Evolving Brains

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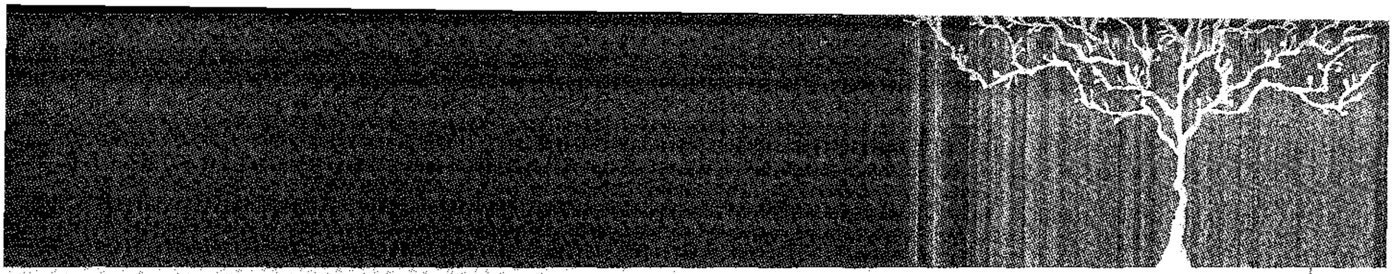


CHAPTER 6

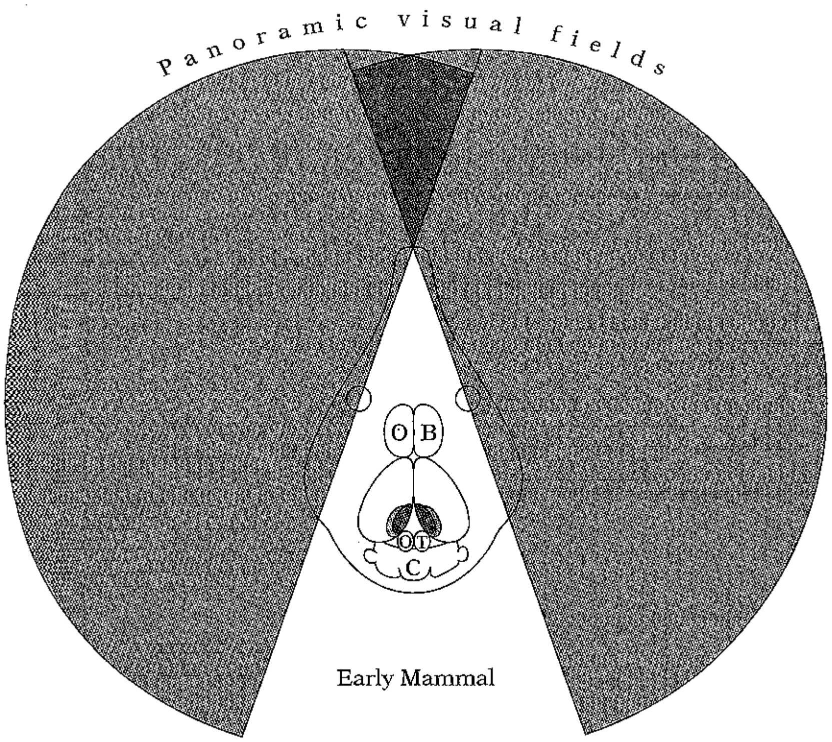
Primate Brains

> In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history.
>
> Charles Darwin,
> *The Origin of Species,* 1859

The 6-mile-wide meteorite that struck Yucatán 65 million years ago caused the earth to be enveloped in a huge cloud of dust and debris that blocked sunlight for many months. This event destroyed the dinosaurs and many other groups of animals. The mammals, however, were well equipped to survive this cold, dark period because they were active at twilight or at night, they were warm-blooded, and they were insulated with fur. When the dust finally settled the mammals found a world in which most vertebrates larger than themselves were dead: the meek had inherited the earth. From the stock of early mammals new forms emerged to seize the niches vacated by the lost animals. Other mammals, including our ancestors, the early primates, created new niches for themselves in this fundamentally altered environment. Once the dust settled, that environment became much warmer than today's world, and tropical rain forests covered a much larger portion of the planet than they do now.

Eyes, Hands, and Brains

The early primates lived in these forests and started to become abundant about 55 million years ago. Much is known about these early primates because they left behind many fossils: they are closely related to the group of living primates called the prosimians, a name that means "before the monkeys." The prosimians include the tarsiers, galagos, lorises, and lemurs. The early primates weighed only a few ounces, and they clung with their tiny grasping hands to the fine terminal branches of trees in the tropical rain forest. Their large eyes faced forward, and their visual resolving power was greatly improved by an increased density of photoreceptors in the center of their retinas. Emerging from this dense array of photoreceptors was a strong set of connections from the central retina via the optic nerve to the brain. The visually mapped structures in the brain contained greatly expanded representations of the central retina. In some of these structures there was a marked segregation of visual processing into two distinct functional streams, one exquisitely sensitive to motion and small differences in contrast, the other responsive to the shape and form of visual objects. The visual cortex, the major site of visual processing in the brains of primates, enlarged greatly, and many new cortical visual areas formed that were not present in the primitive mammals. Another innovation in the early primates was a specialized cortical area devoted to the visual guidance of muscle

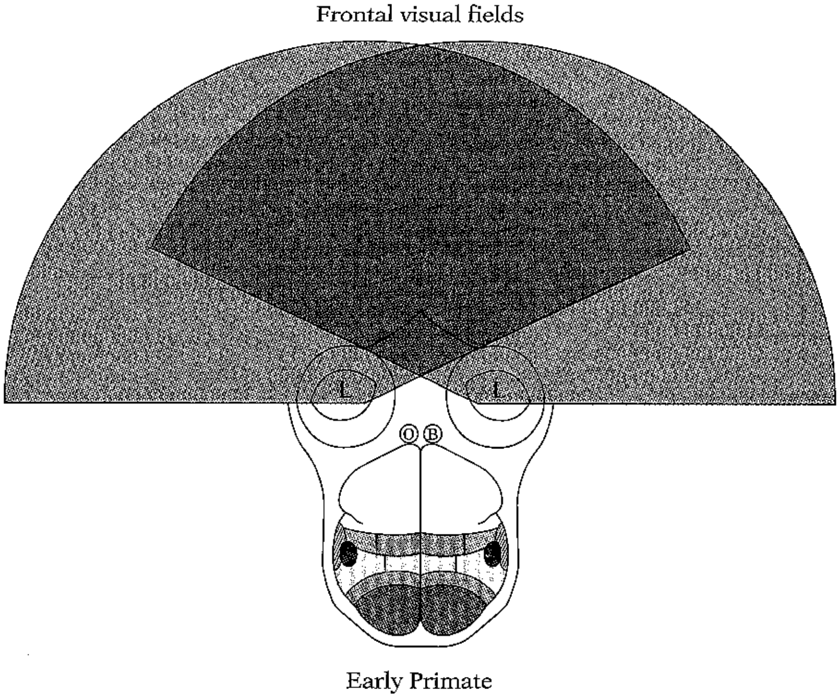


In a primitive mammal, the visual field is nearly panoramic and the cortical visual areas in the brain are small. The first visual area (V1) is shown in red; the second visual area (V2) in orange. The locations of V1 and V2 are based on the studies of Jon Kaas and his colleagues of hedgehogs. The olfactory bulbs, OB, are large, reflecting the heavy emphasis on the sense of smell in primitive mammals.

A hedgehog, *Erinaceous europaeus,* a living nocturnal insectivore that has retained many features of primitive mammals.

movement. This functionally linked set of changes in the visual system and in visuo-motor coordination comprises some of the basic defining features for primates that served to differentiate them from other groups of mammals. About 40 million years ago, a duplication of the gene for a retinal cone pigment in an ancestor of Old World monkeys, apes, and humans, resulted in the development of trichromatic color vision. Also beginning at about this time was an expansion of the system for emotional communication via facial expressions and the concomitant reduction of the olfactory communication in primates.

A prosimian, the slender loris, *Loris gracilis*, using its prehensile hands and feet to cling to a fine branch. By occupying the fine-branch niche primates gained access to a rich array of resources such as fruit and insects, but living in this precarious environment requires superb vision and visuo-motor coordination.



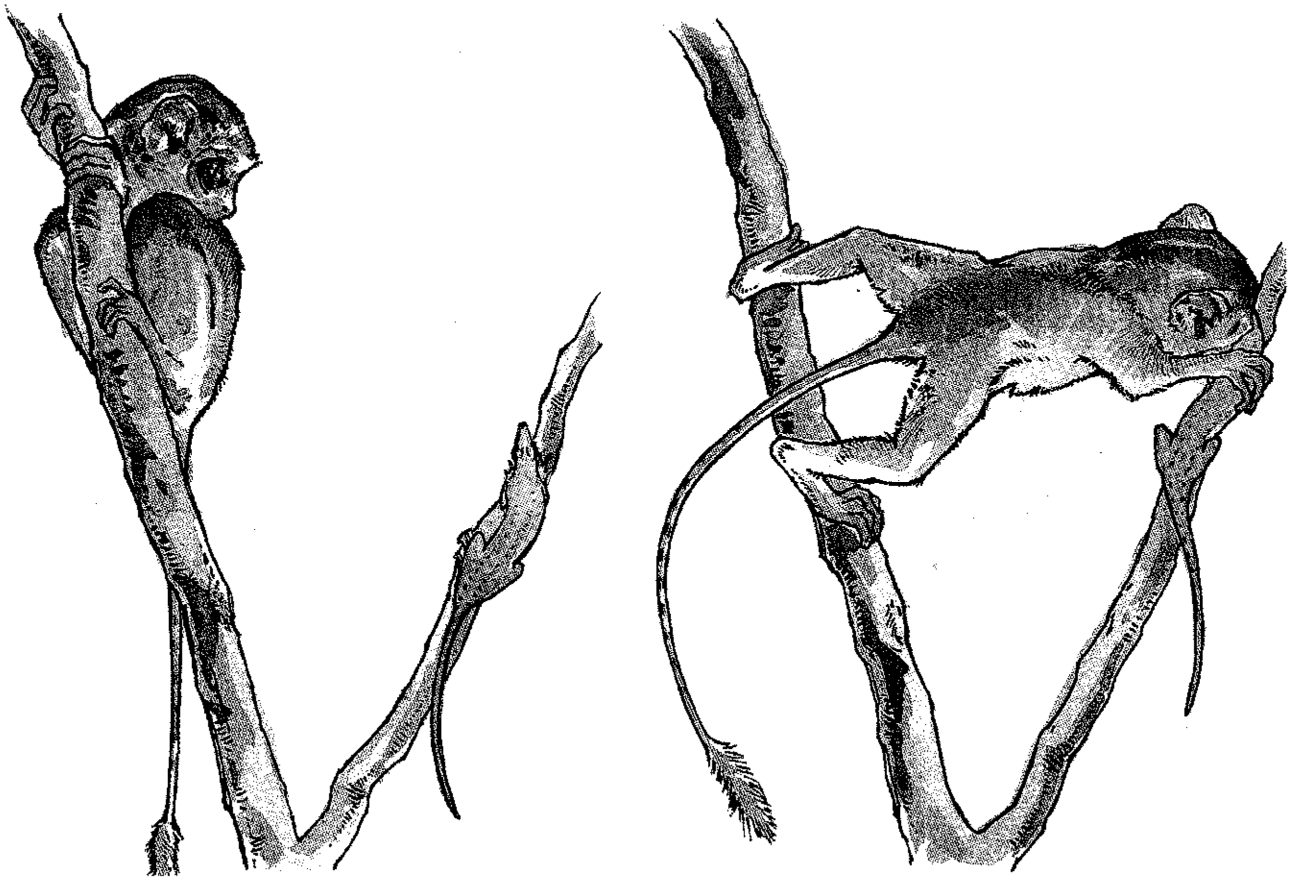
In a primitive primate, the large eyes are directed forward and there is a large amount of binocular overlap between the visual fields of the two eyes (L = lens). The olfactory bulbs are smaller than in primitive mammals. The first visual area (V1) is shown in red; the second visual area (V2) in orange; the third tier of visual areas in yellow; area MT in dark blue; the inferotemporal visual cortex in green; the posterior parietal cortex visual cortex in brown; the temporoparietal visual cortex in purple. The positions of the eyes and the locations of the visual areas are based on the author's studies of prosimians with high-resolution magnetic resonance imaging and neurophysiological recording, and on the remarkably well preserved skulls and brain endocasts of Eocene primates.

The Advantages and Costs of Front-Facing Eyes

Front-facing eyes and the expansion of the size and number of cortical visual areas are distinctive features of primates and are related to the primate capacities for keen vision and eye–hand coordination. Two theories have been proposed to explain the development of high-acuity frontal vision and eye-hand co-ordination in primates: Matthew Cartmill's "visual predator" hypothesis and Robert Martin's "fine-branch niche" hypothesis. The two theories are not mutually exclusive. Cartmill has suggested that the early primates were hunters who relied mainly on vision. He based this inference on the fact that many small prosimian primates, such as tarsiers and mouse lemurs, capture and eat insects and small vertebrates, and that nonprimates with large front-facing eyes, such as cats and owls, are predators. Martin has proposed that the early primates used their grasping hands to move about in the fine branches of the forest canopy and exploit the rich abundance of fruit and insect resources available there. Keen vision and superb eye–hand coordination are required to function in the fine-branch niche, a uniquely complex visual environment in which the branches move and sway, where the penalty for miscalculation can be a fatal fall.

What advantages do front-facing eyes provide to predators? Because of the bilateral symmetry of their limbs, predators generally orient themselves so that their prey is located directly in front of them and they can propel themselves swiftly forward, carrying out a coordinated attack with forelimbs and jaws. Frontally directed eyes provide maximal quality of the retinal image for the central part of the visual field. This is where the prey is located in the crucial moments, just before the final strike, when the predator is evaluating the prey's suitability as food, its evasive movements, and its ability to defend itself. Image distortion tends to increase the farther an object is located off the optical axis of a lens system, and thus it is advantageous to a visually directed predator to have front-facing eyes in which the optical axes are directed toward the central part of the visual field. Such image distortion can be reduced by decreasing the aperture of the lens, but the early primates were probably active at twilight or night when light was at a premium, and the larger aperture was needed to collect as much light as possible. Indeed, the familiar examples of nonprimates with large front-facing eyes are cats and owls, both night hunters.

Front-facing eyes also increase the size of the binocular visual field, enhancing visual capabilities in at least three ways. The first is by the expansion of the stereoscopic visual field. Objects cast slightly different images in each of the two eyes. The visual cortex is sensitive to these small differences, which it interprets as relative differences, in depth. Stereoscopic depth perception provides a relative measure of distance that can guide a predator in seizing its prey.



A tarsier preying upon a lizard. These drawings are based on photographs taken by Johannes Tigges and W. B. Spatz.

Another important function of binocular vision, pointed out by Bela Julesz, is to "break" camouflage. Prey often adopt the protective strategy of matching themselves to their background and are difficult to detect monocularly; the binocular correlation of the images from both eyes may enable the predator to detect prey thus concealed. Finally, under low light conditions, the binocular summing of images from both eyes can facilitate the detection of barely visible prey.

Moving about in the fine terminal branches also requires keen vision in the part of the visual field immediately in front of the ani-

mal. Thus, the fine-branch-niche hypothesis for the origin of primates shares with the visual-predator hypothesis the necessity for high-quality vision in the space immediately in front of the animal, where it can manipulate objects with its hands. Thus both hypotheses predict front-facing eyes for improved image quality and stereoscopic depth perception. However, living in the trees does not in itself lead to front-facing eyes. Squirrels are highly adept at moving from branch to branch in the trees, yet they have laterally directed eyes with nearly panoramic vision. Still, the squirrel's small strip of binocular visual field has a large representation in the visual cortex, suggesting that binocular vision and perhaps stereopsis may be important to the squirrel even though its eyes are laterally oriented.

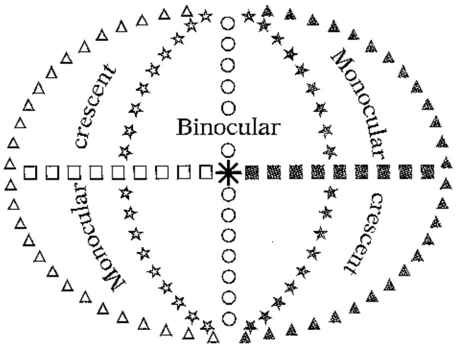
Along with the advantages they confer, front-facing eyes impose a significant cost on primates because the nearly panoramic visual field found in most mammals is constricted, and the ability of primates to detect predators approaching from the rear is limited. This constriction of the visual field predisposes primates to develop other means for detecting predators. Some prosimians, such as the galagos, which can direct the orientation of their ears with delicate precision, have the keen ability to detect the sources of sounds that might signal a predator's approach. The early primates, like most primitive mammals, probably lived a solitary existence. However, the loss of panoramic vision strongly favored the formation of social groups because multiple sets of eyes could overcome the vulnerability imposed by the restriction of the visual field. The response to this limitation may have been the evolution of neural systems for social cooperation and the production of vocalizations that signal the presence of predators. Dorothy Cheney, Robert Seyfarth, and others have found that primates have specific alarm cries for aerial versus ground predators. The evolution of these specific alarm cries presents something of a puzzle since the animal making the cry calls attention to itself, which might increase its risk of being attacked by the predator. It has been suggested that such apparently altruistic acts, while possibly endangering the crier, increase the chances of survival of close relatives that share most of the genes possessed by the animal making the alarm cry. Thus the cooperative behavior enhances the chances that those shared genes will be passed on to the next generation.

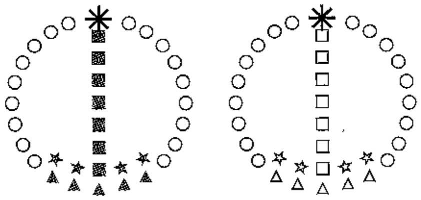
The Optic Tectum: An Ancient Visual System Transformed

The midbrain in primates contains the ancient visual map, the optic tectum, found in all vertebrates. In nonprimates, the optic tectum on one side receives most of its fibers from the retina on the opposite side, and the primitive condition is a nearly completely crossed projection from the retina to the optic tectum. In primates, the front-facing eyes have caused a remodeling of the connections between the retina and the optic tectum: there is a large projection from the

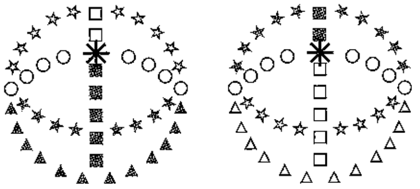
The mapping of the visual field on the optic tecta in primates and nonprimates. The star indicates the center of the visual field; the small circles indicate the vertical midline of the visual field, which separates it into right and left hemifields. The monocular crescent is the part of the visual field that is seen by only one eye. Each tectum—there is one on each side—is the dome- or disk-shaped structure forming the roof of the midbrain. In the diagram, the anterior edge is at the top of each tectum. In primates the representation of the vertical midline of the visual field corresponds to the anterior edge of each tectum: the right visual hemifield is represented in the left tectum, and vice versa. In nonprimates the representation in the anterior tectum extends well beyond the vertical midline, and this part of the visual field is represented redundantly in the optic tectum on both sides of the midbrain.

Visual Field





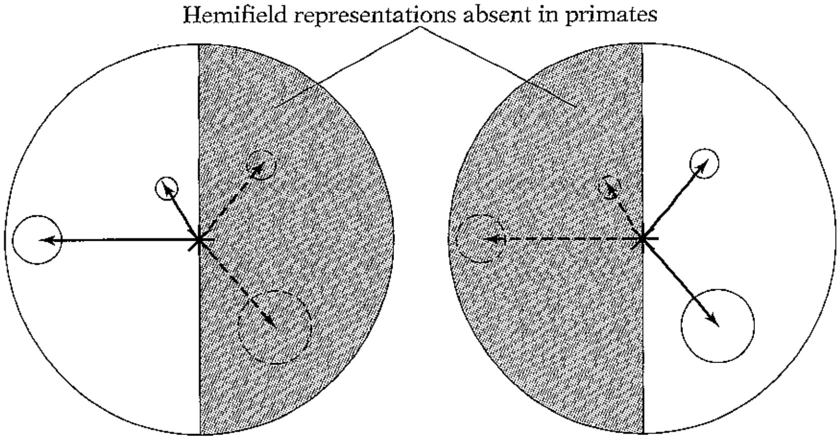
Primate Optic Tecta



Nonprimate Optic Tecta

retina to the optic tectum on the *same* side, and the maps in the tecta have been modified so that only the opposite half of the visual field is represented in each tectum. This change may have come about because the standard vertebrate tectal mapping would have resulted in redundant representations of the visual field in the tectum in primates. However, other animals with frontally facing eyes, cats and owls, have retained the same type of visual mapping that is found in other vertebrates rather than the modified version found in primates, and thus there is some redundancy in the tectal maps in these animals. In fish, amphibians, and reptiles the optic tectum has a broad array of functions consistent with its role as the main visual processing center in the brain. The tectum also serves to integrate visual, auditory, and somatosensory inputs. In primates the function of the optic tectum is more specialized, serving to guide the eyes so that the images of an object of interest fall directly on the central retina in the region of maximum acuity, which is only a very small part of the total retinal area. Thus a major function of the optic tectum in primates is to cause the eyes to fixate on interesting objects.

Primates fixate mainly by eye movements rather than head movements; by contrast, owls and cats rely mostly on head movements to look at interesting things. Part of the visual field map is represented in both sides of the tectum in nonprimates, but not in primates. Perhaps the nonredundant map found in the primate tectum reflects its role in directing the eye to fixate on objects of interest. Tectal map



Peter Schiller and Michael Stryker found a direct correspondence between the visual and visuo-motor maps in the optic tectum in monkeys. They mapped visual receptive fields (the circled areas) in the tectum and then electrically stimulated these sites. Stimulation caused the monkey to direct its eyes so that the center of the retina gazed at the site in the visual field corresponding to the previously recorded receptive field. (The eye movement is indicated by the arrows from the stars marking the fixation point to the receptive fields.) This visuo-motor response is a major function of the optic tectum in primates, causing the animal to look at novel objects that have entered its peripheral visual field. If primates had a redundant visual field map, as do other mammals, there would be ambiguity, indicated by the dashed circles and arrows, in the visuo-motor map that guides fixation. Redundancy in the visuo-motor map might compromise the primate's ability to fixate rapidly and accurately on novel objects.

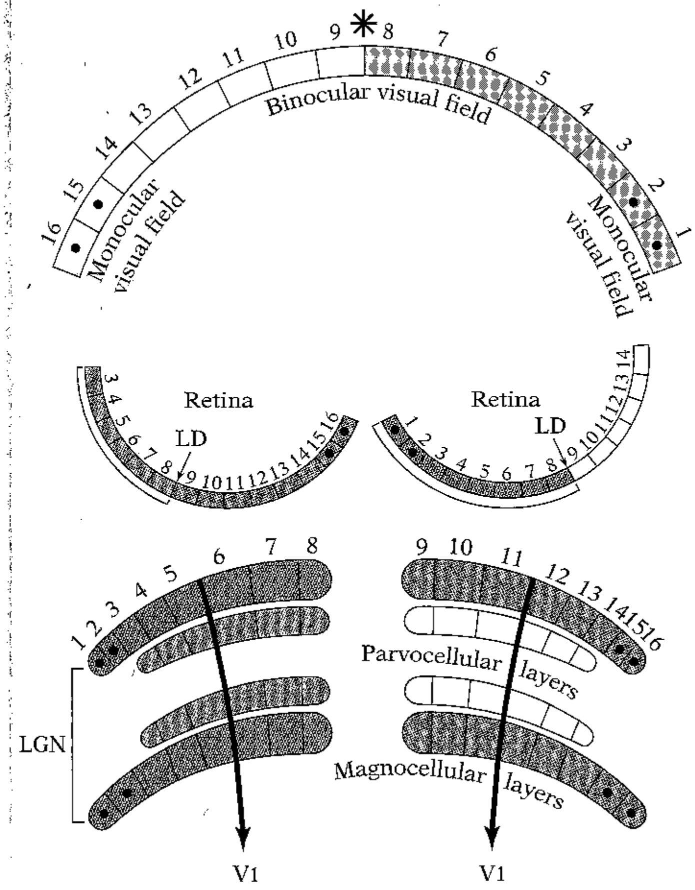
redundancy in primates might have interfered with fixation by providing a superfluous target within the visuo-motor map.

The organization of the optic tectum is fundamentally transformed in primates, but is this transformation unique to primates? In 1977, I suggested that the organization of the optic tectum might be a defining feature that distinguishes primates from nonprimate mammals. A few years later Jack Pettigrew reported that *Pteropus*, a type of large bat from the group known as the megachiropterans, had the primate type of tectal map. He used this observation to argue that this group of bats were "flying primates." His proposal caused a considerable uproar among evolutionary biologists since it would have required a major revision of the basic system for classifying mammals by separating the megachiropterans from the smaller bats (microchiropterans) and lumping them with the primates. The heat of this controversy resulted in several scientific symposia and two detailed mapping studies of the optic tectum in the megachiropterans, *Rousettus* and *Pteropus*. Unlike primates, in which the visual field in each side of the tectum extends only to the midline, both studies found that the representation extended considerably beyond the midline into the visual field on the same side. These parts of the tectal map beyond the midline are thus represented on both sides and are redundant. Bats, like most mammals, have laterally placed eyes and low acuity. Comparative anatomical and DNA data also suggest that megachiropterans are more closely related to microchiropterans than to primates. Thus megachiropterans pos-

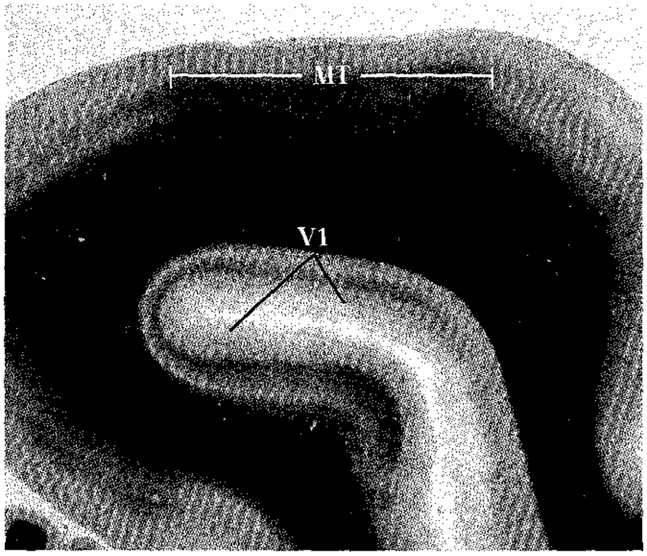
the nonprimate pattern of tectal organization and are unlikely to
lying primates.”

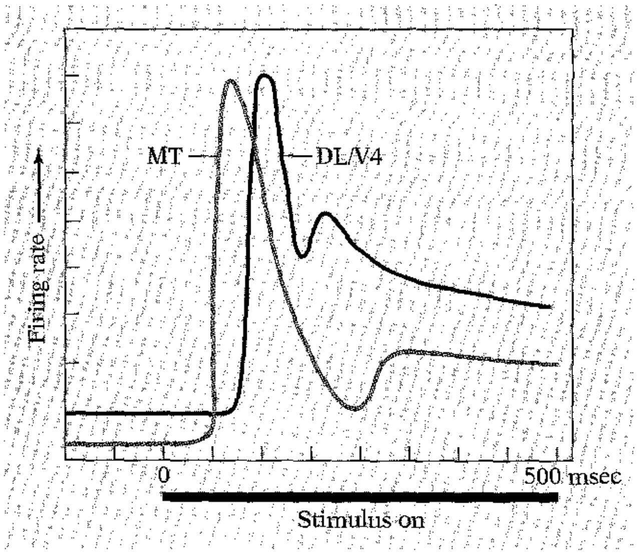
ing Motion and Form

analysis of images requires tracking and identifying objects. The
expansion of the visual system in primates occurred mainly in
orebrain, where two distinct systems evolved for seeing the
on and the form of objects in the visual scene. In primates the
r output from the retina travels in the optic nerve to the lateral
culate nucleus in the thalamus, which in turn connects with the
l cortex. “Nucleus” is the anatomical term for an aggregation



The mapping of the visual field onto the lateral geniculate nucleus in primates. The upper diagrams are horizontal slices through the visual field and the retinas. The retinas are divided into hemiretinas by the line of decussation (LD), or crossing, which corresponds to the vertical midline of the visual field. The green and blue hemiretinas, which view the right half of the visual field, project to the layers of the lateral geniculate nucleus on the left side of the brain. Note that the green input is not quite complete, because it does not include the monocular segment. Each hemiretina projects to an individual layer, and the layers are stacked in such a way that same places in the visual field fall in register. The parvocellular layers contain many small neurons, and their responses are specialized for fine detail in the visual image and in day-active primates for the analysis of color. The magnocellular layers contain fewer and larger neurons, and their responses are specialized for the analysis of low-contrast moving images. The axons of geniculate neurons project with a high degree of topographic precision onto layer 4 of the primary visual cortex (V1). The parvocellular and magnocellular cells project on different sublayers within layer 4, indicating a certain degree of parallel processing of the visual inputs, within the visual cortex.





Left: A myelin-stained section through the brain of an owl monkey illustrates the distinct patterns in MT and V1. The myelinated rectangular fibers appear dark blue. The "white matter" stains black because it is made up almost entirely of myelinated fibers. Area MT is the dark blue rectangular band at the top of the section. The part of V1 that is buried in the calcarine fissure is located in the center of the section and shows the strong banding pattern that has led to its alternative name as "striate" cortex. Right: The responses of MT and DL/V4 neurons to a stimulus presented in their receptive fields. The stimulus was an optimally oriented bar. In each case the curve represents the summed responses for a population of neurons recorded from that area. Note that the responses recorded from MT rise and drop off much faster than do those recorded from DL/V4. The recordings were made in owl monkeys by Steven Petersen, Francis Miezin, and the author.

of neurons; "geniculate" derives from the Latin word for "knee" and refers to the shape of the nucleus; "lateral" refers to its location on the side edge of the thalamus. The lateral geniculate nucleus consists of several sets of layers, each of which receives fibers from either the eye on the same side or from the eye on the opposite side of the head. The layers are further specialized for function. One set, the magnocellular ("large-cell") layers, contains large neurons that receive input from the largest retinal ganglion cells with thick, fast-conducting axons. The magnocellular layers are sensitive to rapid movement and minimal contrast in light intensity. The second set, the parvocellular ("small-cell") layers, contains smaller neurons that receive input from smaller retinal ganglion cells with thinner, slower-conducting axons. The parvocellular layers detect finer detail but are less sensitive to motion and contrast than are the magnocellular layers. A partial segregation of the magnocellular and parvocellular inputs is maintained at higher levels in the visual pathway.

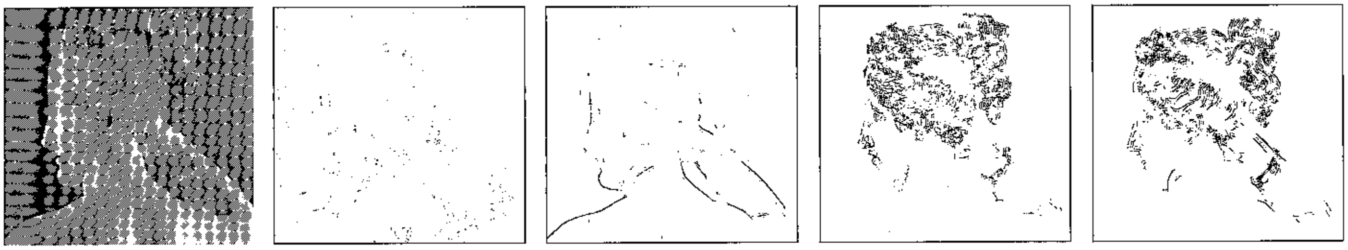
The magnocellular layers project to a separate layer of the primary visual cortex and thence via rapidly conducting axons to the middle temporal visual area, known as MT, where the neurons are very sensitive to the direction of visual motion. The perception of motion requires the fast conduction of the visual input. The fast conduction of information to MT is related to its function in the perception of movement. The speed of axonal conduction is related to the size of the axon and to the thickness of the myelin insulation: the magnocellular neurons have large axons, and the axons in area MT are thickly myelinated.

MT in turn projects to higher cortical areas in the posterior parietal lobe. The studies of Michael Goldberg, William Newsome, Richard Andersen, and their collaborators indicate that the posterior parietal lobe uses the visual input as part of a system to plan movements of the eyes and hands. A parallel stream of connections emerging from the primary visual area is made up of a more slowly conducting set of axons that relays a mixture of parvocellular and magnocellular inputs to the second visual area (V2) and thence to the fourth visual area (V4), where the neurons are very sensitive to size and shape of visual stimuli. Area V4 projects to the inferotemporal visual cortex, which is crucial for the visual memory of objects.

Seeing Spots, Lines, and Curves

In 1958, David Hubel and Torsten Wiesel discovered that most neurons in the primary visual cortex are exquisitely sensitive to the orientation of straight lines and edges within their receptive fields. They also found that neurons within a vertical column extending from the cortical surface to the underlying white matter shared the same preferred line orientation. Neurons that specifically responded preferentially to particular orientations were soon found in other cortical visual areas that received input either directly or indirectly from the primary visual cortex. They also discovered neurons that

An analysis of Paolina, as described by Benoit Dubuc and Steven Zucker. The first image is a photograph of a statue of Paolina Bonaparte, Napoleon's sister, by Antonio Canova. The following four images show how visual cortical neurons could analyze the original image, based on the comparison within the receptive field between points on a line and the flanking regions around the line. Where there are no flanking regions, there are only points, or "dust." Where there are lines without flanking regions, there are curves. Where there are flanking lines at many different orientations, there is turbulence. Where there are flanking parallel lines, there is flow. Thus the system of oriented line detectors can analyze the underlying physical processes that create the visual scene.

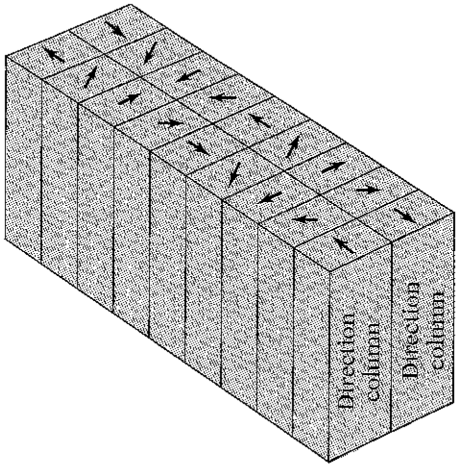


Paolina Dust Curves Turbulence Flow

responded to the ends of lines and to corners defined by intersecting lines. These are probably the basis for the detection of the curvature of lines and the recognition of shapes. Their Nobel-prize–winning work is beautifully recounted in David Hubel's book *Eye, Brain, and Vision*. In 1980, Steven Petersen, Jim Baker, and I found that most neurons in V4 are very sensitive to the dimensions of the stimulus, with some neurons preferring tiny spots while others preferred long rectangles. This set of stimulus preferences by cortical neurons has intrigued theoreticians. Anthony Bell and Terrence Sejnowski have suggested that the orientation selectivity of cortical neurons is a computationally ideal system for analyzing the image properties of natural scenes. Benoit Dubuc and Steven Zucker have proposed that the detection of line endings and curvature form the basis for the visual analysis of complex objects.

Area MT and the Perception of Motion

Area MT, which is present in all primates, is devoted to the analysis of movement in visual images and is one of the clearest examples of the specialization of function in the neocortex. MT also provides some of the best evidence that links neuronal activity to perception. In 1968, Jon Kaas and I first mapped the representation of the visual field in MT and found that it corresponds to a zone of the cortex that contains thickly myelinated axons. Shortly thereafter, Ronald Dubner and Semir Zeki found that the neurons in MT are very sensitive to the direction of movement of stimuli within their receptive fields. MT neurons respond maximally to a preferred direction and are often inhibited by movement in the opposite direction. Like the orientation-selective neurons in V1, the directionally selective neurons in MT are organized in vertical columns. Thomas Albright found that these columns are adjoined by columns containing cells with the *opposite* directional preference.



The columnar organization for direction preference in MT, based on recordings done by Thomas Albright. Each column extends from the cortical surface to the underlying white matter. Along one axis the directional preferences change gradually, but along the other axis adjacent columns are maximally responsive to opposite directions.

Adjacent columns with opposite preferred directions appear to be joined in such a way that activity in one suppresses activity in its antagonistic mate. This relationship is probably responsible for the striking motion aftereffect known as the waterfall illusion. This powerful illusion is elicited if you watch a waterfall for a minute or two and then direct your gaze to the nearby rocks, which will incredibly appear to move *upward* in the direction opposite to the falling water.

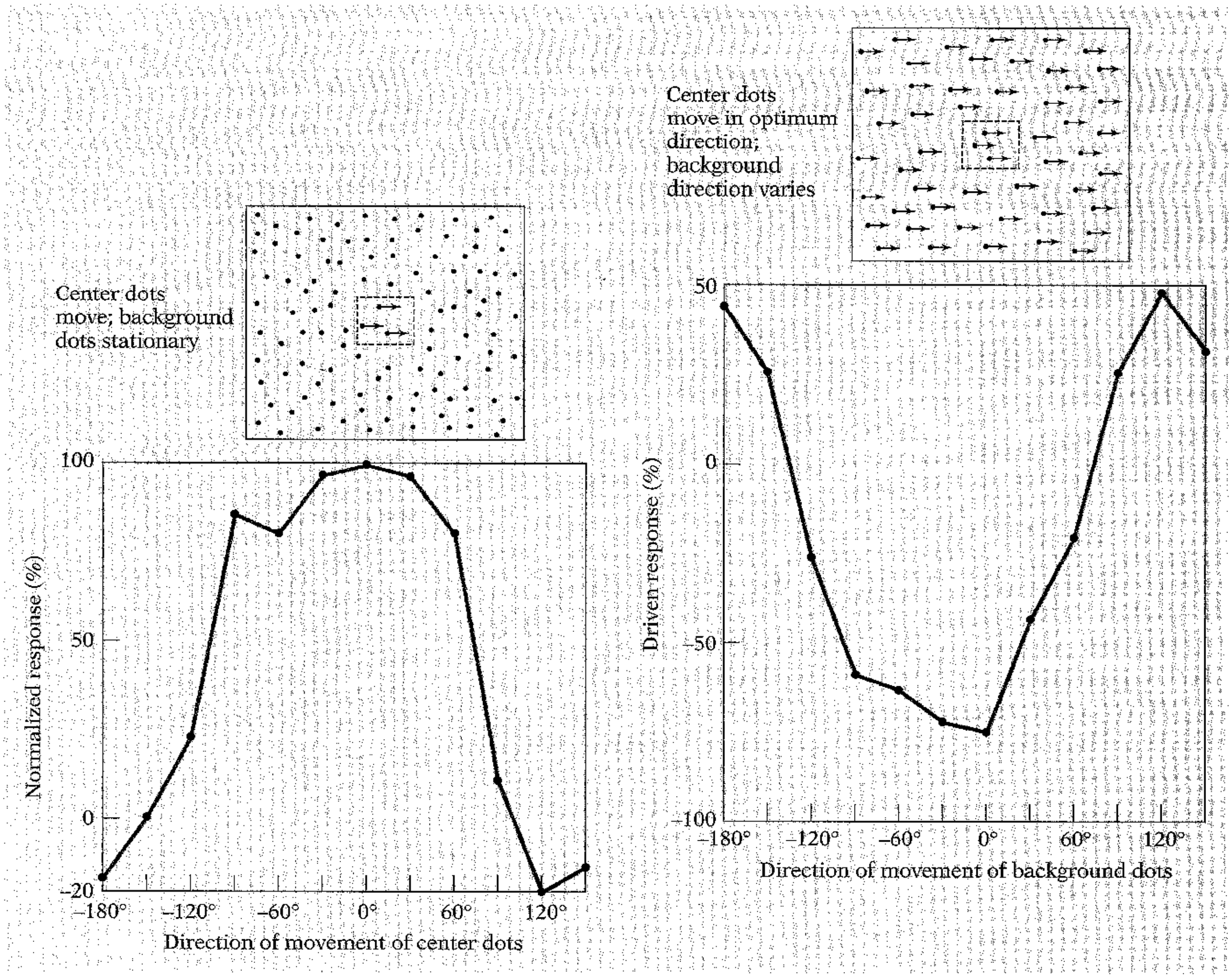
The illusion results when you have exhausted the MT neurons sensitive to the direction of the falling water, thus disrupting the balance between them and their antagonistic partners tuned to the opposite direction. The oppositely tuned neurons are released from inhibition and become active, which leads to the disturbing perception that the stationary rocks are moving upward! Steven Petersen, James Baker, and I showed monkeys continuously moving images, like a waterfall, and then tested the responses of their MT neurons. We found that their responses were suppressed when tested with stimuli moving in the same direction as the prior adapting movement and were enhanced for stimuli moving in the opposite direction. More recently, Roger Tootell and his colleagues have induced the waterfall illusion in humans and have found similar changes in MT monitored with functional magnetic resonance imaging (MRI).

There is additional evidence that the activity of MT neurons is directly related to the perception of motion. Kenneth Britten and his colleagues recorded from MT in monkeys that were observing ambiguous images that could be perceived as moving either in one direction or its opposite. The monkeys had been previously trained to report the direction in which they perceived motion. When the activity of the MT neuron was higher, the monkey tended to perceive the ambiguous image as moving in the preferred direction of the neuron; when the activity was lower, the monkey tended to perceive the image as moving in the antipreferred direction. Daniel Salzman and his colleagues did an analogous experiment in which they induced activity in MT neurons by stimulating them with microelectrodes. The microstimulation caused the monkey to perceive motion in the direction corresponding to the preferred direction of the neuron. Thus the activity of directionally selective MT neurons appears to cause the perception of motion in the preferred direction of the neurons.

Imagine that you are gazing at a waterfall. If you were to stare at the site of the star in the midst of actually falling water for a minute and then at the rocks below, the rocks would appear to move upward in the direction opposite to that of the falling water. Be careful if you try this with a real waterfall; it can be very disorienting to see the rocks move!

Seeing the Visual Context

The perception of qualities of objects depends heavily on the surrounding visual context. In 1982, Francis Miezin, EveLynn McGuinness, and I found that MT neurons are sensitive not only to the direction of motion of objects but also to the movement of the background. We found that when we mapped the receptive fields of MT



neurons on a large featureless screen, as is typically done in most vision experiments, the responses were restricted to what we called the classical receptive field. We invented this term because this field corresponds to that obtained in most visual-receptive–field mapping experiments. However, when the screen was filled with a background of coherently moving dots, we found that the direction of motion of the dots moving entirely outside the classical receptive

Opposite: The graph on the left shows how an MT neuron responded to an array of dots moving in different directions within the classical receptive field enclosed by the dotted rectangular outline. The dots in the surrounding field were stationary. The responses are plotted as percentages of the response to the best direction of movement, which was rightward (0 degrees). The graph on the right shows how the same neuron responded when the classical receptive field was stimulated with the optimum stimulus and simultaneously the direction of motion of dots in the surrounding visual field was varied. Directions of surround motion near the preferred direction suppressed the responses, and directions of motion near the antipreferred direction facilitated the responses. Thus the tuning of the nonclassical field was antagonistic to stimulation within the classical receptive field.

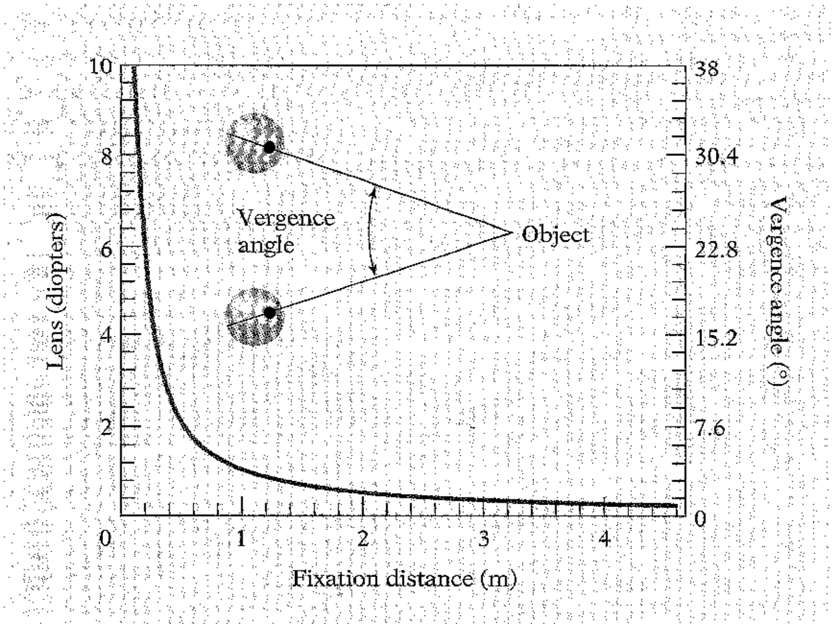
field had a powerful and specific effect on the responses to stimuli presented within the classical receptive field. This was very surprising, because movement of the background had no effect when there was no stimulus within the classical receptive field. Thus the response of the neuron was jointly dependent on stimuli within the classical field and outside it. Background movement in the preferred direction of movement within the classical receptive field suppressed the response, while background movement in the antipreferred direction often powerfully facilitated the response to stimuli presented in the preferred direction within the classical field.

When we mapped the sizes of the nonclassical receptive fields, we were surprised to discover that they often extended over more than half the entire visual field of the monkey. Our results indicate that the responses of cortical neurons are the product of the interaction between local cues and the global context. Analogous results have been obtained for other types of stimuli in other cortical areas. The neural tuning for object distance, described in the next section, is an example of a nonclassical effect. These effects imply that in addition to the set of dense local connections among neurons that is related to the highly ordered retinal topography of the classical receptive fields, there is a second set of connections, broader and sparser, that supports the more global responses from the nonclassical receptive field. These global effects may be responsible for many integrative aspects of visual perception such as the discrimination of figures from their background and perhaps visual memory.

Seeing Size and Distance

Survival depends on knowing whether the furry animal in the distance is large and potentially dangerous or small and a possible meal. Determining the size and distance of objects is a fundamental feature of visual perception that probably developed early in primate evolution. More than 300 years ago, René Descartes reasoned that the perception of the size of nearby objects is related to the motor act of fixating on them, while the perception of more distant objects depends on what the viewer knows about the object and its visual context. Imagine looking at a nearby object. Your eyes converge on it. As you move the object away the angle between the lines of sight from your two eyes will decrease. More than a meter away the lines of sight will become nearly parallel and will not change very much as the object recedes farther into the distance. Thus there are large changes in the vergence angle between the eyes when fixating on objects in the near field, but small changes when they fixate on more distant objects. Similarly, the accommodative reflex causes the lens to change its optical power as a function of fixation distance, with large changes for close distances but small changes for distances of more than a meter.

In an otherwise featureless visual field that offers no clues for comparison, human subjects can discriminate the sizes of objects up to a distance of about 1 meter; at greater distances they underestimate the true sizes. This finding by Herschel Leibowitz indicates that the motor act of fixating on a object is sufficient for accurate size judgments for near objects, but that the visual context is required for judging the sizes of more distant objects. As fixation passes from the nearest possible point out to a distance of 1 meter, the vergence of the eyes and the accommodative state of the lens go through about 90 percent of their potential variation; thus beyond 1 meter there is little further variation upon which to base distance discrimination. This optical constraint means that the accurate judgment of greater distances must be based on other cues. With the full visual context available, adults can discriminate the true size of objects out to at least 30 meters, but 8-year-old children can accurately judge the sizes of objects only to a distance of 3 meters. At greater distances children underestimate the true size of objects, and the farther away the object, the greater their underestimate. Thus children seem to be unable to take full account of the visual context for distant objects because they underestimate the size of distant objects in a manner



Changes in the accommodative state of the ocular lens and the vergence angle between the eyes as a function of the fixation distance between the viewer and the object. The curves for these two functions are identical. Note that for distances greater than 1 meter there is little change in accommodation power or vergence angle. This means that these cues will be of little use in determining the distance of objects greater than 1 meter away, and that, as proposed by Descartes, the visual system must rely on cues that are strongly dependent on learning and experience. This is another example of how physical constraints have influenced brain evolution.

similar to adults who cannot see the visual context. Children develop the capacity to use the visual context to make accurate judgments by constantly probing their spatial environment and refining their impressions. This probing proceeds in infants from the nearby space within arm's reach and extends gradually as the child matures to incorporate the wider world through continual feedback derived from the experience of moving through the environment. It is easy to forget as adults that as children we once saw the world very differently. However, this change in perception with maturation is revealed by the common experience of returning after a long time to a place that we occupied as children, such as a school room, and perceiving it as adults as very much smaller than we experienced it as children.