DEVELOPING HUMAN BRAIN is viewed from the side in this sequence of drawings, which show a succession of embryonic and fetal stages. The drawings in the main sequence (Action) are all reproduced at the same scale: approximately four-fifths life-size. The first five embryonic stages are also shown enlarged to an arbitrary common size to clarify their structural details (EXP). The three main parts of the brain (the forebrain, the midbrain and the hindbrain) originate as prominent swellings at the head end of the early neural tube. In human beings, the cerebral hemispheres eventually overgrow the midbrain and the hindbrain and also partly obscure the cerebellum. The characteristic convolutions and invaginations of the brain's surface do not begin to appear until about the middle of pregnancy. Assuming that the fully developed human brain contains on the order of 100 billion neurons and that virtually no new neurons are added after birth, it can be calculated that neurons must be generated in the developing brain at an average rate of more than 250,000 per minute.
Two views of the world

Adult

Infant
Davida Y. Teller “Teller acuity cards”
Normal acuity development

Grating acuity (c/deg)

Age (weeks)

Snellen equivalent

20/600
20/200
20/60
20/20
20/20
Grating acuity (c/deg) vs. Age (weeks/months) for Monkeys (wks) and Humans (mos). The graph shows a linear increase in grating acuity with age, with monkeys reaching higher acuity values compared to humans. The Snellen equivalent scale is also plotted on the right axis.
a. Monkey

Contrast sensitivity vs. Spatial frequency (c/deg)

- 5 wks
- 15 wks
- 26 wks
- 49 wks
Peak spatial contrast sensitivity

Stavros and Kiorpes, Fig. 6
Stavros and Kiorpes, Fig. 6
Adult macaque temporal contrast sensitivity

Stavros and Kiorpes, Fig. 1
Adult temporal contrast sensitivity

- Human
- Monkey

Temporal contrast sensitivity vs. Temporal frequency (Hz)
Stavros and Kiorpes, Fig. 5
Peak temporal contrast sensitivity vs. Age (weeks)

Temporal resolution (Hz) vs. Age (weeks)

Stavros and Kiorpes, Fig. 5
Growth of the macaque eye

1 week

1 deg

178 µm

Adult

1 deg

249 µm
after Østerberg, 1935; as modified by Rodieck 1988;
micrographs from Curcio et al., 1990
prenatal

15 mos

45 mos

adult
inputs

A  B

media transmittance

optical transfer

receptor optics

receptor sampling

receptor efficiency

neural transfer

decision rule

"A"  "B"
Contrast sensitivity

Ideal observer

24 wk
4 wk
1 wk

Behavioral development

5 wk
20 wk

Spatial frequency (c/deg)
Segmentation of retinal axon terminals in the lateral geniculate nucleus
Development of retinal ganglion cell terminals in the cat’s lateral geniculate nucleus (LGN)

Eye-specific layers: *prenatal* loss of branches in the wrong layer

Topography: *postnatal* loss of exuberant branches
FIGURE 25.17 Wave of Impulse Activity Spreading across Isolated Retina of a neonatal ferret. The isolated retina was placed on recording electrodes, embedded in a regular array in the dish. The position of each of 82 retinal neurons is represented by a small black spot. Electrically active neurons are marked by larger blue spots, the sizes of which are proportional to the firing rates. Each frame represents the activity averaged over successive 0.5 s intervals. During the time represented by the eight frames (3.5 s), action potentials begin with one small group of cells and spread slowly across the retina. A new wave begins shortly after, and then another, each spreading in a different direction. At this stage of development, photoreceptors in the ferret are not responsive to light. (After Meister et al., 1991.)
The developing visual pathway shows patterned spontaneous activity.
FIGURE 25.15 Effect of Abolition of Electrical Activity by Tetrodotoxin on arborization of optic nerve fibers terminating in the lateral geniculate nucleus. (A) In a normal kitten the terminals of optic nerve fibers labeled with horseradish peroxidase are restricted to the single layer where they end. (B) After application of tetrodotoxin for 16 days during embryonic life, labeled axons show much larger arborizations that are not restricted to individual layers. (After Sretavan, Shatz, and Stryker, 1988.)
Cortical synaptogenesis in three species

Rat

Macaque

Cat

Cragg; Hendrickson
ABOVE: Postnatal Age (months and years)
BELOW: Conceptional Age (log scale)
Four stages in the development of eye dominance columns in cat visual cortex
FIGURE 25.3 Age Dependence of Branching Patterns of Axons from Lateral Geniculate Nucleus ending in layer 4, labeled by injection with horseradish peroxidase. (A) Axon of a 17-day-old kitten. The axon spreads over a large uninterrupted territory in layer 4 of the visual cortex. (B) In the adult cat, the geniculate axon ends in two discrete tufts, interrupted by unlabeled fibers coming from the other eye. (After Wiesel, 1982.)

FIGURE 25.5 Retraction of Lateral Geniculate Nucleus Axons ending in layer 4 of the cortex during the first 6 weeks of life. The figure shows the overlap of inputs from the right (R) and left (L) eyes present at birth and the subsequent segregation into separate clusters corresponding to ocular dominance columns. The overlap at birth is greater in kittens than in monkeys. (After Hubel and Wiesel, 1977.)
Spontaneous retinal activity influences the formation of ocular dominance bands.

Control

TTX-reared

\[ \text{layer IV} \]

\[ \text{Cortex} \]

\[ \text{LGN} \]

\[ \text{Eyes} \]

\[ ^{3}\text{H}-\text{proline} \]

TTX P14 to P40

9.18
FIGURE 25.16 Increased Arborization of Lateral Geniculate Fibers ending in layer 4 of visual cortex after application of tetrodotoxin to both eyes. (A) Normal arborization of a labeled geniculate axon in layer 4 (30-day-old animal). (B) Labeled geniculate axon in a kitten in which tetrodotoxin had been applied to the eyes for 12 days (29-day-old animal). The axons of this neuron cover a much larger area of cortex. (After Antonini and Stryker, 1993a.)
Figure 25.4 Ocular Dominance Columns in Layer 4 of the visual cortex in a visually naive monkey and in an older animal that had been exposed to light. (A) The monkey was delivered 8 days prematurely by cesarean section. Infrared night vision goggles were used in complete darkness for the delivery and for the injection of radioactive proline into the right eye 1 day later. The animal was maintained in complete darkness for 7 more days. The autoradiograph shows layer 4 of the ipsilateral primary visual cortex. Ocular dominance columns can be discerned. (B) Similar section through layer 4 in a 16-day-old monkey that had been born naturally and raised under normal lighting conditions. The right eye was injected with radioactive proline at 9 days. The boundaries of the ocular dominance columns are better defined. (After Horton and Hocking, 1996a; photographs kindly provided by J. Horton.)
Figure 2. Photomontage and drawing of the ocular dominance columns in layer IV of the striate cortex of monkey 1, prepared from a series of autoradiographs like the example shown in Figure 1. The ocular dominance columns are well segregated and organized into an adult-like pattern at E165/P0. The dashed line represents the vertical meridian (V1-V2 border). The opercular cortex (representing the central 8° of
FIGURE 25.2  Ocular Dominance Distribution in the visual cortex of newborn monkey. Cells in groups 1 and 7 of the histograms are driven by one eye only (ipsilateral or contralateral). All other cells have input from both eyes. In groups 2, 3, 5, and 6, one eye predominates. In group 4, both eyes have equal influence.

(A) Normal adult monkey. (B) Normal 2-day-old monkey. (After Wiesel and Hubel, 1974.)
FIGURE 25.6 Architecture of the Visual Cortex of Newborn Monkey without visual experience (as in Figure 25.4A), delivered by cesarean section 8 days prematurely and kept in total darkness for 7 days. (A) Cytochrome oxidase staining shows blobs in area 17. (B) Thick and thin stripes in visual area 2, labeled with thick and thin arrows. (After Horton and Hocking, 1996a; photographs kindly provided by J. Horton.)
Reconstruction of an oblique microelectrode penetration through the postlateral gyrus of a 16-day-old kitten without previous visual experience. Longer lines intersecting the electrode track represent single well-isolated cortical cells; directions of these lines represent receptive-field orientations, a line perpendicular to the track standing for a vertical orientation. Shorter lines show regions in which unresolved background activity was observed. At the end of a penetration an electrolytic lesion was made; this is indicated by the circle. Scale, 0.5 mm.
FIGURE 25.1 Orientation Columns in the absence of visual experience. (A) Axis orientation of receptive fields encountered by an electrode during an oblique penetration through the cortex of a 17-day-old baby monkey whose eyes had been sutured closed on the second day after birth. The receptive field orientation changes progressively as columns are traversed, indicating that normal orientation columns are present in the visually naive animal. Red dots are from the ipsilateral eye, blue dots from the contralateral eye. (B) The black dot marks the lesion made at the end of the electrode track in layer 4. (C) Orientation columns displayed by imaging in a 14-day-old kitten with lids sutured at birth. Colored bars (right) represent the orientation of the stimulus. Note that pinwheels are already present. (A and B from Wiesel and Hubel, 1974; C from Crair, Gillespie, and Stryker, 1998; micrograph kindly provided by M. C. Crair and M. P. Stryker.)
Movshon et al., 2005
Parvocellular

1 wk (74)

c

4 wk (64)

e

>24 wk (83)

Proportion of cells

Characteristic spatial frequency (c/deg)

Magnocellular

1 wk (21)

b

4 wk (28)

d

>24 wk (33)

f

A

B

C

D

E

F

-ARVOCELLULAR
-AGNOCELLULAR

HARACTERISTIC

SPATIAL

FREQUENCY

CDEG

W

W

W

W
Parvocellular

a

1 wk (78)

b

1 wk (20)

Magnocellular

c

4 wk (74)

d

4 wk (27)

e

>24 wk (95)

f

>24 wk (32)

Proportion of cells vs Responsivity (imp/sec/contrast)

Figure

WK ET AL
Figure 1. Normalized spatial frequency and contrast sensitivity as a function of age. (a) Normalized spatial frequency. (b) Normalized contrast sensitivity. Different symbols represent different cell types: Behavior, Cones, Magnno cells, Parvo cells.
Temporal vision:
Neuronal performance & behavior

Normalized sensitivity

Behavior
Magnocellular cells

Normalized resolution

Stavros and Kiorpes, Fig. 7
Proportion of cells

1 wk
n=90

4 wk
n=157

16 wk
n=110

Adult
n=240

Eye dominance

V1
1 week (n=82)

4 week (n=129)

16 week (n=113)

Adult (n=106)

Peak response (impulses/sec)
Optimal spatial frequency (c/deg) vs. Temporal resolution (Hz)

1 week (n=82)

4 week (n=121)

16 week (n=105)

Adult (n=100)
Temporal vision:
Neuronal performance & behavior

Stavros and Kiorpes, Fig. 7
Behavioral acuity
Cone distributions

Sensitivity profiles

Spatial tuning

1 week

Adult
Visual system development proceeds according to a prescribed plan

Early visual system structure is mature at birth; refined postnatally

Prenatal development can be influenced by abnormal activity patterns

Visual function is immature in newborns and develops in a stereotypic manner

Visual function is not limited by development of structures prior to striate cortex

Postnatal development also influenced by abnormal activity patterns