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Neurocomputing 58–60 (2004) 807 – 813

NEUROCOMPUTING

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

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Abstract

There is not yet a fully satisfactory and quantitative explanation as to why human cones have their particular distribution on the retina. If this distribution is to maximise the rate of the information transfer, it should be proportional to the probability distribution of locations of attended objects. We derive this probability distribution from experiment data on eye movements to test this hypothesis, which provides a quantitative link between saccadic dynamics and the cone distribution.

Keywords: Photoreceptor distribution; Retinal sampling; Saccades

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1. Introduction

The coding of information by visual receptors is most efficient if the density $D(x)$ of cones, or possibly of retinal ganglion cells (RGCs), at a retinal location x is proportional to the probability density $P(x)$ of attended visual objects. Without eye movements, a uniform cone distribution (assuming that the objects appear uniformly in the visual field) would be most efficient. By shifting our gazes to fixate interesting objects at the fovea, we can increase efficiency by allocating more cones to a small region.

Human cone density peaks sharply at the foveola, declining rapidly in the first few degrees around it and more slowly outside the fovea [3]. RGCs show a similar distribution, with an even sharper peak [7]. Our hypothesis then is that this arrangement maximises the information gathered by the retina. To make this argument quantitative,

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doi:10.1016/j.neucom.2004.01.131

we estimate $P(x)$ from data on the accuracy and frequency of eye movements, and compare it with the density of cones and RGCs.

2. Computing the probability of target incidence across the retina

At this early stage of the investigation into the possible link between retinal sampling and eye movement, we will use a very simple model of the visual world. Lacking detailed knowledge of the sizes and distributions of visual objects, we make the simple assumptions that each object is independent of every other and can be treated as a point. We also restrict ourselves to object probability distribution $P(x)$ and cone density $D(x)$ as a function of eccentricity x along the horizontal axis. Finally, we assume that the visual system attends to one object at a time, so a subject's visual life is treated as a sequence of object locations, each of which is either a sample from an initial uniform distribution $P_0(x)$, or is the result of a saccade (Fig. 1). Consequently, $P(x) = (1 - \omega)P_0(x) + \omega P_S(x)$, where $P_S(x)$ is the probability distribution of target location after a saccade, and $0 < \omega < 1$ represents the proportion of objects which elicit saccades. Note that $P(x), P_0(x), P_S(x)$ are probability densities on the hemisphere, so the probability that a target lies between x and $x + \mathrm{d}x$ is $2\pi P(x)\sin(x)\,\mathrm{d}x$.

Now $P_S(x)$ depends on (1) the probability distribution $K(x, y)$ of the post-saccade eccentricity x of a target initially at y, and (2) the distribution $f(y)$ of positions y of object's which elicit saccades. Thus, over all saccades, the probability that an object's post-saccade eccentricity is between x and $x + \mathrm{d}x$ is $2\pi P_S(x)\sin(x)\,\mathrm{d}x=$

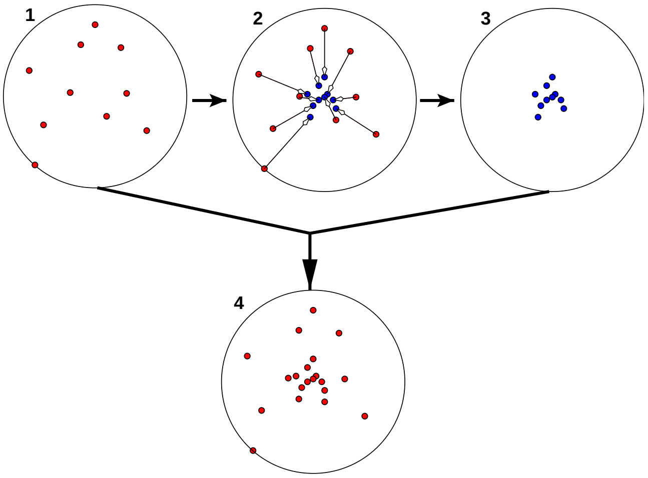

Fig. 1. In a scene with several objects one of them attracts the observer's attention. (1) At the start the object could be anywhere. This gives the initial uniform distribution $P_0(x)$. (2) The chosen object may elicit a saccade, bringing it closer to the fovea. (3) This happens to many objects in an observer's visual life, so the distribution of targets after saccades, $P_S(x)$ is concentrated around the fovea. (4) Combining the distributions of targets before and after saccades, we obtain $P(x)$. In the full model, zero, one or more than one saccade may be made to each target.

$(\int K(x,y)f(y)\,\mathrm{d}y)\,\mathrm{d}x$ and so the full probability distribution $P(x)=P_0(x)+P_S(x)$ can be shown to be

$$P(x)=(1-\omega)P_0+\frac{\omega}{2\pi\sin(x)}\int f(y)K(x,y)\mathrm{d}y. \tag{1}$$

We obtain below both $K(x,y)$ and $f(y)$ from experimental data—more details will be given in a longer paper. ω is a free parameter of the model.

$K(x,y)$ can be thought of as the probability distribution for the error x of a gaze-shift as a function of initial target eccentricity y. The data from many studies are consistent with a simple linear relationship between initial eccentricity y and the mean error $\mu(y)$: $\mu(y)=a(y-y_0)$, where a is typically in the range 0.1–0.2 and y_0 in the range 5°–10° [2]. The scatter in the error of saccades also increases with amplitude [6]. Combined eye–head gazeshifts also have very similar accuracy to eye-only saccades [8]. We therefore model $K(x,y)$ as a Gaussian distribution with mean $\mu(y)=a(y-y_0)$ and standard deviation $\sigma(y)=b+cy$.

$$K(x,y)=\frac{A(y)}{\sigma(y)}\left(\exp\left[-\frac{(x-\mu(y))^2}{2\,\sigma(y)^2}\right]+\exp\left[-\frac{(x+\mu(y))^2}{2\,\sigma(y)^2}\right]\right)\quad \text{if } x<y, \tag{2}$$

where $A(y)$ ensures $\int_0^y \mathrm{d}x\,K(x,y)=1$, and the second term is the contribution from saccades which overshoot the target; we set $K(x,y)=0$ if $x>y$. Using data from [5], we find the following values for the parameters: $a=0.15, y_0=8.5°,\ b=0.5,\ c=0.1$. Since this model of $K(x,y)$ ceases to hold for very small y (for $y<1.11°$ we would have $\mu(y)>y_0$, we take $y=1.5°$ as the lower limit of the range of validity of our model and in our integrals.

To assess the sensitivity of our results to the parameters which define $K(x,y)$, we repeated the calculation of $P(x)$ using parameters which describe saccades to auditory targets, which are much less accurate. Based on [9], we use the parameters $a=0.32,\ y_0=0,\ b=0$ and $c=0.23$ for auditory saccades.

Our main source for the frequency distribution $f(y)$ is an experiment in which eye movements were recorded from subjects wandering outdoors [1], giving a relative frequency of eye-only saccadic amplitudes $f_E(y)\propto\exp(-y/7.6°)$. Since gazeshifts greater than 10° usually involve both eye and head movements, we derive the relative frequency $f_G(y)$ of gazeshifts y from experimental data [8] on $p(y_E\mid y)$, the probability of eye movement amplitude y_E given a gazeshift amplitude y, by the relationship $f_E(y_E)=\int_0^{90} p(y_E\mid y)f_G(y)\,\mathrm{d}y$. Accounting for the error in the gazeshift, the distribution of the target eccentricity $f(y)$ relates to the frequency $f_G(y')$ of gazeshift amplitude y' by $f_G(y')=\int f(y)K(y-y',y)\,\mathrm{d}y$. Hence, combining data from an experiment on eye–head coordination $p(y_E\mid y')$ [1] and gazeshift error $K(y-y',y)$, assuming that $f(y)$ has a similar form to $f_E(y)$:$f(y)=d+e^{-y/\lambda}$, we obtain our model $f(y)$. Parameter values $d=0.017$ and $\lambda=3.2°$ were obtained by averaging the eye-head coordination data for five subjects. The corresponding values for individual subjects range from $\lambda\in(2.0°,7.6°)$ and $d\in(0.004,0.09)$. This does not necessarily mean that the *actual* $f(y)$ varies between individuals, since the subject-dependent eye–head coordination $p(y_E\mid y)$ could couple with the subject dependent $f_E(y_E)$ to give the subject

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

invariant $f(y)$. Indeed, the subject-dependent eye–head coordination data come from experiments in which all subjects saw targets with the same distribution of positions [8]. However, since we lack data on $p(y_E \mid y)$ and $f_E(y_E)$ from the same subjects, the large subject variation in both sets of data means that our estimate of $f(y)$ must be seen as rather uncertain.

3. Results and discussion

The estimated object density $P(x)$ is fitted to the experimental data on cone density $D(x)$ [3] or RGC density [7] by choosing the fitting parameter ω, giving $\omega = 0.09$ for cones, or $\omega = 1.13$ for RGCs, see Fig. 2. The two distributions have the same general form. Both have a peak around the fovea of approximately equal width, and are in close agreement between 5° and 30°. However, they differ at larger eccentricities x, where $P(x)$ is constant while $D(x)$ keeps decreasing with x. The results are similar for both cones and RGCs.

Fig. 3 (left) compares the probability distribution computed using the $K(x, y)$ for auditory or visual saccades. The right plot in Fig. 3 shows how $P(x)$ varies with $f(y)$. Clearly, the estimation of $P(x)$ is very sensitive to variation (or uncertainties) in $f(y)$, but much less sensitive to changes in $K(x, y)$.

These results suggest that the distribution of cones and RGCs in the human eye are to some extent adapted to maximise information flow. However, the differences between of $P(x)$ and $D(x)$, and the uncertainty in the results show that there is a need for considerable improvements in the model.

One possible explanation for the discrepancy between $P(x)$ and $D(x)$ is that our proposal is essentially right but that our simple model of visual experience is inadequate. A first step forward would be to obtain a better estimate of $f(y)$. At present our estimate of $f(x)$ is based on very limited experimental data, combining the distribution of eye-only saccades for three subjects [1] with data for eye–head coordination from five other subjects [8]. Given large subject variations in both sets of data, $f(y)$ can

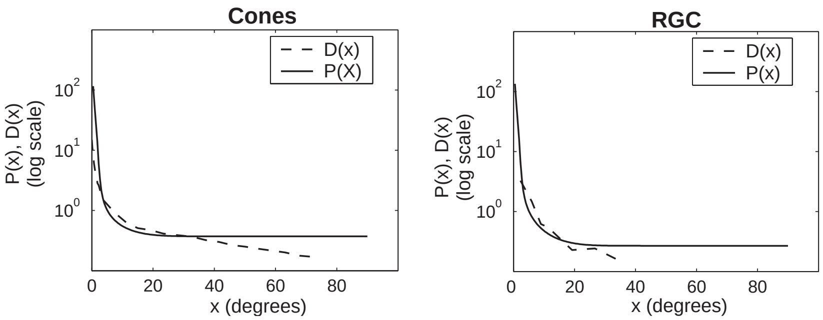

Fig. 2. Probability distribution of positions of objects on retina computed using experimental data on eye-movement dynamics ($P(x)$, solid line); and retinal sampling density of cones (left) or ganglion cells (right), ($D(X)$, dashed line). If the cone (or RGC) distribution maximises information flow, the two curves should coincide.

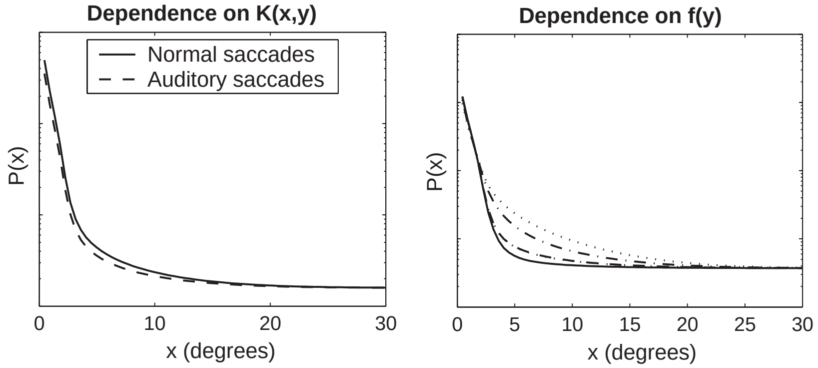

Fig. 3. Sensitivity of results to parameters derived from experimental data. (A) $P(x)$ computed using $K(x,y)$ for visual and for auditory saccades, with the same $f(y)$. (B) $P(x)$ computed using a range of parameters for $f(y)$, all with the same $K(x,y)$.

be better estimated by either using data from the same sets of subjects, or measuring $f(y)$ directly. Possibly the main improvement to our model would come from new experiments to re-evaluate $f(y)$.

It is also important to develop a model which takes account of the interplay of complex visual scenes and visual attention. In particular, saccades with errors greater than 30° are extremely rare, so $P(x) \sim P_0(x)$ for $x > 30^\circ$. Thus, our assumption that $P_0(x)$ is constant leads to the large x discrepancy between $P(x)$ and $D(x)$. This assumption makes sense if positions of objects are unrelated. However, in complex scenes there may be correlations among the positions of some of the objects present. This could induce a persistent decline of $P_0(x)$ at large eccentricities if there were correlations at very large scales (e.g. to have $P_0(60) > P_0(80)$, there should be correlations between objects 60° apart). Another factor omitted by the model is that the cone density affects the visual resolution, and thus the number of interesting objects that are detected. Consequently, $P_0(x)$ might not be independent of $D(x)$.

3.1. Predictions

The theory developed in this paper implicitly relates a species' photoreceptor distribution to its environment and eye movements. The species' habitat would be reflected both in $P_0(x)$ and $f(y)$. For instance, animals living in open environments often have horizontal streaks of high-cone densities. Cone distributions are already known for many species, but study of saccade accuracy and frequency across different species would be needed to test the predicted relationship.

The angular size of the fovea varies widely among primate species (although the absolute areas are approximately equal) [4]. Since the angular width of the cone density peak in humans is a successful prediction of our model, we could use it to predict that primate species with a wider (or narrower) peak will have less accurate (or more accurate) eye movements.

4. Conclusions

This work provides a starting point for further research into how attentional and environmental factors contribute to the distribution of objects on the retina; and whether this in turn determines the distributions of cones and RGCs. It also quantitatively links two apparently disconnected bodies of experimental data: psychophysics of saccades and retinal physiology.

Acknowledgements

We are very grateful to J. Stahl for providing us with data from his experiments. A.L. and L.Z. are supported by the Gatsby Charitable Foundation. R.G. is funded by a Royal Society Dorothy Hodgkin Fellowship.

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