The STANDARDIZED HUMAN EYE

Measured values for in vivo humans except as noted

James T. Fulton

Appendix L of "Processes in Biological Vision"

ABSTRACT: A comprehensive graphic and tabular review of the human eye in 11 categories. An expansion of the archaic tabulations of Gullstrand (1908) and LeGrande (1946), that have never addressed the full field of view of the human eye, is provided. The optical system is expanded from 2 to 4 distinct elements. The measured acuity of the eye as a function of eccentricity is shown. The highest acuity region of the retina is the 1.2 degree diameter foveola behind the fixation point. The acuity achieved by the telephoto capability of the foveola/field lens combination is documented. Understanding the function of the field lens is crucial to understanding the measured performance of the human eye compared to the "acuity" of eagles and other birds of prey. The individual chromophores of vision are described in detail. The parameters of the retina are tabulated. The parameters of the ocular-motor system are summarized. The dynamic parameters of the photoexcitation/de-excitaton equation of transduction are described. The mechanism of adaptation (bleaching) is defined. The electrolytic parameters of the photoreceptor neurons are described. The organization of the optic nerve is presented. The performance parameters of stereoptic vision are summarized. Citations to supporting sections of "Processes in Biological Vision" are provided.

KEYWORDS: Human Vision, ocular optics, retina, chromophores, histology, cytology

REFERENCES TO SECTIONS beginning with a numeric indicate a Chapter in "Processes in Biological Vision" available on line at https://neuronresearch.net/vision/ by clicking on *Download Chapters* on the left navigation panel.

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Excerpts from

PROCESSES IN BIOLOGICAL VISION

including,

ELECTROCHEMISTRY OF THE NEURON

This material is excerpted from the full β-version of the text. The final printed version will be more concise due to further editing and economical constraints.

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The STANDARDIZED HUMAN EYE

Measured values for in vivo humans except as noted

See also note 1 at the end

This tabulation is divided into a series of subparts:

I OPTICS
II RETINAL MOSAIC
III PHOTODETECTOR CELLS
IV SIGNAL PATH PARAMETERS
V OPTIC NERVE PARAMETERS
VI MOTOR PARAMETERS
VII CIRCULATION PARAMETERS
VIII RESOLUTION/ACUITY PARAMETERS
IX BINOCULAR PERFORMANCE PARAMETERS
X PERCEPTION PARAMETERS
XI PRECISION OPTICAL SERVO SYSTEM PERFORMANCE

Characteristic Value Comment

I OPTICS (Chap. 2.4)

The human optical system is a highly anamorphic wide-angle system. It provides a very wide angle (over 100 degrees horizontally in each eye, over 190 degrees total angle) sensing capability at low resolution for purposes of awareness and alarm mode operation. It provides a very narrow angle (1.2 degrees) sensing capability at high resolution for purposes of analysis. Its wide angle capability is seldom described in detail. **Figure 1.1.1-1** shows the wide angle anamorphic capability of the eye based on one Le Grand model reproduced in Lotmar 1971. The optics are both non-spheric (differing significantly from a spheric form) and aspheric (differing marginally from their simple mathematical form). The cornea is an aspheric section of an ellipsoid with its long axis parallel to the optical axis. The “crystalline” lens is an asymmetrical aspheric based on two spherical shapes and employing graded index of refraction as a function of its radius, GRIN, technology.

The formulas usually found in the literature only apply to the “reduced eye” meaning the performance of the eye within one degree of the optical axis. This is the region where the performance can be calculated reasonable correctly using “thin lens” optical equations. The formula of Le Grand, and of Gullstrand are for the reduced eye. This designation refers to the thin lens, Gaussian, or paraxial optical analysis that only applies where sinx = x.; the equations only apply within 1 degree of the optical axis. They do not apply to the peripheral performance of the human eye. The reduced eye does not even apply to the foveal pit and foveola which are more than 5 degrees from the optical axis. The 1.2 degree diameter foveola forms the high acuity central cone of vision.

The models of Gullstrand and of LeGrand did not address the “field lens.” The field lens is formed by the curvature of the “inner limiting membrane” of the retina and the difference in index of refraction between the “vitreous humor” filling the globe of the eye and the neural tissue of the retina.

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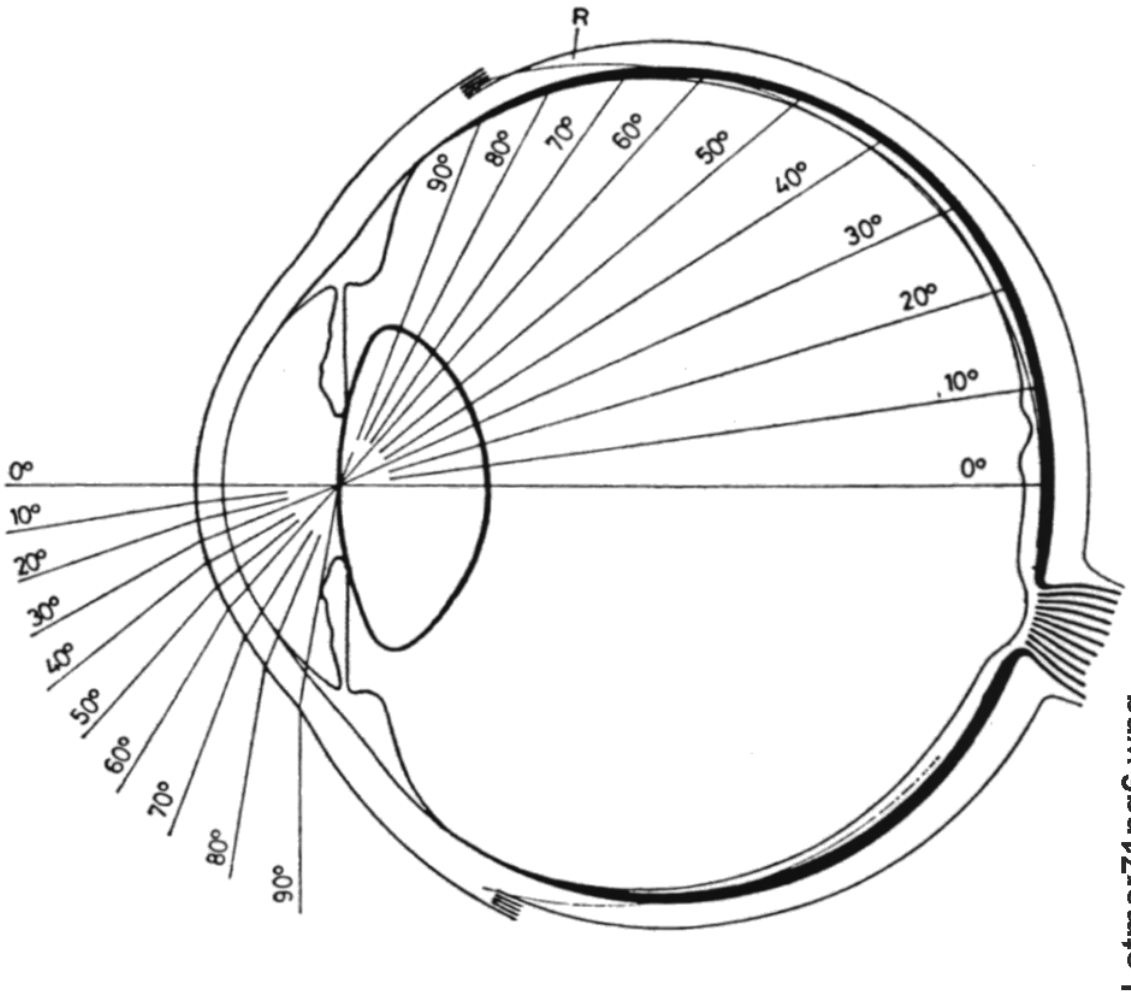

The figure above is meant to emphasize the overall capability of the human eye. Its broad angular field of view combined with superb on-axis acuity are unmatched.

The following figure exhibits how the unmatched visual–axis acuity is achieved. The introduction of a field lens, formed by the walls of the foveal pit, implements a telephoto type telescope within the eye. This telescope has a field of view of less than 3 degrees in diameter centered on the point of fixation. When combined with the 1.2 degree foveola, they account for the well documented peak in the acuity of the eye within this small angle. The peak represents an increase in acuity of between 3:1 and 7:1 over the acuity of the adjoining retina.

Both of these figures are discussed in detail in Section 2.4 of Chapter 2 of "Processes in Biological Vision"

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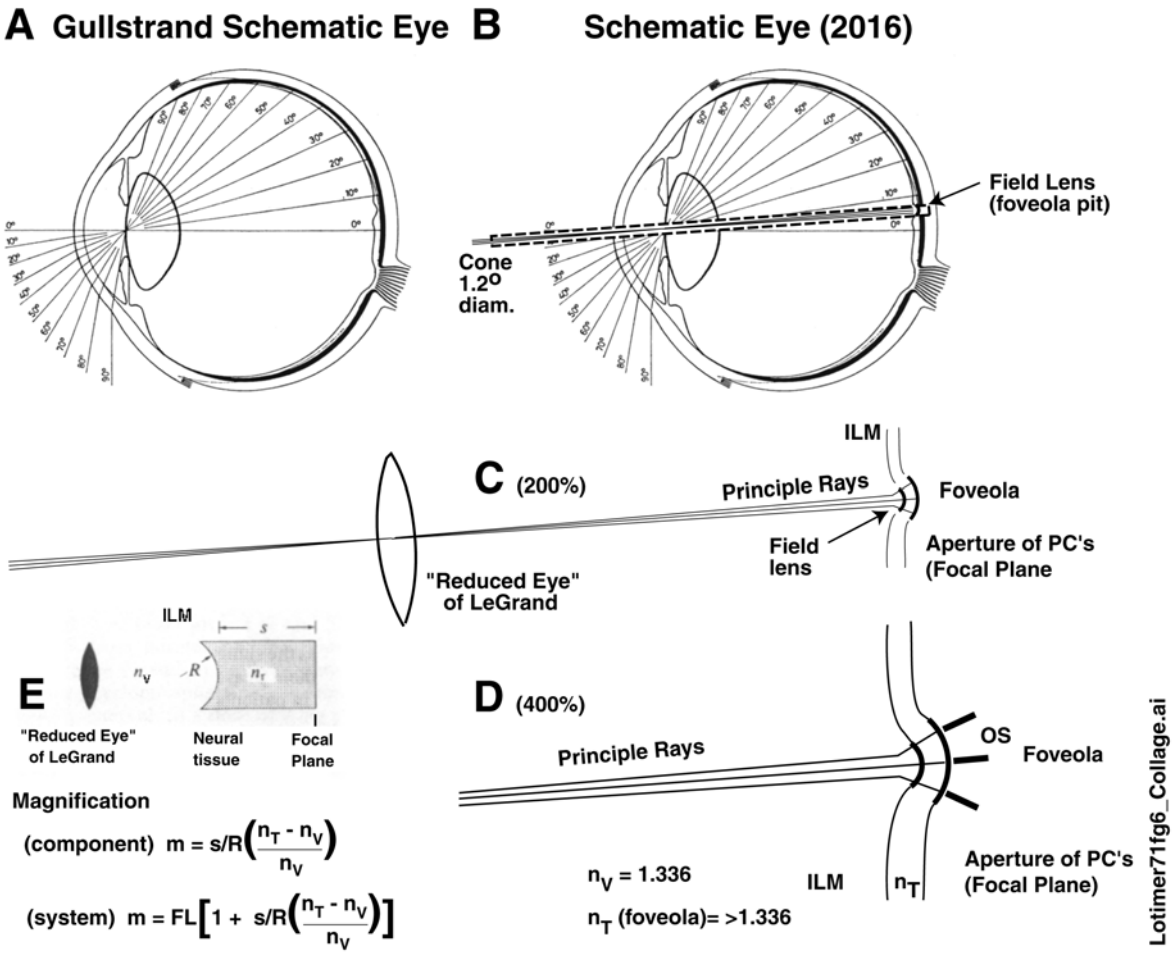

Type: Broadband, immersed, anamorphic, afocal, 4-element with field lens & collimator **

Cornea (element 1)	43 diopters	on-axis, varies with field angle
index of refraction	1.3771/1.336	True/Simplified Eye
surface classification	elliptical	
Crystalline Lens (element 2)	16-26 diopters	on-axis, varies with accommodation and field angle
index of refraction	variable	both axially and radially, see text
surface classification	elliptical	
Field Lens at foveola (element 3)	up to 7:1 magnification Radius of curv.~250 μ	curvature of inner limiting membrane forms a lens but also introduces geom. distort.
Collimator array (element 4)	2.0 μm. diam. sphere	"ellipsoid" in front of many PC
Spectral Width	<405-->1300 nm.	Between ½ amplitude points relative to Rayleigh scattering level
Average in-band transmission	>90%	405 to 1200 nm.

Iris opening, max. to min. 7.0+ to 2.0- mm.		
time constant, open/close	6.0 sec./1.2 sec.	
Focal length of main group		
paraxial F. L. (LeGrand)	22.2888 mm.	(no accommodation, also "image F.L".)
Complete focal equation.	(F. L.)cos θ mm.	lens power varies with angle θ **(in image space**) to maintain focus on a quasi-spherical retina

In object space, the F.L. is divided by the index of refraction (1.336) and the angle is multiplied by the index. Therefore the object F. L. is given by 16.68 cosΘ where Θ =1.336 x θ

Depth of focus (on-axis, diffr. limit)	+/- 8.0 μm.	+/- 3.0 μm @ f/2.4; +/-17.0 μm @ f/8.5
Back focal length (no accom.)		
Geometric demagnification	450:1	Numeric is on-axis value--at 10 meters.
Snell's Law demagnification	1.33:1	Due to immersion optics
Total demagnification	600:1	On-axis value, without field lens/collimator
Field lens		consisting of neural tissue and supporting tissue in the optical path. Typical thickness 500 μ thinning to 100 μ in Foveola
(including the macula lutea)*	2.0 mm horiz./0.88 mm vert.	yellowish in color
Collimator lens	2.0 μ diam.	spherical lens, index = 1.40 or higher
Effective Focal Length	~8 μ (an immersed lens)	nominally fixed, value not critical

* See "Retinal Topography" below for alternate dimensions.
** This optical description incorporates the parameters of Gullstrand's Schematic Eye (1908). Upon elimination of the collimator lens, the field lens, the continuous gradient index of refraction for the lens, and limiting the field angle to ~1.0; the resulting simplified paraxial (Gaussian) optics is identical to that of Gullstrand. Gullstrand used an index of refraction which varied by zone in his calculations. The resulting values are also very similar to those of LeGrand's Full Theoretical Eye which used a single index of refraction for the lens.

Rabbetts' "Clinical Visual Optics" (1984 & 2007) provide much more detailed parametric values than here.

With the availability of the data of both Blaker (1980) and Glasser & Campbell (1998), it is no longer appropriate to use a static model of the eye. Equations are available describing the change in focal length and spherical aberration as a function of age.

Introduction of the Field Lens and resulting Telephoto generated increase in foveola acuity

The field lens occurs in two distinctly different configuration within the animal kingdom. It is used primarily to increase the acuity of the eye among the anthropoids (humans and a few Old World Primates) and to provide a superior motion detector among the eagles, falcons and a few other birds of prey. These features are developed in detail in **Section 2.4.4**. The author recently encountered a failure in the application of the field lens following a detachment of the retina from the choroid of the left eye (reported in **Appendix ZH** of this work)

Tabulation of individual optical parameters. Based generally on Westheimer (1972)

The following values are for educational purposes only. They are not adequate for optical design purposes where five decimal place accuracy is needed. See Chapter 2 of the text or contact the author for more precise values.

Refractive indices (at 500 nm.)

These values are a function of wavelength and temperature
``

Air	1.000(32)
Cornea	1.376
Aqueous humor	1.336

lens (average)	1.386	
vitreous humor	1.336	
Muller cells	1.380	In foveola where they are the dominant tissue forming the field lens
Photoreceptors	1.406	In some portions of the inner segment, IS, leading to the OS waveguide

The lens is formed of a material of variable index with respect to both radius and axial position. Therefore, the above index is an average. Smith, W. gives 1.406 for the maximum index of the lens. Glasser & Campbell have recently determined an "equiv. refractive index" of 1.4160 based on their curve fitting a paraxial equation to each surface of the lens. The wavelength was not specified in their 1999 paper. It was 632.8 nm in a 1998 paper. This 2% difference from above is too large to be assigned completely to chromatic dispersion in the lens material. The various calculations used do not exhibit sufficient precision to be relied upon. Good optical design and analysis work usually requires 5 place accuracy.

Details of the indices for the zones of the photoreceptor cell are shown in **Figure 2.2.2-6**

Diopter power of surfaces for simple lens of constant index of refraction

The following numbers are based on LeGrand. See the next paragraph for more realistic values.
These numbers are based on curvature and do not recognize the change of index of refraction across the cornea. The net of 58 diopters corresponds to a focal length of 17.24 mm in air. When the index of the aqueous and viscous humors are introduced, the focal length becomes 22.2888 and the net power of the cornea and lens are reduced to about 45 diopters. The numbers are for the un-accommodated state.

anterior surface of cornea	+49D
posterior surface of cornea	-6D
anterior surface of lens (nominal)	+6D
posterior surface of lens (nominal)	+9D

Prescription for the axial gradient index lens representation of human eye (from Blaker, 1980)

Element	Unaccommodated	Accommodated
Power	60.80 D	70.06 D
First Principal point	1.532 mm	1.839 mm
Second Principal point	1.737 mm	2.052 mm
First nodal point (Gaussian only)	7.049 mm	6.635 mm
Second nodal point (Gaussian only)	7.240 mm	6.936 mm
Focal plane	23.71 mm	21.12 mm
Near point		11.76 cm (4.6 inches)

Accommodation range of eye (From Blaker quoting Fincham)

Individual eyes	accommodation range
#1, 20 year old male eye	11 D
#2 20 year old male eye	9 D

Absorption of the lens in the region of 310-400 nm

Average peak value	3.5 optical density units	See Chapter 6
Average absorption	0.7 optical density units per mm.	

Lapuerta & Schein have provided smilar data for the macaque monkey (*Macaca fascicularis*) of 3 to 4.5 kg. Their calculations were based on Gaussian optics only and less than 4 digit precision calculations[1]. Gaussian optics are not adequate for the wide field of view of primate eyes. Their cornea was assumed to be spherical! They were well aware of the limitations of Gaussian optics and provide citations to the calculations of others.

[1]Lapuerta, P. & Schein, S. (1995) A four-surface schematic eye of macaque monkey obtained by an optical method *Vision Res* vol 35(16), pp 2245-2254

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Diffraction Limited Spot Size

On axis (nominally encompassing the foveola) the lens of the young adult human eye appears to be diffraction limited. However, good measurements defining the optimum diameter of the pupil for the smallest diffraction limited spot size has not been found in the literature. With a maximum pupil diameter of 7 mm and a nominal focal length of 22.2888 mm, the corresponding *F*-number would be 3.18. At a wavelength of 500 nm (in the green), the resulting Airy Disc would be nominally two microns in diameter. This is a good match for the nominal diameter of the photoreceptors taken here as 2.0 microns in diameter.

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II RETINAL MOSAIC (Chap. 3)

Retinal Topography

Zones of the Retina (following Hogan, 1971)

....**Central**

Area	Diameter	Diam in PC's	Area in PC's	External Angle
Foveola	0.35 mm diam	~175	~23,000	1.18°
Fovea	next zone out to 1.85 mm diam.	~750	~4 x 10^5	8.68°
Parafovea	next zone out to 2.85 mm diam.	~1,250		14.4°
Perifovea	next zone out to 5.85 mm diam.	~3,000		

....**Peripheral**

Near periphery	1.5 mm zone around the central retina
Mid periphery	3.0 mm zone around near periphery
Far periphery	9-10 mm wide on temporal side, 16 mm wide on nasal side
Ora serrata	2 mm wide on temporal side, 0.7-0.8 mm. wide nasally

....Macula (a.k.a. Macula Lutea)

Overlay of retinal area 2.0 mm. wide (~8 degrees) and 0.88 mm. vertically (~3.5 degrees) centered on the Fovea Glaser (1999) described the macula as 25 degrees in diameter with the fovea described as a 5 degree disk containing a smaller foveola. See **Section 2.2.2**. Generally believed to be colored due to presence of cytoplasmic inclusions of Xanthophyll. See **Section 3.2.1.3.3**.

[The generic term macula used in the clinic corresponds to the area within the parafovea in most cases. The size of the macula is seldom given a specific diameter in the literature. In 1977, Bunt specifically labeled a circular area with a diameter of 6 degrees centered on the point of fixation as defining the macula. In more recent times (1980's forward), many clinicians have described a macula of 2–3 degrees diameter based on the prominent ring of vascularization surrounding the foveola and overlaying the inner circular region of the fovea.]

Midena, writing in 2007 uses the term macula in a generic form and labels the "macula at 8 degrees diameter," "macula at 10 degrees diameter," etc. out to 22 degrees. See **Section 2.2.2.2**.

The values above are based on the Gullstrand Schematic Eye (1911) and do not include the magnification present due to the field lens in the new Schematic Eye (2016).

Total number of photoreceptors

The number of photoreceptors per eye varies from 106 million (Newell, 1986, pg 88) to about 100 million (Rodieck, 1998, pg 14) to 54 million (Glaser, 1999, pg 8) depending on author. The order of magnitude is the important value.

Retinal Placement of photoreceptors

The arrangement of photoreceptors within the retina is poorly understood at present. The global array appears to be a fractal pattern. The sub-arrays associated with each spectral range have only in 2019 been documented by Zhang et al., including an "unidentified" spectral type; this unidentified type probably corresponds to the UV spectral type common to all mammals. They found the sub-arrays to lack any recognizable organization. See **Section 3.2.4**.

The overall array in the foveola can be described in terms of a close-spaced array of hexagonal and pentagonal units formed by the photoreceptors. The pattern is that found on a sewn basketball or volleyball. The density of this configuration can be described in terms of a Nyquist frequency associated with each axis of the array. The Nyquist frequency along each major axes of the array, in the foveola, is 108-100 cycles/degree in humans. A higher Nyquist frequency of 125-128 cycles/degree has been found along one axis perpendicular to one of the three principle axes.

See **Section 16.6.3.5**. Whether this higher frequency is found in all subjects is not currently known.

Retinal Cross-section (following Rodieck, 1973 -vitreous humor to choroid)

Inner Limiting Membrane	chemical isolation: vitrea from INM
Optic fiber layer	axons of ganglion cells
Ganglion cell layer	ganglion cells
Inner plexiform layer	bipolar to ganglion connections/lateral cells
Inner nuclear layer	bipolar/lateral cells
Outer plexiform layer	dendrites of bipolar cells/lateral cells
(synapse area)	pedicels and spherules of photoreceptors
Fiber layer	axons of photoreceptors
Outer nuclear layer	photoreceptor cell nuclei
Outer limiting membrane	isolation; IPM from INM
Inner segment layer	translation region
Outer segment layer	transduction region
Retinal epithelium layer	chromophore production & maintenance
Bruch's membrane	chemical isolation; retina from choroid
Choroid	structural support

Total thickness between the Inner Limiting Membrane & Bruch's membrane varies from 0.11 mm. at the edge to 0.23 mm. adjacent to the Foveola. Within the foveal pit, the thickness is reduced to on the order of 150 microns.

III PHOTODETECTOR CELLS (Chap. 4 & 5)

Type: Neuro-secretory cell with attached quantum-mechanical transducer

Secretory function

Secretes structural protein, Opsin which provides a spaceframe of disks to hold transducer material. A part of the inner segment. In foveola, inner segments are typically have the shape of a truncated cone and are 40-50 microns long. Their minimum diameter matches that of the outer segment at their junction

Absorption function structure

The outer segment varies in size considerably with position in the retina. Polyak (1957) presented the broadest discussion of these measured sizes. The minimum diameter is found at the very center of the foveola and may only include a few hundred outer segments, they exhibit a minimum diameter of 2.0 microns, as required by their waveguide character, and a length of up to 75 microns. Much of the retina is populated with outer segments of 3-4 microns in effective diameter. The values below are nominal for the foveola to allow a consistent discussion in the text.

Spaceframe (cylindrical disk stack)	50 μm x 2.0μm diam.	2000 disks, 250 Angstrom spacing
Angular cross-section (fl=22.28)	0.09 milliradians	0.3 arcmin, 18.5 arcsecs.
Aspect ratio of stack	25:1	nominal
Disk thickness	220 Angstrom	at the fold
	160 Angstrom	at the center
Protein (Opsin) thickness	64 Angstrom	single layer
Coating thickness	15 Angstrom	each side of each disc
Chromophore mol. diam.	5 Angstrom	
Disk formation rate	10 per hour/stack nominal / warm blooded mammals	
Disk transport velocity	300 nm/hr–7.2 μ/day	
Disk operating life	7 days	nominal/ warm blooded mammals

The total number of chromophore molecules per outer segment is approximately $4 \cdot 10^{10}$ (**Sec. 4.3.5.3.5**)

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Transduction function	Two step process:		photo/excited state in transducer; Excited state/electric transfer to neuron
Transducer type: quantum mechanical			
Material	Rhodonine$_1$		1 of 4 retinoids emanating from the retinal pigmrnt epithelium and coating discs of above spaceframe as a monomolecular liquid crystal.
Anisotropic Spectral Peak** (Functional spectra)	Rhodonine 9 Rhodonine 7 Rhodonine 5	0.437 μ 0.532 μ 0.625 (0.610) μ	½ amplitude width, 0.075 μ ½ amplitude width, 0.065 μ ½ amplitude width, 0.060 μ
Anisotropic Spectral Peak (Blocked in large chordates)	Rhodonine 11	0.342 μ	½ amplitude width, ~0.080 μ
(values are accurate to two places; more specific values are given in next table)			
Isotropic Spectral Peak* (Non-functional)	Rhodonine(iso)	0.498m	½ amplitude width 0.100 m (typ.)

* The non-functional spectrum is that measured in dilute solutions of Rhodonine or when excited by light transverse to the axis of the Outer Segments. It is the spectrum usually labeled Rhodopsin in the older literature. The peak is ill-defined and variously reported as 495-502 m depending on environment. The listed width was measured with a spectrometer using a filter width of >30 nm.
** The value of 610 μ for Rhodonine(5) is based on inappropriate psychophysical flicker measurements. The value may also be affected by recent (2016) x-ray crystallography showing retinol is not a planar molecule (**Section 7.1.1.4**). The value of 625 μ is the 1st order value based on a planar stick model of retinol found commonly in the earlier literature.

Active transduction materials

The chromophores of human vision are four members of the Rhodonine family of retinoids, existing in the liquid crystalline state, and derived from retinol (Vitamin A_1) available in the bloodstream. The chromophores form a film on the surface of the protein substrate, opsin, by hydrogen bonding. This film has the smectic type A structure. The unique properties of this family are directly related to the length of the resonant conjugate chain existing between the two auxochromes of each of these molecules. The following notation follows Karrer. The numbers in parentheses indicate the carbon number of the conjugated chain. See **Section 5.2.6** for alternate notations. Freshwater fish employ Vitamin A_2 and some scavengers (at least among the arthropods) use Vitamin A_3 in the formation of their chromophores.

The half amplitude wavelengths given below are nominal for a human subject. They vary with the length of the outer segments and the area of the retina stimulated. The lengths vary with position within a retina. The half amplitude values vary within a few nanometers among individuals. The variations are measurable psychophysically.

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Transducer	Resonant chain length	λ_l μ	λ_m μ	λ_h μ	Q	Half-amplitude Bandwidth in Wave numbers*
Rhodonine (5)***	5	0.595	0.625	0.655	10.4	1539 cm^{-1}
Rhodonine(7)	4	0.500	0.532	0.565	8.2	2301
Rhodonine(9)	3	0.400	0.437	0.475	5.8	3948
Rhodonine(11) [UV]	2 **	0.300	0.342	0.385	4.0	7359

where l, m and h indicate the low half amplitude point, the mid wavelength point and the high half amplitude point. The mid wavelength point is the average of the low and high values because the function is so broad that the center point is ill defined. The bands are separated by 0.095 +/-0.005 microns which is a typical spacing for these homologs.

* The bandwidths corresponding to the difference between the short and long wavelength limits of each band expressed in reciprocal wavelengths (wave numbers) are given for easier comparison with some of the literature. The common units are reciprocal centimeters.
**The UV photoreceptors of the human eye are effectively shielded by the limited transmission of the optical system. They do influence the spectral discrimination capability of the eye in the region between 400 nm. and 437 nm.
*** See footnote to the above table concerning Rhodonine(5).

The above values can also be presented in terms of electron-volts of energy.

Transducer	Resonant chain length	λ_l ev.	λ_m ev.	λ_h ev.	Q
rhodonine (5)***	5	2.083	1.983	1.892	10.4
rhodonine(7)	4	2.479	2.329	2.194	8.2
rhodonine(9)	3	3.098	2.836	2.609	5.8
rhodonine(11) [UV]	2 **	4.132	3.624	3.219	4.0

To express the above wavelengths in terms of energy per mole, the equation $X= (1.2 \times 10^5)/\lambda(nm)$ kJ/mol. can be used.

The molecular weight of the chromophores are:

rhodonine(5)	285
rhodonine(7)	299
rhodonine(9)	285
rhodonine(11)[UV]	299

Translation function

Band gap of microtubules*	2.2 eV	equiv. to 565 nm.
Quantum-mechanical/electric	high gain	junction type transistor, typically 220:1 electron (current) amplification

Synaptic function @ pedicel

Electrotonic synapses containing multiple synaptic disks

Synaptic disk diam.	0.3-0.5 microns	Each contains a hexagonal array of Activa (frequently labeled boutons)
Activa diam.	50-60 Angstrom	
Activa spacing	90 Angstrom	center to center in array

Presynaptic lemma thick.	70 Angstrom	emitter of Activa
Post synaptic lem. thick.	70 Angstrom	collector of Activa
Synaptic gap	45-100 Angstrom	Base of Activa
Gap material	hydronium	
Activa type	PNP	

Mass properties of photoreceptor cells Estimates from Lolley, et. al. (1986)

Volume
Total 234×10^{-12} cm^3

Weight
Total cell $42\text{-}64 \times 10^{-12}$ g
DNA 6.4 “
RNA 2.3 “

* The 2.2 eV band gap of the microtubules is the controlling parameter that requires the L-channel sensory neuron to operate in a 2-exciton to 1-electron mode. The 2-exciton mode requires the sensory neuron to operate non-linearly.

IV SIGNAL PATH PARAMETERS (Chap. 12 & 13)

Input parameters

Usable dynamic range:	$>10^{10}$:1, as much as 10^{15}:1
Photopic dynamic range:	56000:1
Instantaneous photoreceptor dynamic range:	200:1
Usable spectral range:	400 to 650 nm.
Minimum exposure time for a single field of imagery:	0.25 to 1.25 seconds as a function of wavelength and intensity
Maximum image retention time after exposure:	Not precisely defined
Maximum image retention time in absence of tremor/motion:	3-6 seconds

Energy Threshold of Adaptation Amplifier

Nominal energy threshold of photoreceptor adaptation amplifiers 2.2 Electron-volts, equiv. to 565 nm. Not over 2.34 EV based on Sliney data

Poles and zeros of the Adaptation Amplifier

The transfer function of the adaptation amplifier is conventional. It contains both poles and zeroes.
There is a naked frequency term in the numerator of the adaptation amplifier transfer function.

This results in a “zero” in the function at - -. 0.0 Hz

Lowest frequency pole Est. 0.3-0.5 Hz
Next higher pole Est. 8-12 Hz

Time Constants

Iris-- closing 1.2 sec
opening 6.0 sec

Photoexcitation/De-excitation process
Based on the complete P/D Equation of this work, **Section 7.4**.

Intrinsic, τ 0.0125 sec. dominant during falling edge in P/D

		equation.
Dynamic, $\sigma*F*\tau$	$\sigma*F*0.0125$	dominant during rising edge of P/D equation. Where F = radiant flux in photons/sec micron^2; σ = absorption coefficient in electrons-microns^2/photon
		Product greater than 1.00 in photopic region.
absorption coefficient, σ	0.76	(From Fulton_Rushton79 fg 3.ai for the scotopic region)

Adaptation amplifier

Attack	<12.5 ms	dominant during increase in illum.

The attack characteristic is due to a "charging" circuit and depends on the illumination level.

Recovery,

1st	12.5 ms	time constant of P/D at 310 K
2st	0.1 seconds	recovery of adaptation amp. (RC of axon)
3nd (1st vascular)	2 minutes	vascular, est. from Spillmann
4rd (2nd vascular)	~10 minutes	vascular " " ""

The recovery time constants become effective at varying intensities of stimulus. The 12.5 ms recovery time constant is always present. The 3 second neural time constant only applies when the DC value of the adaptation amplifier axon has changed during stimulation. The longer time constants only apply when the vascular balance within the retina is upset.
The recovery time constants vary dramatically with position in the retina mosaic. They are a function of the impedance of the cell wall, the vascular supply and the capacitance shunting the collector of the Activa. The first time constant, interpreted from the recording of the Class C waveform by Baylor (1984), is electronic and has a value of three seconds (related to the low frequency pole given above, 0.3 -0.5 Hertz).

The 2nd through 4th recovery time constants are actually features of a single function, the exposine function, exhibiting an exponential time constant and a sinusoidal component. See **Section 17.6.1**.

Nominal pass band of signaling channels

Low frequency (RC type) pole	3 Hertz	Due to adaptation amplifier collector circuit
High frequency pole	500 Hertz	Due to operating limit of Stage 3 modulators

Nominal transmission velocity of signaling channels

Typical delay associated with the P/D Equation at photopic levels 3.36 milliseconds.

Phase velocity of tonic signals within an electrolyte ~7 millimeters/sec at 37°C

Phase velocity of action potentials along amyelinated axon 4,400 m/sec. at 37°C

Group velocity of action potential signals between regenerative nodes 44 m/sec. at 37°C
(The group velocity in the giant axon of Squid has been reported at 21.2 m/s at 18.5°C, Kandel)

Typical transmission delays: 0.23 ms per cm between Stage 3 nodes (between two engines)

Typical transmission delays (latencies)

retina to midbrain*	1.0 ms	Based on 4 cm path
midbrain to area 7	1.0 ms	Based on 4 cm path
midbrain to area 17	1.0 ms	Based on 4 cm path

area 17 return to area 7	2.0 ms	Based on 8 cm path

*The midbrain, diencephalon, is represented by the lateral & peri-geniculate nuclei

(The following times do not count any processing time within intermediate engines)
area 7 to eye muscles
area 7 to fingers

Cumulative loop delays between stimulus and response (including processing in intermediate engines)

Lens accommodation delay	350 ms (with 8 Hz filter)	Based on Beers & Van der Heijde, 1994
Oculomotor delay	160-200 ms	Range depends on P/D delay
finger tip delay		
verbal delay		

Nominal spectrum of P/D equation (& generator potentials)

No low frequency pole

High frequency poles at

$1/\tau = 2\pi \times f = 1.9$	0.3 Hz	from LaPlace of P/D equation
$\sigma \times F =$	Variable	Depends on stimulus intensity & state of adaptation*

See **Section 7.2.4** & **Appendix A** for more details: the rising time constant can be in the microsecond region, representing a quantum-mechanical high frequency pole in the megahertz range for the chromophores. This value is then limited by the photoreceptor neuron to the few hundred Hertz range. The quantum-mechanical value also accounts for the very rapid bleaching of the retina.

Nominal action potential parameters (Chap. 13)

Nominal action potential pulse shape @ 37 C

Time constant of pulse rise, τ_R	0.012 msec
Time constant of pulse fall, τ_F	0.25 msec
Switching time, τ_S	0.075 msec

[For V_Q = zero; V_M = -95 mV, V_S = -94 mV, τ_R = 0.012 msec, τ_S = 0.075 msec & τ_F = 0.25 msec, Temp. 37 Celsius. Parameters from Schwarz & Eikhof]

Nominal action potential frequency

dark adapted luminance, R–channels	zero	no pulses are generated absent illumination
dark adapted chrominance channels	30 Hz	33 ms. between pulse peaks
dark adapted polarization channels	30 Hz	assumed, lacking data

Maximum action potential frequency

most signal projection channels	100 Hz	nominal value, may be exceeded
reported foveola projection channels	150 Hz or higher, probably limited to 500 Hz	
(Reported in some auditory channels)	800 Hz	

Perceived Spectral Response Characteristics (Chap. 17)

There are four distinctly different regions of the luminosity function; the hyperopic, photopic, mesopic and scotopic. Each exhibits different absolute maxima and various relative maxima depending on the state of adaptation of the three individual spectral channels. Confirmation experiments **must use narrow band filters, express the state of adaptation of each spectral channel individually** and **specify the color temperature of the source.** The nominal peaks in each are:

Name	Absolute maxima	Type	Relative maxima or inflection point

Hyperopic	580 nm.	Perceived	437, 494, 523, 625(610)
Photopic	523 nm.	Chromophoric	437, 494, 580, 625(610)
Mesopic	523 nm.	Chromophoric	details change significantly with intensity
Scotopic	494 nm.	Perceived	437,494

Note that none of these absolute maxima are related directly to a perceived chromophoric peak, red, blue, yellow or green. The above peaks are obtained with instrumentation of less than five nanometers spectral bandwidth. The following values were defined based on averaging, **and smoothing**, of wideband filter data collected at relatively uncontrolled color temperatures.

CIE Photopic	555 nm.	Smoothed
CIE Scotopic	507 nm.	Smoothed

V Optic Nerve Parameters (Chap. 11)

(Includes vascular support to the ocular globe and retina)
optic nerve artery divides into choroid and retinal portion.

Total number of neurons	10^6
Efferent	few dozen
Afferent	
non-signal	few dozen
signal to Lateral geniculate nucleus (LGN)	10^6
signal to Perigeniculate nucleus (PGN)	2×10^4 (2% of total number)

Important features
First transposition at the optic chiasm to support binocular vision
Second bifurcation following the chiasm to support both the LGN and PGN

VI MOTOR PARAMETERS (Chap. 7.3)

Spatial Pointing

Field of Rotation--

Saccadic Motion	Large Saccades	Small Saccades
Control	largely voluntary	involuntary
Amplitude--	a few to >30 degrees	a few down to minutes of arc
Max. Velocity		
Horizontal	700 degrees/sec.	
Vertical	400 degrees/sec	

See **Section 7.3.4.1.3**.

Flicks, preprogrammed minisaccades used to develop the 3D neural image used in stereopsis to evaluate a scene. They are typically less than one degree in amplitude.

See **Section 7.3.2**

Tremor

There is very little data available on tremor. The numbers found in the literature are summarized below.

Size of high frequency tremor--20-40 arc seconds in object field, 1 to 2 photoreceptors in foveolaa
Reported frequency of tremor--30-90 Hertz (reports to 150 Hertz), nominal center frequency--50 Hz.
Baseline frequency of tremor–center frequency of ~90 Hz with sidebands extending from 40 to 130 Hz.

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A candidate tremor system based on the requirements of the two-dimensional correlator proposed for the pretectum of the brain, a two-stage oculomotor plant proposed in this work and a sawtooth tremor waveform are:

Tremor of horizontal and vertical oculomotor twitch responses are in quadrature.
Amplitude of each high frequency tremor component– Typically, one to 2.5 photoreceptor diameters where the photoreceptor diameter is 2 microns or about 20 arc seconds of field angle.

Fundamental tremor frequency– 30 Hz.
Significant harmonics– third through fifth
Nominal tremor velocity during scan– 2.5 cm/sec

See **Section 7.3.3**

Servo-loop delay for shutters, iris and lens

Approx. 50 ms. (Ditchburn, pg. 162.)

Blink duration, Several tenths of a second (Yarbus, pg. 123)
During blink, ocular makes a characteristic motion; up, medial, and back again that typically takes 0.1--0.2 seconds

OCULOMOTOR PARAMETERS

Name	Wet wt. (gms)	Length (mm)	Peak isometric tension (gms.)*
Lateral rectus	0.89	40.8	146
Medial rectus	0.97	40.6	158
Superior rectus	0.76	41.8	122
Inferior rectus	0.837	40	140

For a 67 Kg male at autopsy
* estimated by Robinson, 1964, based on assumed equivalence of stresses with cat muscle

Moment of Inertia of the eye 4.3×10^{-5} gm. tension/deg per sec^2

VII CIRCULATION PARAMETERS

HYDRAULIC PARAMETERS

Retinal rate of flow	1.6-1.7 ml. per mm. per gm. of retina (est.)	Anderson et. al., 1964
Mean retinal circulation time	4.7 +/- 1.1 sec.	Hickman & Frayser, '65
Mean retinal transit time	3-4 sec.	Friedman et. al., 1964
1st vascular time constant	2 min.	"working number"
2nd vascular time constant	~10 min.	"working number", see Section IV time constants above

BINDING PROTEIN PARAMETERS (mostly from Ganguly, 1989)

Name	Mol Wt.	Synthesis rate	Half Life	Serum Concentration
apo-SRBP	~21,000	190 mg/m^2/day	11.1-11.7 hrs	40-50 μg/ml
TTR	~55,000			200-300 μg/ml
SRBP+retinol+TTR	~80,000			
CRBP	~14,600			
CRALBP	~33,000			
IRBP	~144,000			

VIII RESOLUTION/ACUITY RELATED PARAMETERS (Chap.

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17)

The eyes of Hominoidea (anthropoids and humans in particular) employ an analytical signal processing channel not shared with other animals, the foveola/PGN/pulvinar pathway. It is the primary determinant of the resolution performance and acuity of these animals. It relies upon tremor as a fundamental mechanism and employs two dimensional correlation of the signals within the pulvinar based on signals from the foveola.

Spatial Resolution

Calculated based on pixel size in fovea—0.31 minutes or 18.5 seconds		Based on a framing camera approach, 2. 0 micron diameter Outer Segment and a F. L. of 22.2888 mm. from Le Grande.
Actual performance based on tremor–	5-15 seconds of arc	Based on a scanning camera and telephoto capability in foveola/PGN/pulvinar pathway
Measured vernier acuity–	5.0 seconds	about 1/6th of a photoreceptor diameter (Westheimer & McKee, 1977)

Limiting Resolution in foveola 45 line pairs per mm (one black & one white line)

Peak Signal Amplitude versus spatial frequency--30 line pairs per mm

Both above values measured using a high resolution monitor

Angular Acuity

Angular acuity: 50 and 40 c/deg for man with stimulus luminances of 20 and 2 cd/m^2 respectively, 72 c/deg at 2000 cd/m^2 (Reymond & Cook, 1984).

[Angular acuity: 114 and 57c/deg for Eagle, *Aquila audax*, at the first two stimulus luminances (Reymond , 1985 using the same psychophysical methods).]

Temporal Resolution

The temporal performance of the human eye is a function of which signal path is involved and the irradiance level. The following selected values have been gleaned from the literature.

Maximum detectable frequency at high irradiance	Luminance	Chrominance	Appearance
Foveola	45 Hertz	30 Hertz	
Parafovea [outer limits]	~60 Hertz		

Electrical Passband

Tremor in the eye causes a sharp edge in the object field to be sampled at up to 90 Hertz. For larger repetitive patterns, the small saccadic motion causes similar sampling of fixed images at up to a few hundred Hertz. These frequencies appear in the image information presented to the photoreceptors of the eye. If the light level is sufficiently high, the P/D equation will support the transmission of information at a up to 500-800 Hertz to the signal circuitry of the retina. The ganglion neurons of the retina can not project information at frequencies above 500 Hertz due to the pulse width of the action potentials (slightly more than one millisecond wide).

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Tremor (repeated from Motor Parameter Section)

Size of high frequency tremor--20-40 arc seconds in object field, 1 to 2 photoreceptors in foveola
Reported frequency of tremor--30-90 Hertz (reports to 150 Hertz), nominal center frequency--50 Hz.
Baseline frequency of tremor–center frequency of ~90 Hz with sidebands extending from 40 to 130 Hz.

Above values in agreement with recent psychophysical experiments and review in Wuerger, Owens & Westland, 2001

Measured Acuity of Human Eye

The maximum acuity of the human eye is highly dependent on the surround illumination, the spectrum of the light employed in the test, the illumination level used in the test and the test technique. Flicker tests using a finite size target does not give as high acuity as do moving edge experiments. There is little data on the acuity of the human eye at the research level. Clinical testing is usually limited to the acuity of the foveola, as measured along the line of fixation, of each eye. **Section 2.4.8** reviews the data in the academic literature, that is summarized in the following figure. Collecting data at only 0.5 degree eccentricities, or larger, does not portray the acuity of the foveola adequately.

Note 1: The values in this compendium are for the human at 37° Centigrade. Temperature plays a major role in the biology of vision. However, it does not follow the Arrhenius Rule. Biological activity essentially stops at zero Centigrade and fails due to denaturing of bodily proteins near 50° Centigrade.

While specific references are not given for every parameter in the compendium, the parameters are all discussed, and references provided, within the Chapters and sections given in parenthesis next to the main titles.

Other recent sources providing parameters related to the Human Eye are;

Foundations of Vision, (1995), Wandell, B.	Primarily psychophysical analyses
The first steps in Vision (1998), Rodieck, R.	An introductory text
The Human Eye (1999) Oyster, C.	An introductory text
Retina (2001) Ogden, T. & Hinton, D.	An introduction to clinical vision

Many of the values in these texts were drawn from disparate sources without attempting to correlate the values within a consistent framework. One of the authors actually solicited individual parametric values over the INTERNET. Many of the values in these texts are archaic and not supported here and must be interpreted in the light of the Theory of this work. *Example*, the terms "rods" and "cones" are poorly defined morphological ones that have no functional significance. *Example*, the Posterior nodal distance of LeGrand's Theoretical Eye only applies to the on axis condition. This parameter varies by more than ±10% within the population.

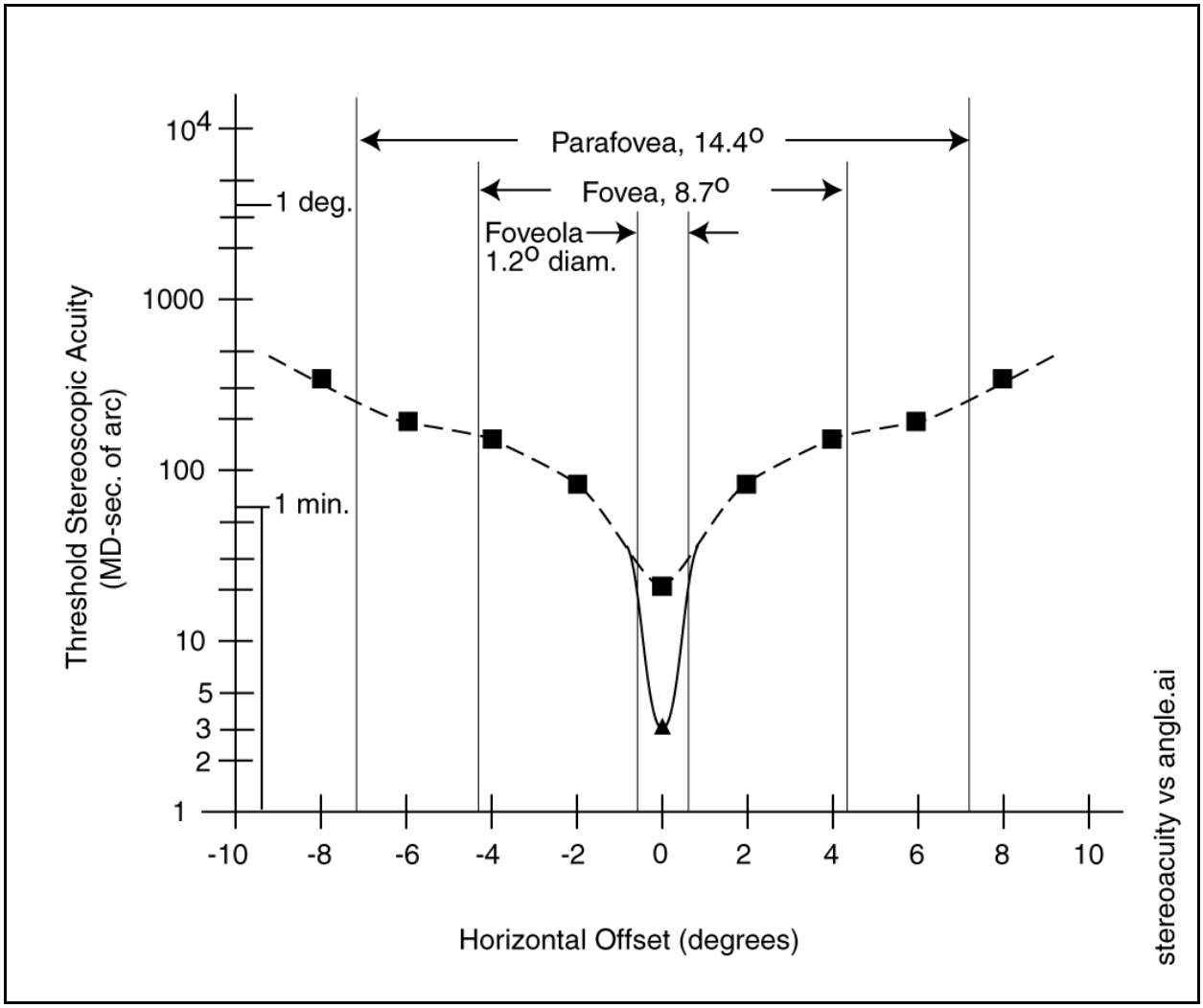

Figure 1.1.1-1 The Stereoacuity of the human eye, with magnification of field lens. Multiple scales have been added to simplify understanding of the graph. In the absence of the field lens, the acuity of the eye would follow the dashed line. The spatial sampling interval is not small enough to properly define the acuity within the foveola. See text.

The peripheral acuity associated with the cornea and crystalline lens (dashed line) associated with the Gullstrand Schematic Eye and the LeGrand Reduced Eye, is shown. The hyperacuity shown for the foveola is addressed in **Section 2.4.10** and explained physiologically by an extension of the model to a new Schematic Eye (2016) presented above.

IX BINOCULAR AND STEREOPTIC PERFORMANCE PARAMETERS

BINOCULAR PERFORMANCE

Nominal distance between nodal points of human eyes	6.4 cm	s.d. =0.31, range 5.7-7.2
Nominal distance to fixation point at rest (in the dark)	–	range 39-197 cm
Nominal vergence angle at rest	–	1-7 degrees
Nominal anatomical vergence angle	–	Up to 70 degrees at birth
Nominal total field of human vision	198 degrees	(Howard & Rogers, 2002)
Nominal field of monocular vision	150 degrees	"
Nominal field of binocular vision	114 degrees	"
Nominal field of global stereopsis	1.2 degrees	centered on line of fixation within binocular field of vision
Nominal end point precision following a saccade	2 arc min.	object misalignment rel. to line of fixation
Nominal end point precision following a flick	2-6 arc sec.	small signal correction
Nominal bandwidth of (tonic) pointing subsystem	4 Hz.	
Nominal bandwidth of subsystem with version overlay		
Nominal bandwidth of subsystem with vergence overlay	0.4 Hz.	Rashbass & Westheimer, 1961

STEREOPSIS

Nominal range of scene disparity that can be fused	10-20 arc min.	on axis
Nominal range of local stereopsis mechanism	2 arc minutes	within global stereopsis range
Nominal precision of (lateral) stereopsis (on axis)	2-5 arc seconds	

Just-noticeable change in disparity is very small (~10 arcseconds) at fixation but increases dramatically in front of and behind fixation (Held et al., 1979)

Nominal bandwidth of (twitch) pointing subsystem	30 Hz	see "tremor" above.

X PERCEPTION PARAMETERS

COLOR DISCRIMINATION PERFORMANCE

Dominant signal processing channel in color discrimination

400-437 nm	O–channel
437-532 nm	P–channel
532-650 nm	Q–channel

XI PRECISION OPTICAL SYSTEM PERFORMANCE

Loop delay		
Alarm (routine) mode	135 ms	including a 1.2° saccade and necessary computation time