

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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2 September 2004

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 PARAMETERS

IX BINOCULAR PERFORMANCE PARAMETERS

X PERCEPTION PARAMETERS

Characteristic	Value	Comment
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I OPTICS (Chap. 2.4)

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

Cornea (element 1)	43 diopters	on-axis, varies with field angle
index of refraction	xxx	
surface classification	elliptical	
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	
Retina (element 3) field plate	variable with location	variable thickness of retina acts as corrector element (geom. distort.)
Collimator array (element 4)	2.0 μ m. diam. sphere	“ellipsoid” in front of each PC
Spectral Width	<405-->1300 nm.	Between 1/2 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		

2 September 2004

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 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 $16.68 \cos\Theta$ where $\Theta = 1.336 \times \theta$

Depth of focus (on-axis, diff. limit)+/-	8.0 μ m.	+/- 3.0 @ f/2.4; +/-17.0 @ f/8.5
Back focal length (no accom.)		
Geometric demagnification	450:1	Numeric is on-axis value--at 10 m.
Snell's Law demagnification	1.33:1	Due to immersion optics
Total demagnification	600:1	On-axis value, without collimator
Field Corrector		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
Focal length of collimator	XXX	nominally fixed

** This optical description incorporates the parameters of Gullstrand's Schematic Eye (xxx). Upon elimination of the collimator lens, the field corrector, the continuous gradient index of refraction for the lens, and limiting the field angle to ~ 0.0 ; 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.

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.

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

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Air	1.000(32)
Cornea	1.376
Aqueous humor	1.336
lens (average)	1.386
vitreous humor	1.336

The lens is formed of a material of variable index with respect to both radius and axial position. Therefore, the

2 September 2004

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 work usually requires 5 place accuracy.

Details of the indices for the zones of the photoreceptor cell are shown in Figure

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 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.	

II RETINAL MOSAIC (Chap. 3)

2 September 2004

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 and 0.88 mm. vertically centered on the Fovea
Generally believed to be colored due to presence of cytoplasmic inclusions of Xanthophyll

Total number of photoreceptors

The number 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 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 is not known. The overall array in the foveola can be described in terms of a close-spaced hexagonal array formed by the photoreceptors. 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 distal to proximal)

Inner Limiting Membrane	chemical isolation: vitrea from IRP
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

2 September 2004

Fiber layer	axons of photoreceptors
Outer nuclear layer	photoreceptor cell nuclei
Outer limiting membrane	isolation; IPM from IRP
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. at the Fovea.

III PHOTODETECTOR CELLS (Chap. 4 & 5)

Type: Neuro-secretory cell with attached photo/piezic 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 cone shaped and 40-50 microns long. Their diameter matches that of the outer segment at their junction. It is frequently less than half that diameter at their other end.

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 are as small as 1.0-1.3 microns in diameter and 75 microns long. Much of the retina is populated with outer segments of 3-4 microns in diameter. The values below are nominal to allow a consistent discussion in the text.

Spaceframe (cylindrical disk stack)	50 μm x 2.0 μm diam.	2000 disks, 250 Angstrom spacing
Angular cross-section (fl=23.71)	0.042 milliradians	2.4 millidegrees, 8.6 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 bilayer
Disk formation rate	10 per hour/stack	nominal / warm blooded mammals
Disk transport velocity	300 nm/hr-7.2 $\mu\text{/day}$	
Disk operating life	7 days	nominal/ warm blooded mammals
Transduction function	Two step process:	photo/piezic in transducer; piezo/electric transfer to neuron

Transducer type: photo/piezic

2 September 2004

Material	Rhodonine ₁	1 of 4 dyes emanating from the retinal epithelium and coating the disks of above spaceframe as a monomolecular liquid crystal.	
Anisotropic Spectral Peak (Functional spectra)	Rhodonine 9	0.437 μ	½ amplitude width, 0.075 μ
	Rhodonine 7	0.532 μ	½ amplitude width, 0.065 μ
	Rhodonine 5	0.625 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)	0.498μ	½ amplitude width 0.100 μ (typ.)
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* 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 μ depending on environment. The listed width was measured with a spectrometer using a filter width of >30 nm.

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 A₁) 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 A₂ and some scavengers (at least among the arthropods) use Vitamin A₃ 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.

Transducer	Resonant chain length	λ _l μ	λ _m μ	λ _h μ	Q
Rhodonine (5)	5	0.595	0.625	0.655	10.4
Rhodonine(7)	4	0.500	0.532	0.565	8.2
Rhodonine(9)	3	0.400	0.437	0.475	5.8
Rhodonine(11) [UV]	2 **	0.300	0.342	0.385	4.0

where l, m and h indicate the low half amplitude point, the mid wavelength point and the high half amplitude

2 September 2004

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 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.

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 $X = (1.2 \times 10^5) / \lambda(\text{nm})$ 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 1 st dendrites piezo/electric	2.2 eV very high gain	equiv. to 565 nm. piezo/electric transistor, typically 3500:1 electron (current) amplification
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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	

2 September 2004

Mass properties of photoreceptor cells

Estimates from Lolley, et. al. (1986)

Volume		
Total		$234 \times 10^{-12} \text{ cm}^3$
Weight		
Total cell		$42-64 \times 10^{-12} \text{ g}$
DNA		6.4
RNA		2.3

IV SIGNAL PATH PARAMETERS (Chap. 12 & 13)

Input parameters

Usable dynamic range:	$10^{15}:1$
Photopic dynamic range:	56000:1
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:	XXX
Maximum image retention time in absence of motion:	3-6 seconds

Energy Threshold of Adaptation Amplifier

Nominal energy threshold of photoreceptor adaptation amplifiers	>2.0 Electron-volts, equiv. to 600 nm. Not over 2.34 EV based on Sliney data
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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.

2 September 2004

Intrinsic, τ	0.0125 sec.	dominant during falling edge in P/D equation.
Dynamic, $\sigma \cdot F \cdot \tau$	$\sigma \cdot F \cdot 0.0125$	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	(Very fast)	dominant during increase in illum.

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

Recovery,		dominant during decrease in illum.
1 st	3 seconds	electronic
2 nd (1 st vascular)	2 minutes	vascular, est. from Spillmann
3 rd (2 nd vascular)	~10 minutes	vascular “ ” “”

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.

The longer adaptation characteristic is actually a higher order function exhibiting an exponential time constant and a sinusoidal component. See text.

Nominal pass band of signaling channels

Low frequency (RC type) pole
High frequency pole

Due to adaptation amplifier collector circuit

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 an axon	4,400 m/sec. at 37°C
Group velocity of action potential signals between regenerative nodes (The group velocity in the giant axon of Squid has been reported at 21.2 m/s at 18.5°C, Kandel)	44 m/sec. at 37°C

2 September 2004

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 to area 7	2.0 ms	Based on 8 cm path

(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
$\sigma \times F = 2\pi \times f =$	XXX	

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, $\tau_R = 0.012$ msec, $\tau_S = 0.075$ msec & $\tau_F = 0.25$ msec, Temp. 37 Celsius. Parameters from Schwarz & Eikhof]

Nominal action potential frequency

dark adapted luminance 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	

Perceived Spectral Response Characteristics (Chap. 17)

2 September 2004

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
Photopic	523 nm.	Chromophoric	437, 494, 580, 625
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 chromophoric peak. Additional selective adaptation must be employed to observe the other chromophoric peaks. 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

Under nominal (not chromatically adapted) photopic conditions, the relative coefficients in the Equation of Vision for human eyes are:

Spectral Band	complete eye	aphakic eye
	C_U' 0.0003	C_U' 0.3
	CS' 0.1	CS' 0.1
	CM' 1.000	CM' 1.000
	CL' 0.1	CL' 0.1

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 LGN	10^6
signal to Pretectum	2×10^4

Important features

- First transposition at the optic chiasm to support binocular vision
- Second bifurcation following the chiasm to support both the LGN and Pretectum

2 September 2004

VI MOTOR PARAMETERS (Chap. 7)

Spatial Pointing

Field of Rotation--

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

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 fovea
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.

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-- one nominal foveola photoreceptor diameter, 2 microns
(about 20 arc seconds)

Fundamental tremor frequency-- 30 Hz.

Significant harmonics-- third through fifth

Nominal tremor velocity during scan-- 2.5 cm/sec

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

2 September 2004

Moment of Inertia of the eye 4.3×10^{-5} gm. tension/deg per sec²

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
1 st vascular time constant	2 min.	"working number"
2 nd 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 RELATED PARAMETERS (Chap. 17)

The eyes of Hominoidea (Human in particular) employ an analytical signal processing channel not shared with other animals. 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 foveola.

Spatial Resolution

Calculated based on pixel size in fovea—0.31 minutes or 18.5 seconds Based on 2.0 micron diameter Outer Segment and a f. l. of 22.2888 mm. from Le Grande (check this re: index)

Actual performance based on tremor— 5-15 seconds

Measured vernier acuity— 5.0 seconds about 1/6th of a photoreceptor diameter (Westheimer & McKee, 1977)

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

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

2 September 2004

Both above values measured using a high resolution monitor

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
Fovea		45 Hertz	
Parafovea [outer limits]			

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 XXX 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 these frequencies to the signal circuitry of the retina.

Tremor (repeated from Motor Parameter Section)

Size of high frequency tremor--20-40 arc seconds in object field, 1 to 2 photoreceptors in fovea
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

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 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

2 September 2004

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 not supported here and must be interpreted in the light of the Theory of this work. *Example*, the terms “rods” and “cones” are 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 $\pm 10\%$ within the population.

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

X PERCEPTION PARAMETERS

COLOR DISCRIMINATION PERFORMANCE

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Dominant signal processing channel in color discrimination

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