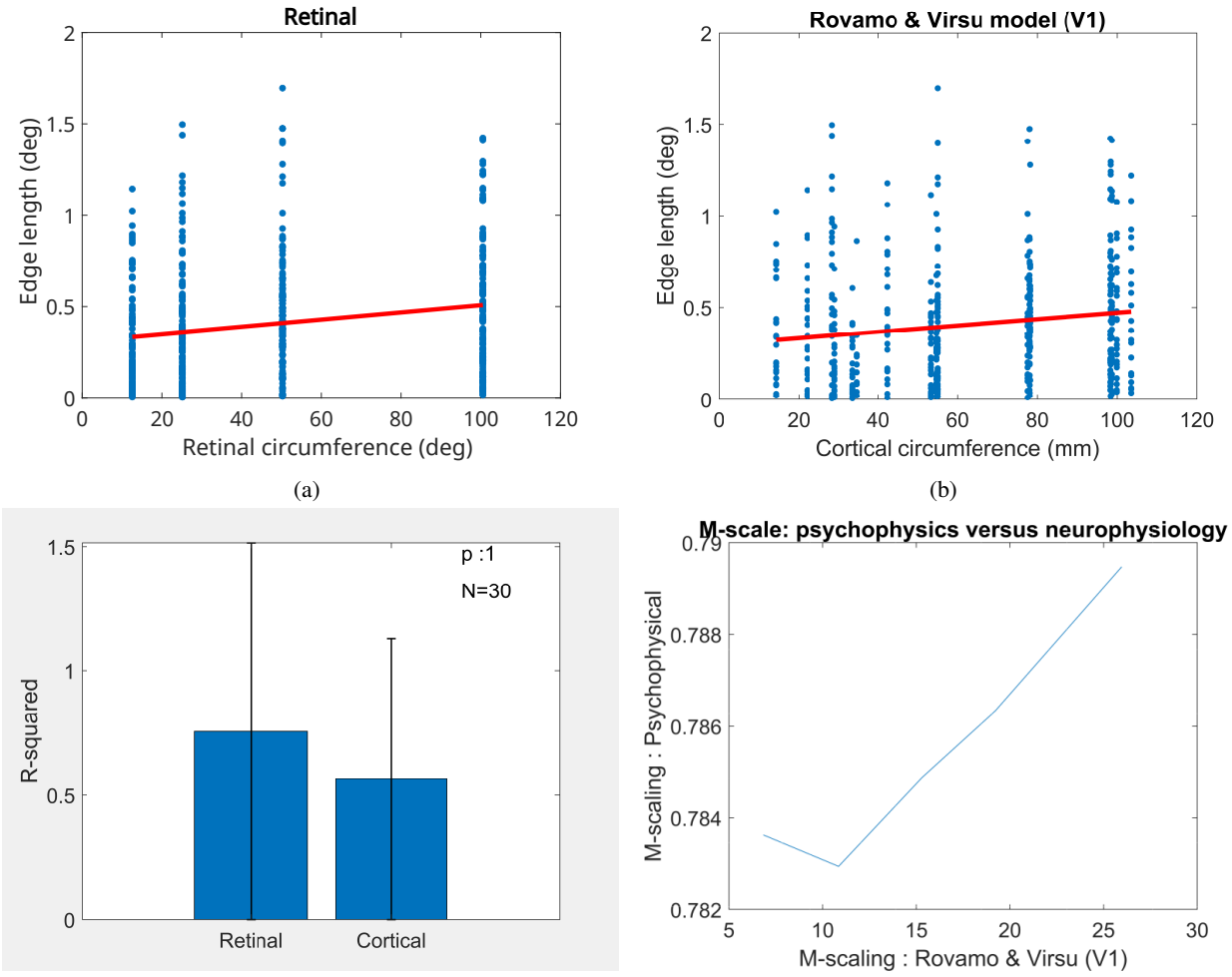


Figure 9: (a) Edge length versus retinal circumference r2: 0.04 (b) Edge length versus cortical circumference r2: 0.023 (c) r-squared from bootstrapped samples for retinal circumference function and cortical circumference function (d) A ratio of the M-scaling from experimental observer data and neuro-physiological study does not observe a flat slope indicating that animal studies and human data show a linear co-relation but are not equivalent.

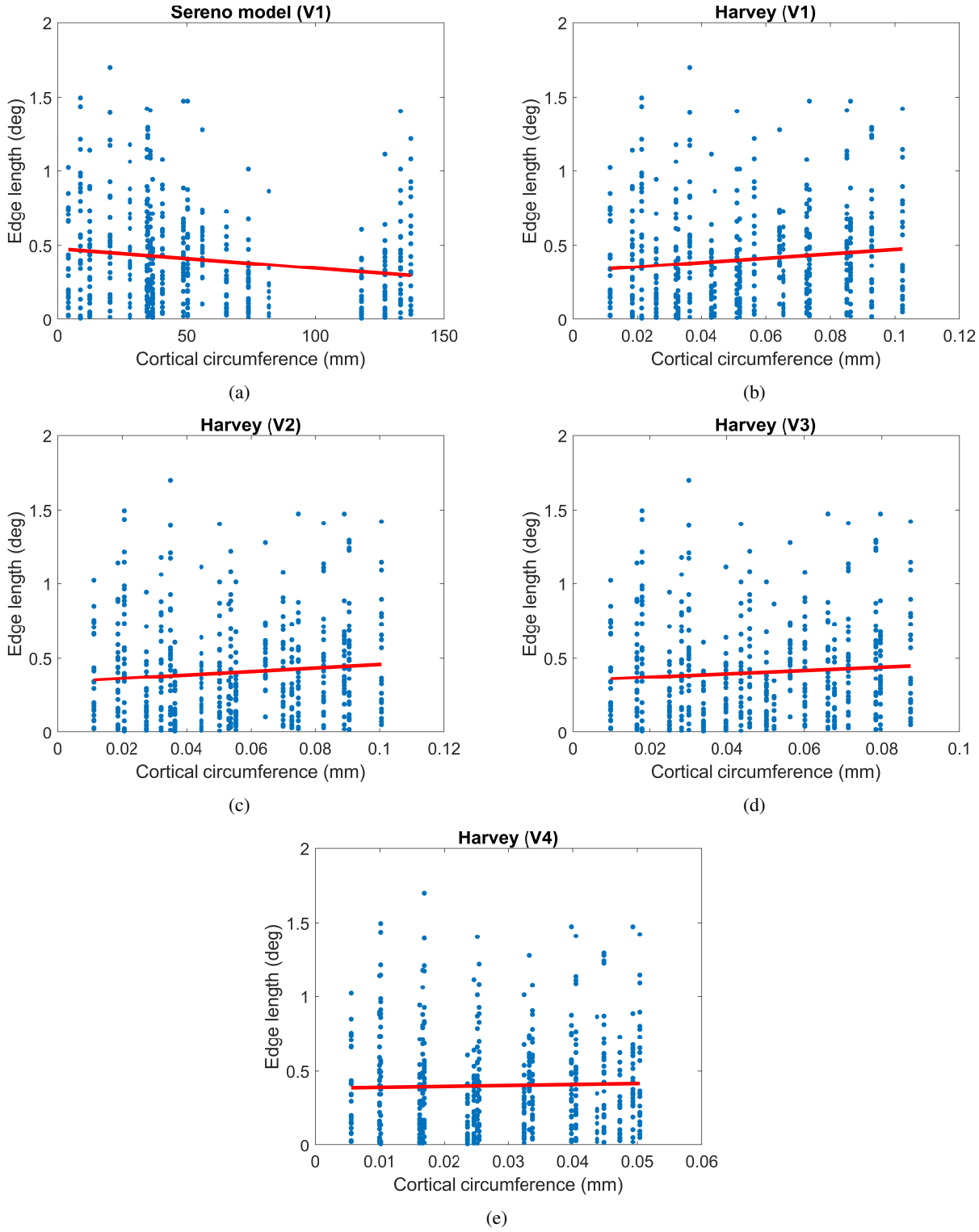


Figure 10: (a) Retinal circumference versus edge length using the Sereno model r2: 0.028 (b) Retinal circumference versus edge length using the Harvey model V1 r2: 0.0135 (c) Retinal circumference versus edge length using the Harvey model V2 r2:0.0084 (d) Retinal circumference versus edge length using the Harvey model V3 r2:0.0057 (e) Retinal circumference versus edge length using the Harvey model V4 r2:0.0007.

Algorithm 1 Cortical mapping function

[1]
Computing 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.

computeLengthOnCortex(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:

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

Cortical magnification factor for region V1. Rovamo's value used as an example
M= $25.19 * (eccentricity + 0.09)^{-1.53}$
Cspeed=M*speed

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

model	loglikelihood	model equation
edgelength $\sim$1 + size + $(1\|user)$	13.6695	0.496 + 0.0394 * size
edgelength $\sim$1 + eccentricity + $(1\|user)$	-150.796	0.755 + 0.0135 * eccentricity
edgelength $\sim$1 + size + eccentricity + $(1\|user)$	27.80	0.433 + 0.04 * size + 0.0176 * eccentricity
edgelength $\sim$1 + eccentricity_min + $(1\|user)$	-127.2	0.683 + 0.038 * eccentricity_min
edgelength $\sim$1 + eccentricity_mean + $(1\|user)$	11.84	0.529 + 0.0568 * eccentricity_mean
edgelength $\sim$1 + size + eccentricity_mean + $(1\|user)$	24.49	0.498 + 0.0214 * size + 0.0286 * eccentricity_mean
edgelength $\sim$1 + size + eccentricity_min + $(1\|user)$	14.85	0.487 + 0.038 * size + 0.0062 * eccentricity_min

tion 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. As evident from regression, a better summary of the relationship between the edge length seen during adaptation is provided by a cortical function than a retinal function. 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 level V4 (Harvey model).

When subjects are reporting edge lengths, they are usually reporting a single edge length for the entire illusion but may not factor for peripheral influence. The peripheral factor could either be the minimum eccentricity since we know that foveal representations are stronger than flanking representations. The peripheral factor could also be characterized by an averaged mean eccentricity. This is the eccentricity that is formed as a function of the distance from fixation, integrated over the circle that is being presented.

We use the edge length that is initially reported by the user, and compare it as a function of retinal eccentricity, cortical eccentricity and peripheral eccentricity - both averaged mean and minimum representations. We show the interactions between the models that have only size, only eccentricity, mean and minimum eccentricity and size and eccentricity together with the user as a random effect.

From the table above, using loglikelihood, the model that best describes the response from users is size and eccentricity together. Size, as the sole fixed parameter, offers the best explanation to the edge length reported by the participants.

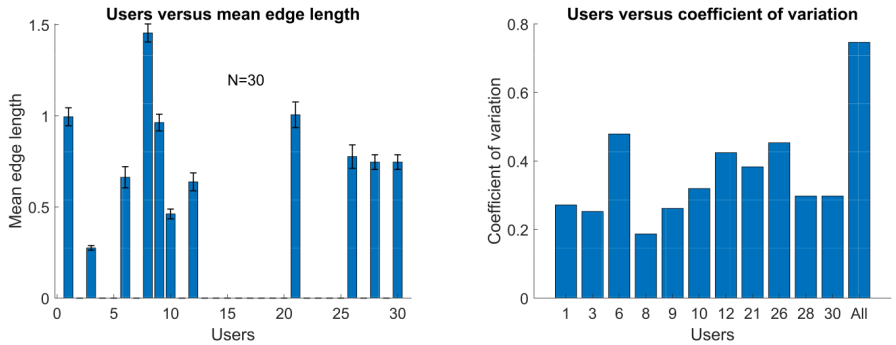
Do participants matter? What is the inter subject and intra subject variability with respect to edge length when considering all participants?

From Fig 11 (b), the users that report edge lengths (i.e. they see polygons instead of circles only) are reported as users 1-10. Over all stimulus conditions and all trials, as the coefficient of variation is much less than 1, the inter-subject variability is very low for users reporting edge lengths and thus, inter-subject values can be averaged as it does not carry wide subject-specific information. The 'All' bar, being less than 1, also shows that the inter-subject and intra-subject variability is relatively low.

A simple ratio of variance of the users versus the overall variance shows that the users individually do not contribute significantly to the mean. Below, we show the inter class coefficient (ICC) as a ratio of the overall variance and the variance of the users, which is a random effect.

$ICC = \sigma^2_{users}/(\sigma^2_{overall} + \sigma^2_{users})$

We find that most of the time, inter class coefficient, ICC, reported are much less than 0.5 indicating not much inter-reliability between the two variances. The users do not significantly influence the general mean reported for edge length. The various ICCs for the model designs are listed in the model table above.



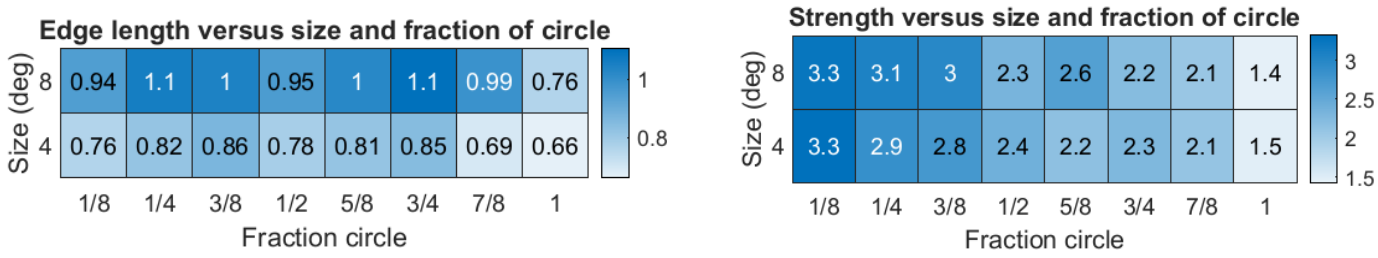
(a) (b)

Figure 11: Experiment: (a) Inter subject variability: Edge length is extracted from each subject. The bar for each subject encompasses all trials across all stimuli conditions. Some users report all circles. Their means are 0. (b) Coefficient of variation: The 'All' bar is calculated from all subjects and all repetitions. It reflects both inter-subject and intra-subject variability.

model	**ICC**	**Do participants influence the edge length mean?**
edgelength $\sim$1 + size + $(1\|user)$	0.0008256	No
edgelength $\sim$1 + eccentricity + $(1\|user)$	1.1057905	Yes
edgelength $\sim$1 + size + eccentricity + $(1\|user)$	0.151666 [Best Model]	No
edgelength $\sim$1 + eccentricity_min + $(1\|user)$	0.19844	No
edgelength $\sim$1 + eccentricity_mean + $(1\|user)$	0.941114	Yes
edgelength $\sim$1 + size + eccentricity_mean + $(1\|user)$	0.183109	No
edgelength $\sim$1 + size + eccentricity_min + $(1\|user)$	0.17636437	No

Results from Experiment 2

Participants did not report twice as large edge length with twice as large a stimulus. The edge length reported per arc length did not change greatly with arc length but changed with actual circle size. This demonstrates that sampling is based on the quality of the curve or curvature rather than the length of the curve. The strength reported was slightly lower for full circles compared to fractional arc lengths, alluding that the visual system has an affinity for closure and prefers to see shapes as composited closed circles where possible.



(a) (b)

Figure 12: (a) Mean edge length (in pixels) for different arc lengths 1/8 ,1/4 ,3/8 ,1/2 , 5/8, 3/4 and 1 of the circle, circle of deg 4 and 8. (b) Strength reported for different arc lengths 1/8 ,1/4 ,3/8 ,1/2 , 5/8, 3/4 and 1 of the circle, circle of deg 4 and 8. Strength was marked on a scale of 1-10 for polygonal percepts. Lowest strength was reported for full circles.

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