

Understanding cone distributions from saccadic dynamics. Is information rate maximised?

Alex Lewis¹, Raquel Garcia² and Li Zhaoping¹.

¹Department of Psychology, UCL, Gower Street, London WC1E 6BT, UK.

²Theoretical Physics, Imperial College, London SW7 2BY, UK.

Abstract:

Although the retinal cone distribution is known for all retinal locations, there is not yet a satisfactory explanation as to why cones are so distributed. We use experimental data on eye movements to model the probability that a target's image lies at any position on the retina. The rate of information transfer is maximised if this probability is proportional to the local receptor density. This establishes a quantitative relation between saccade dynamics and the retinal cone distribution.

1 Introduction

The distribution of photoreceptors on the retina is known for all eccentricities (fig. 1A). The density of cones is highest at the foveola, and declines by a factor of 10 within 4° . Outside the fovea the density declines more slowly [1]. Our hypothesis is that this arrangement maximises the information gathered by the retina, given a fixed number of cones that could be distributed in many different ways, when eye movements are taken into account.

The coding of information by visual receptors will be most efficient if the cone density is proportional to the density of targets in the visual field. In the absence of eye movements it would be most efficient to have a uniform cone distribution. Eye movements ensure that interesting objects are fixated at the fovea, and so it is more valuable to have a high cone density, and hence a high resolution, at the fovea than in the periphery of the eye.

To make this argument quantitative, we must the nature of the fixating movements, since they determine the distribution of target images on the retina.

Indeed, such an explanation must take into account the nature of the eye movements which bring objects towards the fovea, since it is these movements which determine the distribution of images of objects on the retina. We use experimental data on the accuracy and frequency of saccadic eye movements to compute the probability distribution of objects appearing in visual space. By comparing the resulting distribution with the distribution of cones, we assess the extent to which information is maximised. This provides a link between the previously unrelated bodies of experimental data on photoreceptor distributions and eye movements (fig. 1).

2 A model for the probability of target incidence across the retina

When an object appears in the visual field of an observer, a series of saccades may follow to bring its image to the fovea. Because saccades are generally inaccurate, more than one saccade may be

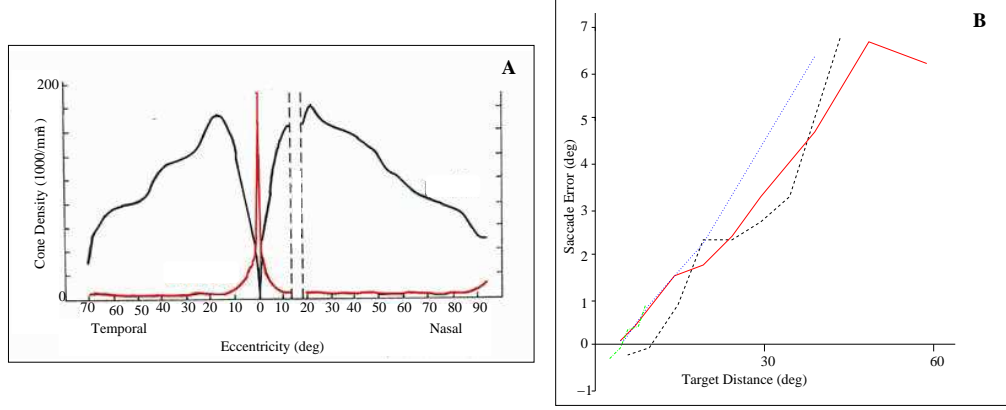


Figure 1: **A** Distribution of cones and rods on the human retina. **B** Results of four experiments on saccade accuracy – mean saccade error increases with target distance (from [7]).

required to fixate the target. To find the probability that an object lies at a point in the visual field, we sum the probability that it initially appears at that point, and the probability that it will be taken to that point by a saccade.

Given an initial probability distribution $P_0(\mathbf{u})$ of objects in the visual field, we can express $P_1(\mathbf{u})$, the probability distribution that results after a gaze-shift has taken place as:

$$P_1(\mathbf{u}) = \int p_G^0(\mathbf{u}, \mathbf{v}) P_0(\mathbf{v}) d\mathbf{v} \quad (1)$$

Here \mathbf{u} and \mathbf{v} are two points in the visual field, which we characterise as a hemisphere, with respective spherical polar coordinates $\mathbf{u} = (\theta_{\mathbf{u}}, \phi_{\mathbf{u}})$, $\mathbf{v} = (\theta_{\mathbf{v}}, \phi_{\mathbf{v}})$. $p_G^0(\mathbf{u}, \mathbf{v})$ is the probability of a gaze-shift towards an object initially at \mathbf{v} that leaves the object at a final position \mathbf{u} . The angle θ is the eccentricity relative to the fovea, so that the volume element for the two-dimensional integral is $d\mathbf{v} = \sin(\theta_{\mathbf{v}}) d\theta_{\mathbf{v}} d\phi_{\mathbf{v}}$. We assume here that $P_0(\mathbf{u})$ is a constant. Similarly, we can express the probability distribution after a sequence of n saccades in terms of the probability distribution after n saccades, P_{n-1} , and $p_G^n(\mathbf{u}, \mathbf{v})$, the probability of a corrective saccade towards a target at \mathbf{v} which leaves the target at \mathbf{u} , after n saccades have already occurred. In principle the probability of making a saccade towards a target could depend on the number of saccades already made, so that p_G^n could depend on n . The full probability distribution of targets on the retina is then given by the sum: $P(\mathbf{u}) = \sum_n P_n(\mathbf{u})$

Because cone density variations and gaze-shifts are much more strongly associated with changes in θ , we consider ϕ to be fixed, and hence the integral in 1 to be one-dimensional. From now on we call the eccentricities $\theta_{\mathbf{u}}$ and $\theta_{\mathbf{v}}$ simply x and y , and reinterpret p_G as the probability of a movement towards an object at eccentricity y with an error x . Then, since the probability of a target lying between x and $x + dx$ is $P(x) \sin(x) dx$, eq. (1) becomes:

$$\sin(x) P_1(x) = \int p_G^0(x, y) P_0(y) \sin(y) dy \quad (2)$$

The experimental data on which we base our model suggests the following decomposition for p_G :

$$p_G^n(x, y) = K(x, y) \alpha^n(y) \quad (3)$$

where $K(x, y)$ is the probability distribution for the error x of the gaze-shift (ie. the eccentricity of the target after a saccade) as a function of initial target eccentricity y , and $\alpha^n(y)$, is the probability

that an object at eccentricity y (after a sequence of n saccades) elicits a fixation. However, we will not need to know the explicit form of the functions $\alpha^n(y)$. The equation for P_n is then:

$$P_n(x) = \int_0^{90} K(x, y) \alpha^{(n-1)}(y) P_{(n-1)}(y) \frac{\sin(y)}{\sin(x)} dy \quad (4)$$

It would be very difficult to determine the functions $\alpha(x)$ from experiments. It is more convenient to eliminate $\alpha(x)$ in favour of the relative frequency of saccades of amplitude x , which we call $f(x)$. Unlike $\alpha(x)$, $f(x)$ has a simple interpretation – it is the proportion of all saccades which have a target at eccentricity x – and almost precisely this has been measured in [2]. $f(x)$ is related to $P_n(x)$ and $\alpha^n(x)$ as $f(x) = \sum_i \alpha^{(i)}(x) P_i(x) \sin(x)$

Given $f(x)$, we can express $P(x)$ in terms of P_0 and the probability distribution of target position after a saccade, P_C :

$$\begin{aligned} P(x) &= \frac{1}{1+w} [P_0(x) + w P_C(x)] \\ P_C(x) &= N_C \frac{1}{\sin(x)} \int_0^{90} K(x, y) f(y) dy \end{aligned} \quad (5)$$

Where N_C is a normalisation constant ensuring that the total probability P_C is 1, and w , the relative weight given to P_C compared to P_0 . The size of w will depend on the proportion of objects in the visual field which do not elicit saccades, but as we have no data from which to determine this number, we will treat it as a free parameter of the model. In fact it will be the only free parameter.

To compute the full probability distribution, which we will compare to the retinal cone distribution, we therefore need to know the kernel (probability distribution of saccade errors) $K(x, y)$, and the frequency distribution of saccades $f(x)$.

The data from many studies are consistent with a simple linear relationship between initial target eccentricity x and the mean error $\mu(x)$: $\mu(x) = a(x - x_0)$ where a is typically in the range $0.1 - 0.2$ and x_0 in the range $5^\circ - 10^\circ$ [7]. Saccades with amplitudes greater than x_0 (the neutral distance) usually undershoot the target, while saccades to targets closer than x_0 typically overshoot (fig. 1B). The scatter in the error of saccades also increases with amplitude [8]. We therefore model $K(x, y)$ as a Gaussian distribution over x with a mean and standard deviation which both depend linearly on the initial target position y .

$$\begin{aligned} K(x, y) &= \frac{1}{2\sqrt{2\pi} \sigma(y)} \left(\exp[-(x - \mu(y))^2 / 2 \sigma(y)^2] + \exp[-(x + \mu(y))^2 / 2 \sigma(y)^2] \right) \\ \mu(y) &= a(x - x_0), \quad \sigma(y) = b + cy \end{aligned} \quad (6)$$

except that we impose $K(x, y) = 0$ when $x > y$, since we do not expect that any saccades occur which move the eye further away from its target. The second term takes care of the overshoots under the assumption of no asymmetry between saccades to nasal and temporal targets (since targets that are on the nasal side of one eye are on the temporal side of the other).

Using data from [3], we find the following values for the parameters a, x_0, b, c : $a = 0.15$, $x_0 = 8.5^\circ$, $b = 0.5$, $c = 0.1$.

In most experiments, gaze-shifts occur through eye movements only, with the head fixed. However studies on eye-head coordination do not show differences in accuracy for eye-only gaze-shifts and combined eye-head gaze-shifts [6]. Therefore $K(x, y)$ adequately describes the redistribution of target eccentricities under a general saccadic gaze-shift, involving both eye and head movements.

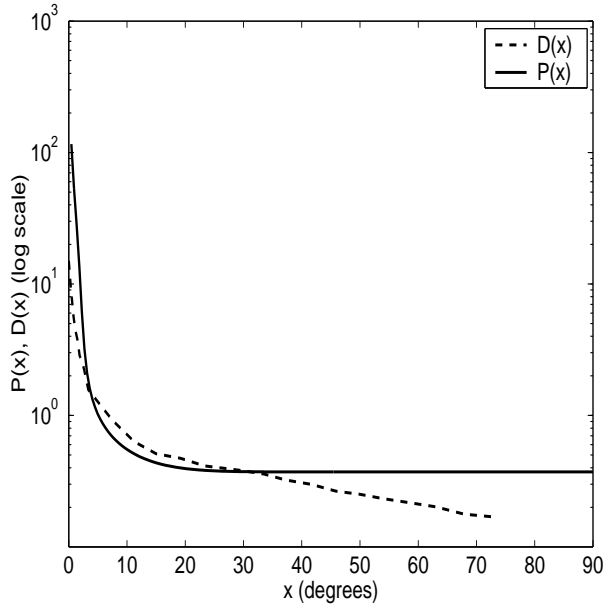


Figure 2: Probability distribution of positions of objects on retina computed using experimental data on eye-movement dynamics ($P(x)$, solid line); and retinal sampling density of cones ($D(X)$, dashed line). $D(x)$ is the average of the cone density on the nasal and temporal side of the horizontal meridian, from [1]. If the cone distribution maximises information flow, the two curves should coincide.

Our main source for the frequency distribution $f(x)$ is an experiment in which three subjects were asked to wander freely outdoors while their eye movements were recorded [2]. The relative frequency of saccades was found to decay exponentially with amplitude, that is $f_E(x) = \exp(-x/7.6^\circ)$. The mean saccade size of 7.6° is only slightly larger than the mean sizes of saccades recorded viewing a picture of a natural scene, performing a visual search task or reading, in an experiment where various stimuli were presented on a screen, with the head immobile [4]. However, the relative frequencies $f_E(x)$ correspond only to eye-movements relative to the head. Saccades with amplitudes larger than about 10° usually involve both the eye and head, and so the full gaze shift amplitude is larger than the eye-only saccade amplitude, and $f(x)$ will be larger than $f_E(x)$ for larger values of x . We therefore model $f(x)$ as having an exponential form similar to $f_E(x)$, but with a constant term included:

$$f(x) = d + e^{-x/\lambda} \quad (7)$$

Using data from an experiment on eye-head coordination¹ [5, 6] we obtain $d = 0.017$, $\lambda = 3.2^\circ$.

We can now use eqns. (5,6,7) to compute $P(x)$, which is to be compared to the sampling density of cones, $D(x)$.

3 Results and Discussion

According to our model, if cones are arranged so as to maximise information, then the density of cones on the retina should be proportional to the target probability distribution $P(x)$ as determined by eye movements. (fig. 2). The two distributions have the same general form, with a peak around the fovea of equal width. They are in close agreement between 5° and 30° , but show a different

¹The authors are very grateful to J. Stahl for providing the data from his experiments.

behaviour within the fovea and at large eccentricities. The hypothesis that information flow is maximised therefore goes some way towards explaining the distribution of cones.

The discrepancies between the model and the empirical cone distribution, at very large and small eccentricities, may be indications of factors which have not yet been included in the model. These could be factors which affect the rate of information flow, or constraints on the densities of cones which are biologically feasible. Within the fovea, the model does not incorporate the biological limits on the maximum cone density that is achievable or useful, such as the optical resolution of the eye and the need for capillaries within the retina. Also, we have not taken account of the different functions of the fovea and periphery of the eye (the periphery is mainly used to detect objects, which may then be brought to the fovea by eye movements, while the fovea itself is used for object recognition).

Since saccades with errors greater than 30° are extremely rare, the model simply predicts that the cone density is proportional to the initial probability distribution $P_0(x)$ for large values of x . However, the density of cones declines continuously at all eccentricities. If there is only one target at a time in the visual field, the initial distribution will be independent of eccentricity, as we have assumed. However, when viewing complex scenes there are many potential targets in view at the same time. In that case $P_0(x)$ may depend on the correlation between the objects, and not be constant. For this to explain the distribution of cones at large x , there would have to be significant correlations at scales up to 90° .

There is some uncertainty in the parameters which we have used to describe both the accuracy of saccades and their frequency. In the case of the frequency distribution, the main problem is the limited experimental data available. We have combined the distribution of eye-only saccades for three subjects from [2] with average values for eye-head coordination from four subjects to obtain $f(x)$. However, the parameters describing eye-head coordination are highly variable between individuals (and even between left and right movements for the same individual) [5, 6], and the average size of saccades with the head fixed also varies [4]. We therefore do not know whether $f(x)$ is also highly variable. This can only be resolved by further experiments.

For saccade accuracy, we used values of the parameters which are in line with many experiments, but there are circumstances in which saccades can be either more or less accurate. For example, in [9], errors as small as 0.5° for saccade amplitudes as large as 70° were found for repeated saccades between two fixed targets. If this level of accuracy were found to be typical for natural saccades, our theory would predict a probability distribution which was very sharply peaked in a region about 1° wide and almost constant everywhere else. This is therefore a potential falsification of the model.

On the other hand, saccades to auditory rather than visual targets can be much less accurate. For example, the accuracy of saccades to both visual and auditory targets was studied in [10], and while auditory saccades for target eccentricity up to 10° were as accurate as visual saccades, auditory saccades to targets at 20° or 30° were significantly less accurate, with errors of 10° for targets at 30° . In addition, the frequency distribution $f(x)$ may well be different for targets of auditory saccades, if only unlike because visual saccades can be at any eccentricity up to 180° . Thus including auditory saccades could change the results of the model, if the frequency of auditory saccades were known.

So far we have only considered horizontal eye movements and cone distributions. The cone distribution shown in fig. 2 is the average density along the horizontal meridian, but the cone distribution is not radially symmetric. The density declines more sharply along the vertical meridian than along the horizontal meridian, so that at 3.5° the density is 20000 cones/mm² on the horizontal meridian and 16000 cones/mm² on the vertical meridian [1]. This radial asymmetry

has three possible explanations within our model. Vertical saccades could be less accurate or less frequent, so that $K(x, y)$ or $f(x)$ would be different. The initial probability $P_0(x)$ could also be different. Of these, there is some evidence that vertical saccades are less accurate than horizontal saccades [7]. When saccades are less accurate $P_C(x)$ is smaller at small values of x ; however, the effect of this alone is not large enough to explain the asymmetry of the cone distribution. We do not know of any experiments on vertical eye-head coordination (which we would need to find $f(x)$ for vertical saccades). Therefore, the model can in principle account for the radial asymmetry of the retinal cone distribution, but we cannot yet verify if it does so correctly.

These results, which relate experimental data on eye movements and on cone distributions, confirm that information flow through the retina is maximised to some extent. Further research, both theoretical and experimental, is still needed to fully understand the distribution of photoreceptors in the eye.

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