The Receiving End of the Cooperative Eye: a test by construction

M Schmettow, C. Willemse, S. Borsci

## Introduction

The human eye region plays a central role in non-verbal communication. Beyond reading emotional states, humans are exceptionally quick and accurate at discerning one another’s gaze direction. The Cooperative Eye Hypothesis (CEH) proposes that this ability evolved alongside the emergence of human hyper-cooperation and altruism. A key anatomical feature supporting CEH is the conspicuous white sclera, which is present in Homo sapiens but absent in all other extant great apes, whose scleras are largely obscured by pigmented conjunctiva (Kobayashi & Kohshima (2001)).

In most great apes, scleral camouflage likely evolved to protect against predators by masking eye position. The CEH, however, interprets the depigmentation of the human sclera as an adaptation for signalling gaze direction, facilitating joint attention in coordinated activities such as hunting and child-rearing. Developmental studies show that even newborns respond to direct gaze and display early forms of gaze following, suggesting an innate cognitive basis for this ability (Farroni et al. (2004)).

Evolutionary theory demands that a mutation must have an immediate reproductive benefit in order to stabilize in a species. The evolution of communicative traits is often difficult to to explain because of the inherent reciprocity. A novel signal can only evolve when a matching receiver mechanism exists, and vice versa. While a specialized eye direction detector (EDD) has been proposed even before the CEH (BARON-COHEN (1995)), the conundrum to solve is which of the two emerged first.

Two extreme scenarios are possible: (1) a pre-existing gaze-reading ability in early hominids, which became more effective with scleral depigmentation, or (2) the co-evolution of the white sclera and a new cognitive mechanism for gaze perception. Comparative studies indicate that chimpanzees rely mainly on head orientation rather than eye cues, supporting the idea that human-level gaze reading is a relatively recent adaptation. A reasonable middle ground between these extremes is that early hominids may have possessed a rudimentary visual mechanism for gaze estimation, such that scleral depigmentation had some immediate benefits. Subsequent selective pressure may then have produced a specialized, more effective EDD.

We argue that mutations leading to depigmentation are more likely to happen than mutations producing novel neural pathways. Under this hypothesis, the pre-existence of a rudimentary receiver, as well as the evolution of a specialized EDD are more likely if the signal is well aligned with general visual-cognitive functioning in humans, as well as computational simplicity of processing the signal.

The present work addresses this question in two steps. First, we test the computational simplicity of eye direction reading by introducing the QuadBright method, a eye-tracking algorithm that estimates gaze direction from visible-light brightness patterns using simple statistical learning. We evaluate its accuracy to test whether such a minimalist approach suffices for reliable gaze estimation—thereby “testing CEH by construction.”

Second, we explore the possibility that the QuadBright algorithm approximates what the human cognitive system uses for gaze perception. If so, QuadBright could serve as a candidate computational model for the hypothesized EDD. By comparing machine and human performance under identical visual constraints, we aim to test whether human gaze perception operates within these limits.

In summary, this paper has two aims:

1. Empirical test of CEH — demonstrating that a simple, biologically plausible algorithm can accurately determine gaze direction supports the claim that the human eye evolved as an efficient visual signal.
2. Extension of CEH — proposing a co-evolved, specialized cognitive receiver mechanism and offering QuadBright as a testable model for it.

### The White Sclera in human eyes

Among all extant great apes, only Homo sapiens displays a conspicuous white sclera (Kobayashi & Kohshima (2001)). While other apes possess anatomically white scleras, theirs remain largely concealed by pigmented conjunctiva, creating minimal contrast with the iris and surrounding facial features. This distinction is particularly striking given that maintaining scleral pigmentation requires sustained metabolic investment through complex biosynthetic pathways, while depigmentation reduces energetic costs.

The common explanation for scleral pigmentation follows a camouflage hypothesis (Kobayashi & Kohshima (2001), Wolf et al. (2022)): the high contrast between a dark pupil and white sclera makes an animal more visible to predators and competitors and may even reveal the focus of attention. For species facing predation pressure or intense intraspecific competition, concealing the white sclera provides a clear survival advantage by preventing others from detecting an individual or predicting its next move. The ubiquity of pigmented scleras across great apes indicates strong, persistent selection pressure favoring camouflage despite its energetic costs.

The human pattern represents a remarkable evolutionary reversal. Despite the energetic advantage of reduced pigmentation, the conspicuous white sclera could only have evolved if it provided fitness benefits that outweighed the costs of increased visibility to predators and competitors. The depigmented sclera creates maximum contrast with the iris, making the eye region highly salient even at distance or in peripheral vision. This implies that either the original selection pressure disappeared for humans, or by another selection pressure depigmentation became so advantageous in human ancestors that it overcame the universal great ape pattern of scleral camouflage.

### The Cooperative Eye Hypothesis (CEH)

The Cooperative Eye Hypothesis proposes that scleral depigmentation evolved as an adaptation for enhanced gaze signaling, facilitating rapid joint attention in cooperative activities such as coordinated hunting, foraging (Kobayashi & Kohshima (2001)), and child-rearing (@). This hypothesis situates the unique human eye morphology within the broader context of human hyper-sociality and the emergence of unprecedented levels of cooperation among early hominids.

Supporting evidence comes from developmental studies demonstrating that human infants respond to direct gaze and exhibit rudimentary gaze-following behaviors from birth (Farroni et al. (2003), Farroni et al. (2004), Farroni et al. (2007)). These findings suggest that gaze perception operates through innate cognitive mechanisms that are functional in early development, before extensive learning could account for such abilities. The early emergence and universal nature of gaze sensitivity across human populations indicates deep evolutionary roots for this capacity.

Comparative studies with chimpanzees provide additional support for the CEH. Despite their close genetic relationship to humans, chimpanzees rely primarily on head orientation rather than eye cues when interpreting gaze direction (Tomasello et al. (2007)). This finding suggests that sophisticated eye-based gaze reading represents a derived human trait rather than an ancestral great ape characteristic, supporting the hypothesis that enhanced gaze signaling co-evolved with human cooperative behaviors.

This interpretation raises a critical evolutionary puzzle: for the white sclera to confer fitness benefits for the sending individual, observing individuals must possess mechanisms capable of extracting and utilizing gaze information from this visual signal. The existence of such a specialized receiver system becomes essential to complete the evolutionary account.

### The Eye Direction Detector (EDD)

The existence of a specialized Eye Direction Detector represents a necessary corollary to the CEH. For scleral depigmentation to provide fitness benefits, human cognitive architecture must include mechanisms capable of rapidly and accurately extracting gaze direction from visual input. BARON-COHEN (1995) even puts the EDD as the starting point for Theory of Mind in human social cognition.

The existence of specialized neural networks for gaze processing is supported by neuroimaging studies showing that certain brain regions are preferentially activated when individuals view eye regions or interpret gaze direction (Babinet et al. (2021)).

What presents an open question is the temporal order of evolutionary appearance of white sclera and the EDD, but there are some indirect cues. Comparative evidence suggests that scleral depigmentation occurred relatively recently in human evolution—likely within the past two million years following divergence from the last common ancestor with chimpanzees. At the same time, the biosynthetic pathways of melanin are complex and several mutations are known in humans and apes (Dessinioti et al. (2009), Mayhew & Gómez (2015)). Non-fatal mutations leading to less pigmentation must therefore have been common. Mearing et al. (2022) found that sclera pigmentation varies stronger in anthropoid ape faces than was previously held. In contrast, there is practically no variation in the human sclera, which hints that it first appeared as a one-point mutation, rather than a slow genetic drift.

This raises the reciprocity conundrum: how could the white sclera produce immediate reproductive benefits? One possibility is that the white sclera encountered a rudimentary precursor of the EDD. As Laidre & Johnstone (2013) points out, it is a common assumption that “many signals have evolved from what once were cues.” Alternatively, early humans may have been able to learn to read glance directions, with the white sclera providing a signal clear enough to facilitated this learning process.

A plausible hypothesis is that cues are more likely to evolve into fully fledged signals when they can be processed with relatively low computational demands by potential receivers. Under this view, the likelihood that a cue becomes ritualized into a communication signal depends not only on its reliability but also on the ease with which the receiver’s perceptual and cognitive mechanisms can extract the relevant information. Consequently, evolutionary novel receiver mechanisms are expected to exhibit computational simplicity, as selection favors processing architectures that minimize energetic costs and reduce neural complexity while maintaining functional efficiency (Guilford & Dawkins (1991)).

The simplicity requirement is underlined by the fact that gaze reading emerges in human infants before the visual system has fully developed (Babinet et al. (2021)). This suggests that the EDD relies on low-level visual cues that can be processed quickly and efficiently, rather than complex feature extraction or high-resolution image processing.

The computational simplicity of the white sclera can indirectly be tested by designing a technical receiver device using minimal input and computational resources, and evaluate its accuracy compared to human gaze reading capabilities.

### Bio-plausible eye tracking

If the CEH, extended by the receiver mechanism, is correct, the human eye should be computationally simple to read: its morphology and coloration should allow for fast, accurate gaze estimation using only the visual cues available to a human observer. That should also hold for *eye tracking* devices designed to read gaze directions. However, most modern eye-tracking devices typically use signals that are not available to the human visual system, such as infrared reflections or magnetic fields (Singh & Singh (2012)). Only video-oculographic devices use visible light (Zhou & Geng (2004)) and recently gave rise to the development of webcam, smartphone and VR eye tracking (Ciesla & Koziol (2012)). Several algorithms have been developed in this line, often making use of advanced machine learning or computer vision techniques (Krafka et al. (2016)).

However, most these techniques are computationally complex and demanding, especially with the partial occlusion of the pupil by the eye lids. They also require more advanced processing methods, such as filtering, edge detection or neural networks. These, in turn, are based on iterative optimization methods, which are computing intensive.

If the eye ball sends such easy to decipher signals that humans can still read glance directions in highly degraded images (Yorzinski et al. (2021)), then it must be possible to build an eye tracking device that effectively uses purely visual information by rather simple methods of data processing. While not guaranteed, it is possible that designing an eye tracking algorithm under these constraints even results in a good model, how human glance reading works.

From the characteristics of human glance reading, the following *bio-plausibility requirements* can be derived for the algorithm:

1. based on visible light
2. based on low-level visual features available in infants
3. effective in degraded images and from a distance
4. universal, requiring only minimal calibration

We now introduce the QuadBright method, which instead employs the simple fact that the moving pupil produces a change in *horizontal and vertical brightness distribution* in the visible plane of the eyeball. The most simple approach to capture a bi-directional brightness distribution is to split the image horizontally and vertically in four quadrants (NE, SE, SW and NW, see Fig X) and taking the average brightness (Br). This effectively produces a 4 pixel grayscale image. The four quadrants are used as input for a multiple linear regression model, which predicts the horizontal and vertical position of the eye ball. The following equation shows the model for the horizontal eye position, the vertical position is analog.

### YET Zero prototype

To test the QuadBright algorithm, a simple eye tracking device was constructed, called Yet Zero (YET = Yet is your Eye Tracker). The main design goal was to create a low-cost, easy-to-build device that can be used in various experimental settings.

Most important for the physical design of the eye tracking device is a small footprint of the camera to minimize obstruction of the field of view when it is mounted in frontal position. In contrast, the resolution of the camera barely matters, as QuadBright essentially compresses the input into a four pixel frame. The choice fell on a type of commercially available USB endoscope cameras. These cameras with a diameter of 5.5mm create almost no obstruction when mounted in the visual field and the built-in LED lights provide a stable light source for better accuracy. A simple 3D-printed part was created to be able to glue the camera to a stick, which in turn can be connected to an improvised head mount.

The YET Zero application was written in Python, using PyGame for the GUI and basic image processing routines from OpenCV. The regression model was implemented using the Scikit-learn library. As usual in eye tracking, a calibration phase trains the model on Quadbright data obtained on (nine) initial calibration points. To account for small deviations between trials, intermediate single-point quick calibrations are performed to realign the parameters and .

In first tests this system seemed worked well, but it was susceptible to changes in computer screen brightness introduced by the presented stimuli. While the best solution is to use a frontal brightness sensor and extend the model accordingly, as a quick fix the quick calibration was augmented with a highly degraded preview of the next stimulus, just enough to keep the brightness level stable.

# Study 1: Accuracy of the QuadBright algorithm

The first study was conducted to evaluate the accuracy of the QuadBright algorithm. The algorithm was tested on a 36 participants, who were asked to glance at an orange target on a white background, moving in a random pattern between 24 positions in a six-by-four grid.

## Methods

The experiment was carried out with the YET Zero prototype. A headmount was constructed from an old headphone and a kitchen paper roll was used as a chin rest. Participants were seated in 45cm viewing distance using a 16:9 screen with a 41cm diagonal. The experiment consisted of 24 trials per condition. The target moved in a random pattern between 24 positions on the screen. The participants were asked to follow the target with their eyes. The QuadBright algorithm tracked their eye movements and the accuracy of the algorithm was measured by calculating the angular standard error of predicted eye movements of the participants.

The original experiment tested three lighting conditions (visible, infrared, no light), as well as consistent/inconsistent screen brightness levels at quick calibration. As expected, inconsistent brightness levels led to a strong decline in accuracy, whereas the light source conditions differed very little. For the analysis here, data from inconsistent background brightness was discarded and the lighting conditions were pooled. Full details of the experiment can be obtained from Bender & Schmettow (2024).

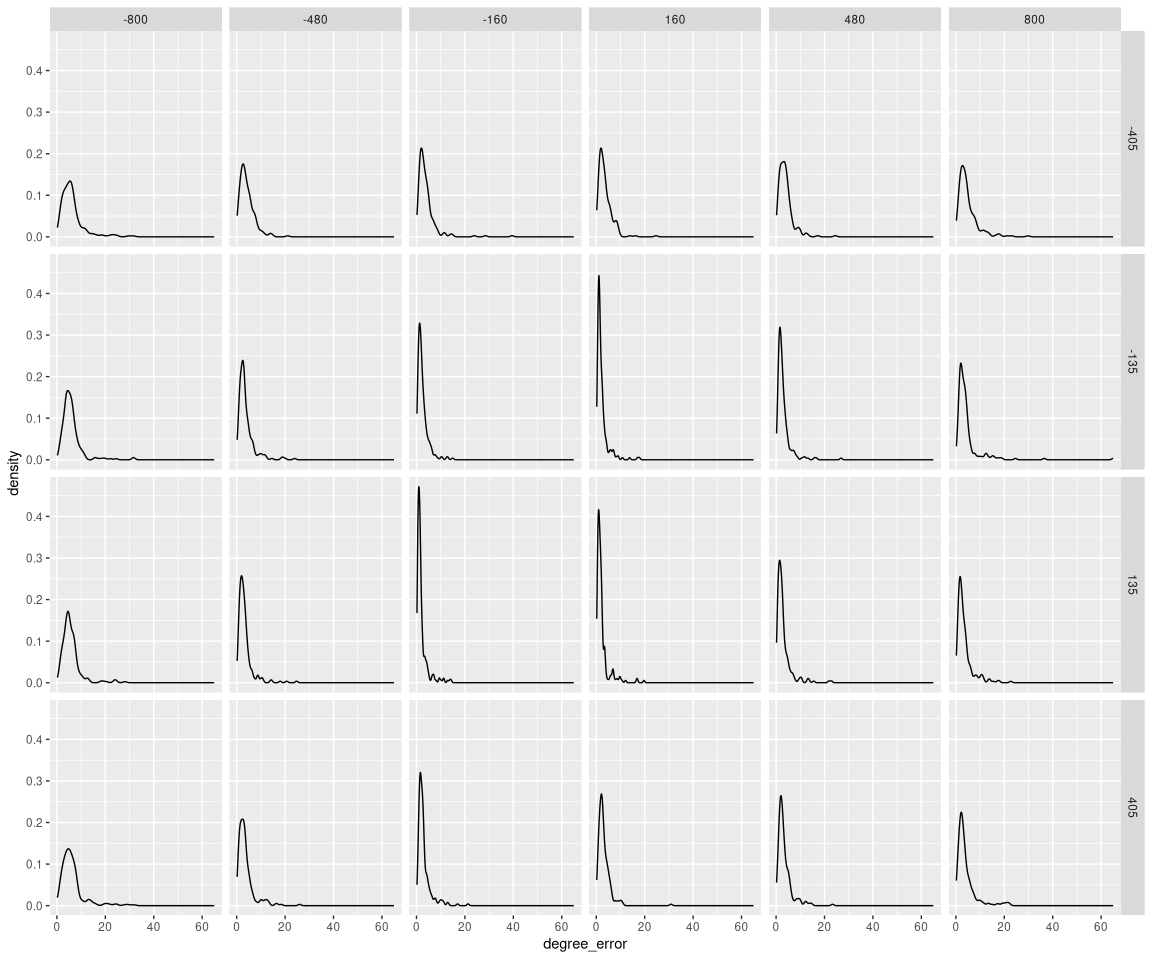
A multi-level linear model was used to analyze the data, with random intercepts for participants and target positions. The dependent variable was the degree error, calculated as the angular distance between the actual target position and the predicted gaze position. The model was fitted using the lme4 package in R.

|  |
| --- |
| Figure 1: Measurement error by target position. Histograms show the distributions of angular errors (in pixel), with a density distribution shown in Red. Blue vertical lines indicate the median accuracy. Note the logarithmic scale on the x-axis. |

## Results

The effectiveness of the Quadbright method is measured as degree errors between real target position and measured position. The sample median of degree errors 2.7 degree, with a mean of 3.2 degree. 95 percent of all measurements are below 10.3 degree error. Extreme errors mostly occurred on three (out of 36) participants.

|  |
| --- |
| Figure 2: Distribution of degree errors across all trials and participants. Vertical lines indicate the mean (green), median (blue) and 95% quantile (red). Note the logarithmic scale on the x-axis. |



We ran a polynomial multi-level model with Intercept to map angular errors to target positions. To account for the curvature of measurement error across the screen, we used a second-order polynomial term, where the intercept represents the point of minimum angular error in screen center. To account for individual differences, we included the same term on participant level (random effects).

In the center of the screen the error is xy. Both square terms are positive, which means the error increases towards extreme positions. However, the linear terms are both positive, which means the point of minimum error is xy to the right and xy up from screen center, with quite some uncertainty.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Table 1: Coefficient estimates with 95% credibility limits   | fixef | center | lower | upper | | --- | --- | --- | --- | | Intercept | -1.2614164 | -2.7666335 | 0.4749971 | | x\_linear | -0.0009461 | -0.0012579 | -0.0006482 | | x\_square | 0.0000036 | 0.0000025 | 0.0000050 | | y\_linear | -0.0006679 | -0.0011998 | -0.0001857 | | y\_square | 0.0000049 | 0.0000029 | 0.0000069 | |

The model predicts the degree error in the center of the screen to be 2.3 degree, with a high level of certainty ([Table 1](#tbl-fixef-M1)). The square terms for both axis are positive, which means that the error increases towards extreme positions. The linear terms are both negative, which means there is a lateral difference, with the largest error in the lower, mount-side (non-nasal) corner.

[Figure 3](#fig-predicted-degree-error) shows interpolated degree errors per participant. While for all participants the horizontal and vertical errors is lowest near the center region, there appear to be strong individual differences in the curvature. At the same time, there is a surpising lack of crossings between the individual curves, which means that participants with low error in the center region also have low error in extreme positions.

|  |  |  |  |
| --- | --- | --- | --- |
| |  | | --- | | (a) Horizontal | | |  | | --- | | (b) Vertical | |

Figure 3: Predicted degree error by target position and participant. Points show center estimate per trial with LOESS lines for interpolation.

In conclusion, eye tracking using the Quadbright algorithm typically produces accuracy in the range of 2-5 degree error. This is a magnitude above what is achieved by commercial eye tracking devices using corneal reflections (e.g. Pastel et al. (2021)), but in the same range as other video-oculographic devices (Heck et al. (2023)). In the study of Gale & Monk (2000) similar levels of accuracy were observed on participants when they judged glance directions from eye and head positions. Another similarity is the effect of eccentricity on accuracy, which has been observed for human participants by Loomis et al. (2008). Altogether, the Quadbright device qualifies as a candidate model for human eye direction reading.

## Study 2: Human glance perception with QuadBright information

The second study tested the possibility that human direction reading uses a Quadbright device by a gaze reading experiment, where accuracy was measured in a control condition and in a condition where eye regions were reduced to four brightness levels. To approximate the depth of processing in both conditions, exposure times were varied from 70 milliseconds to one second.

### Experimental design

In this experiment, participants see a frontal face glancing at the hours positions on a clock face (**?@fig-X-a**) and are asked to read the correct hour position. The Quadbright condition was created by masking the eyeball region by a two-by-two grid of brightness levels (**?@fig-X-b**). A Python script using the library (**OpenCV?**) was used to automate the task (**Julian?**). Exposure times varied in five steps (70, 140, 400, 600 and 1000 milliseconds).

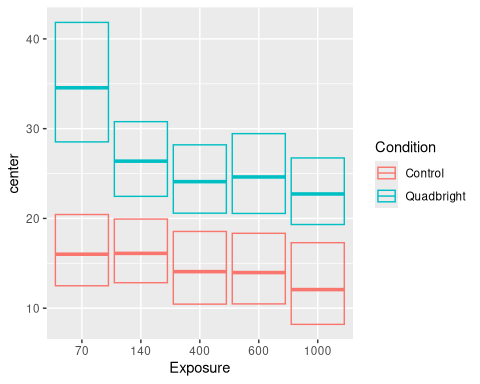
### Sample

### Data analysis

The outcome variable is the deviations between true and reported hour positions, resulting in a discrete outcome. A two-factorial linear term with conditional effects for exposure time and QuadBright degradation was used for population-level (fixed effects), as well as on Stimulus and Participant level (random effects). To account for over-dispersion, a negative-binomial outcome distribution with logarithm link function was tried first, but the extremely large reciprocal dispersion parameter suggested that the data is not over-dispersed and the final model was therefore fitted using the Poisson family. All computations were carried out using the (**brms?**) package in (**R?**).

### Results

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Table 2   | Population-level effect | center | 2.5% CrI | 97.5% CrI | | --- | --- | --- | --- | | Intercept | 15.8° | 11.9° | 20.9° | | Quadbright | 222% | 170.7% | 288.7% | | 140 | 99.7% | 89.4% | 111.5% | | 400 | 90.6% | 81.6% | 100.5% | | 600 | 89.8% | 80.3% | 100.1% | | 1000 | 81.9% | 69.9% | 93.3% | | Quadbright:140 | 75.3% | 65.6% | 86.2% | | Quadbright:400 | 75.7% | 65.7% | 87.2% | | Quadbright:600 | 78.4% | 67.3% | 91.4% | | Quadbright:1000 | 78.6% | 67.6% | 93.1% | |



In [Table 2](#tbl-fixef-M4) the Intercept is the average error in the baseline condition (Control, 70 milliseconds), which is around 16° with moderate certainty. In the control condition, error rates remain stable (99.7%) with 140 ms exposure, but with 400ms and 600ms the error rate drops to around 90% and finally to 81.9%.

In the Quadbright condition with 70 ms exposure, the error is around twice as high compared to the control condition, although with considerable uncertainty. Initially, the expected degree error is around 35°. Different to the control condition, error rates take the first drop at 140ms to around 75%. From that point on, the error rates drop similarly to the control condition.

If human eye direction reading is similar to a Quadbright device, we expect that it is a universal trait in the population. Figure [Figure 4](#fig-participant-trajectories) shows the participant-level performance trajectories. Initially, all of them showed lower performance in the Quadbright condition. The second dominant effect that can be observed is an enormous variance in the Quadbright conditions. Initially, the sample appears to fall into two clusters, one in the region below 40 degree errors, and a few participants dramatically failing with Quadbright signals. Starting with 140ms, a third group appears with almost stable performance around 10 degree.

|  |
| --- |
| Figure 4 |

A related question is whether the population-level pattern is representative for all displayed eye directions on stimulus level. [Figure 5](#fig-stim-trajectories) shows that this is not so.

|  |
| --- |
| Figure 5 |

## Discussion

### Evolution of the effective sender

The Cooperative Eye Theory implies that the eyeball is a very effective sender of glance direction signals, to allow for the most simple receiver mechanisms, as these are more likely to evolve. By construction of the most simple eye tracking device that can come to mind, we tried to establish a limit on how effective the sender is.

Overall, the Quadbright device showed very similar characteristics as human observers. Overall accuracy is in the same range as observed by Gale & Monk (2000), and the effect of eccentricity is also similar. In comparison with any other method of eye tracking the Quadbright device is extremely simple in hardware and software. In fact, hardware requireḿents can be further reduced to using a single 2x2 array of brightness sensors.

Quadbright is extremely efficient in memory consumption, as it works with four brightness levels, which makes a total of 4 byte in the input buffer. Computationally, Quadbright is extremely efficient, as it uses a linear model with only 12 parameters to calculate eye directions. By the method of minimizing the sum of squares, all calculations in the process have closed solutions, requiring no costly numerical approximations, recursions, or iterative procedures.

A limitation of the first study is that the YET Zero prototype fixes the camera close to eye, which does not match the conditions of a human observer. However, extreme data reduction of Quadbright input suggests that the algorithm will work for distant images as well. While the Quadbright device is not robust to adverse lighting conditions, this may not limit the conclusions of the study, because humans light adjustment capabilities of the human visual system (and that of many mammalian clades) are superb. A straight-forward technical approximation could be the addition of a few simple brightness sensors, and add these signals as control variables to the linear model. Finally, face detection and object tracking are required to find the eye region in a face. However, these are well-established techniques in computer vision, and the human visual system is extremely good at these tasks.

The simplicity of the Quadbright device is proof that the human eyeball is an extremely effective sender of glance direction signals, to the extent that it would be hard to believe that nature has never found a similar solution.

### Evolution of the receving end

Is the Quadbright algorithm equivalent with human glance reading? Is input organized as an image of four areas and the visual system performs a series of simple linear equations? If Quadbright is a good model of human glance perception, then all humans should be able to read glance directions from brightness differences between four grey areas.

Our second study assessed the impact of Quadbright degradation on human glance reading. It showed that for most participants performance dropped significantly and for some even catastrophically. Quadbright is definitely not the mechanism that drives modern human glance reading.

This puts alternative theories of human glance reading into perspective. Kano et al. (2021) used computer vision methods to show that the human eye has excellent sender characteristics. This work can also serve as a starting point for a more complex model of human glance reading.

Anderson et al. (2016) argued that there may be different mechanisms for precise gaze triangulation and coarse judgement of direction. By using a contrast reversal manipulation they showed that the first depends on geometric cues, whereas the second depends on luminance andf motion cues. Farroni et al. (2003) observed gaze cueing effect of 4 month old infants only in moving eyes, and only when the move is preceded by direct eye contact. The latter effect bears some resemblance to the calibration procedure used in eye tracking devices. Altogether, our experiment supports the hypothesis that multiple processing modes interact in human glance reading.

(**Loomis2008b?**) found that eye direction detection is only reliable within 4° foveal eccentricity, which indicates that the EDD makes use of higher image processing features, such as edge and geometry detection. If the mechanism were instead based on brightness processing, we would not expect peripheral performance to degrade that much. Moreover, this mechanism alone would have rather limited utility in natural settings as it requires the observer to already attend to the senders eyes. In cooperative situations, especially in a group-in-action scenario, a secondary mechanism for peripheral change detection would strongly enhance the utility of the overall system.

Interestingly, some participants were not affected by the Quadbright image reduction and by tendency even performed better on a good level. This has two possible explanations: One is that Quadbright processing can be learned, and these individuals somehow have acquired this skill prior to the experiment. The second, more speculative explanation is that Quadbright processing is an innate capability that is just not present in every human.

Finally, detection of spatial and temporal brightness gradients are universal functions in habitats where light exists, and have evolved at least as often as eyes have evolved in the animal kingdom. The fact that people can read Quadbright images has implications for the question of order of evolution. We posited the conundrum that the white sclera has a much higher chance of appearing through a one-point mutation than the eye direction detector (EDD), but it would only stay with an immediate benefit. Our observations support scenarios, where the white sclera started as a cue for an existing receiver mechanism based on brightness processing, providing the necessary baseline reciprocity for a specialized EDD to evolve.

### Future research

Speculating about how receiver mechanisms evolved, and how many there exist is fascinating, but much more research needs to be conducted to make good for the fact that you cannot truly experiment with evolution. The eye tracking device, we developed, can be used to emulate other algorithms, for example using more fine-grained brightness distributions (“Hexabright”) or processing geometric cues.

The dominant effect of the Quadbright manipulation is how differently it acts on individuals. The divide spans two magnitudes and must therefore have correlates in everyday performance. We would expect that performance in the Quadbright condition is correlated with the ability to read glances under poor conditions, for example with peripheral viewing or when the sender is wearing glasses.

Studying how people read glances to establish shared attention also has impact in at least two modern fields of application. One problem with the emerge of automated cars is how they can effectively communicate with humans. For example, making eye contact is often observed in communication between drivers and street-crossing pedestrians. External human-machine interfaces (e-HMI) are displays have been tested for communication on the outside of cars, which communicate with pedestrians through text, icons and facial expressions. Understanding glance processing can be used to design efficient animations, which are perceived as glances.

Another field of application is the design of artificial faces. In social robotics, robot faces are often designed to be expressive, and the role of glance reading in human-robot interaction is well established. However, designing more human-like eye regions for this purpose may result in an adverse effect known as the Uncanny Valley. Artificial faces that are too human-like, but not quite right, are perceived as creepy. The results of this study suggest that degraded eye regions can convey glance directions, which could facilitate the quality of interactiuon, without falling into the Uncanny Valley.

Finally, the eye tracker we build to test our ideas about the receiving end has already been used extensively for bachelor-level student projects. With some refinement it could deliver sufficient accuracy for many psychological experiments and applied research studies, with the added benefit of being much easier to replicate for everyone than with using commercial eye tracking devices.

# References

Anderson, N. C., Risko, E. F., & Kingstone, A. (2016). Motion influences gaze direction discrimination and disambiguates contradictory luminance cues. *Psychonomic Bulletin and Review*, *23*, 817–823. <https://doi.org/10.3758/s13423-015-0971-8>

Babinet, M.-N., Cublier, M., Demily, C., & Michael, G. A. (2021). Eye direction detection and perception as premises of a social brain: A narrative review of behavioral and neural data. *Cognitive, Affective, &Amp; Behavioral Neuroscience*, *22*(1), 1–20. <https://doi.org/10.3758/s13415-021-00959-w>

BARON-COHEN, S. (1995). The eye detection detector (EDD) and the shared attention mechanism (SAM) : Two cases for evolutionary psychology. *Joint Attention : Its Origin and Role in Development*, 41–59. <https://cir.nii.ac.jp/crid/1572261550899222144>

Bender, F. R., & Schmettow, M. (2024). *Evaluaton of the low budget do it yourself eye tracking system: Your eye tracker (YET) human factors and engineering psychology* [PhD thesis, University of Twente]. <https://purl.utwente.nl/essays/104538>

Ciesla, M., & Koziol, P. (2012). Eye pupil location using webcam. *Computer Vision and Pattern Recognition*, 1–11.

Dessinioti, C., Stratigos, A. J., Rigopoulos, D., & Katsambas, A. D. (2009). A review of genetic disorders of hypopigmentation: Lessons learned from the biology of melanocytes. *Experimental Dermatology*, *18*(9), 741–749. <https://doi.org/10.1111/j.1600-0625.2009.00896.x>

Farroni, T., Mansfield, E. M., Lai, C., & Johnson, M. H. (2003). Infants perceiving and acting on the eyes: Tests of an evolutionary hypothesis. *Journal of Experimental Child Psychology*, *85*(3), 199–212. <https://doi.org/10.1016/s0022-0965(03)00022-5>

Farroni, T., Massaccesi, S., Menon, E., & Johnson, M. H. (2007). Direct gaze modulates face recognition in young infants. *Cognition*, *102*(3), 396–404. <https://doi.org/10.1016/j.cognition.2006.01.007>

Farroni, T., Massaccesi, S., Pividori, D., & Johnson, M. H. (2004). Gaze following in newborns. *Infancy*, *5*(1), 39–60. <https://doi.org/10.1207/s15327078in0501_2>

Gale, C., & Monk, A. F. (2000). Where am i looking? The accuracy of video-mediated gaze awareness. *Perception & Psychophysics*, *62*, 586–595. <https://doi.org/10.3758/BF03212110>

Guilford, T., & Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour*, *42*, 1–14. <https://doi.org/10.1016/S0003-3472(05)80600-1>

Heck, M., Becker, C., & Deutscher, V. (2023). Webcam eye tracking for desktop and mobile devices: A systematic review. *Proceedings of the 56th Hawaii International Conference on System Sciences*. <https://doi.org/10.24251/HICSS.2023.825>

Kano, F., Furuichi, T., Hashimoto, C., Krupenye, C., Leinwand, J. G., Hopper, L. M., Martin, C. F., Otsuka, R., & Tajima, T. (2021). What is unique about the human eye? Comparative image analysis on the external eye morphology of human and nonhuman great apes. *Evolution and Human Behavior*, *43*(3), 169–180. <https://doi.org/10.1016/j.evolhumbehav.2021.12.004>

Kobayashi, H., & Kohshima, S. (2001). Unique morphology of the human eye and its adaptive meaning: Comparative studies on external morphology of the primate eye. *Journal of Human Evolution*, *40*(5), 419–435. <https://doi.org/10.1006/jhev.2001.0468>

Krafka, K., Khosla, A., Kellnhofer, P., Kannan, H., Bhandarkar, S., Matusik, W., & Torralba, A. (2016). Eye tracking for everyone. *IEEE Conference on Computer Vision and Pattern Recognition (CVPR)*. <http://gazecapture.csail.mit.edu.>

Laidre, M. E., & Johnstone, R. A. (2013). Animal signals. *Current Biology*, *23*, R829–R833. <https://doi.org/10.1016/j.cub.2013.07.070>

Loomis, J. M., Kelly, J. W., Pusch, M., Bailenson, J. N., & Beall, A. C. (2008). Psychophysics of perceiving eye-gaze and head direction with peripheral vision: Implications for the dynamics of eye-gaze behavior. *Perception*, *37*(9), 1443–1457. <https://doi.org/10.1068/p5896>

Mayhew, J. A., & Gómez, J. (2015). Gorillas with white sclera: A naturally occurring variation in a morphological trait linked to social cognitive functions. *American Journal of Primatology*, *77*(8), 869–877. <https://doi.org/10.1002/ajp.22411>

Mearing, A. S., Burkart, J. M., Dunn, J., Street, S. E., & Koops, K. (2022). The evolutionary drivers of primate scleral coloration. *Scientific Reports*, *12*(1). <https://doi.org/10.1038/s41598-022-18275-9>

Pastel, S., Chen, C. H., Martin, L., Naujoks, M., Petri, K., & Witte, K. (2021). Comparison of gaze accuracy and precision in real-world and virtual reality. *Virtual Reality*, *25*, 175–189. <https://doi.org/10.1007/s10055-020-00449-3>

Singh, H., & Singh, J. (2012). Human eye tracking and related issues: A review. *International Journal of Scientific and Research Publications*, *2*. [www.ijsrp.org](https://www.ijsrp.org)

Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: The cooperative eye hypothesis. *Journal of Human Evolution*, *52*, 314–320. <https://doi.org/10.1016/j.jhevol.2006.10.001>

Wolf, W., Thielhelm, J., & Tomasello, M. (2022). Five-year-old children show cooperative preferences for faces with white sclera. *Journal of Experimental Child Psychology*, *225*, 105532. <https://doi.org/10.1016/j.jecp.2022.105532>

Yorzinski, J. L., Thorstenson, C. A., & Nguyen, T. P. (2021). Sclera and iris color interact to influence gaze perception. *Frontiers in Psychology*, *12*. <https://doi.org/10.3389/fpsyg.2021.632616>

Zhou, Z.-H., & Geng, X. (2004). Projection functions for eye detection. *Pattern Recognition*, *37*, 1049–1056. <https://doi.org/10.1016/j.patcog.2003.09.006>