Behavioral Development: Effects of Environments

An animal's environment early in its life can have a pronounced effect on its subsequent behavior. The effects of environment on behavior are, however, often difficult to distinguish from the effects of genes on behavior. Investigators who study visual and communicative behavior have recently found ways to specify when and, in some cases, how environments affect neural connections. A theory has emerged that the nervous systems, and hence the behavior, of animals may be permanently modified during critical periods of early life in response to environmental stimuli.

Neurobiologists have determined how nerve cells interact at early stages of the visual pathway in animals of several species, including rabbits, cats, and monkeys. This work paved the way for studies of how visual experience affects these neural networks. It has become clear that animals that are visually deprived when they are young subsequently have nerve cells that respond abnormally to visual stimuli. Such an effect was first described about 10 years ago by Torsten Wiesel and David Hubel of Harvard Medical School, who analyzed the consequences of visual deprivation in kittens.

In their original experiments, Wiesel and Hubel sewed one of a kitten's eyes shut shortly after birth. Since kittens are born with their eyes closed, this kitten never had an opportunity to see with its deprived eye. When Wiesel and Hubel opened the kitten's eye a few months later, they found that it could not see with that eye. This deprivation affected the way visual stimuli are processed in the kitten's brain, since only a small fraction of the nerve cells in the animal's visual cortex responded with electrical signals when light was shined on the deprived eye. Nearly all of those cortical cells, however, responded when light was shined on the normal eye. In a normal kitten, the vast majority of cortical cells respond to stimuli of either eye.

Wiesel and Hubel discovered that this sort of visual deprivation can only exert an effect when a kitten is young—between about 4 and 16 weeks old. As few as 3 or 4 days of visual deprivation when a kitten is 4 or 5 weeks old will substantially reduce the number of cortical neurons that respond to visual stimuli of the deprived eye. An adult cat, in contrast, is insensitive to such deprivation, even when its eye is sewn shut and not opened for more than a year.

What, as well as whether, an animal sees may be affected by early visual experience. Some investigators report that abnormal visual stimuli can modify what an animal is able to see by altering the orientation specificity of its cortical neurons. A neuron in the visual cortex of the brain responds when a particular area of the retina, called the receptive field of that neuron, is stimulated by lines oriented in a particular direction. Thus, one cell of the cortex responds when a particular area of the retina is stimulated by a horizontal line and another cell responds when that area is stimulated by a vertical line. The orientation of the lines that cause a cortical cell to respond is the orientation specificity of that cell. Normally, any orientation of a line will cause some cortical neurons to respond.

Colin Blakemore and G. F. Cooper of the University of Cambridge in England reared kittens so that their only visual experience consisted of vertical lines. The kittens were reared in the dark except for a few hours of each day when they were put in a cylinder painted with black and white vertical stripes. The kittens, these investigators reported, subsequently had no cortical neurons that responded to horizontal lines. Presumably, if tested these animals would not be able to see horizontal lines.

Helmut Hirsh of the State University of New York at Albany and D. N. Spinelli of the University of Massachusetts reared kittens with masks so that one of a kitten's eyes saw only vertical stripes and the other saw only horizontal stripes. The cortical cells that responded to stimuli of the eye that had seen only horizontal lines did not respond when that eye was stimulated by vertical stripes, and conversely.

Experiments Are Questioned

The experiments indicating that orientation specificity can be affected by early visual experience have recently been questioned by several groups. For example, Michael Stryker and Helen Shark of the Massachusetts Institute of Technology reared kittens so that they only saw either horizontal or vertical lines and found no effect of these abnormal environments on the orientation specificities of the kittens' cortical neurons. Their experimental techniques differed, however, from those used by Blakemore, Hirsch, and their associates. First, they tested cortical neurons at regular intervals across the cortex, so as to minimize sampling errors. Second, they stimulated the receptive fields of the kittens' retinas with computer-driven optical displays rather than with hand-held optical stimuli, which were used by other investigators. Third, they ensured that the person testing the kittens for orientation specificity did not know whether the kitten had previously seen only horizontal, or only vertical, lines. Stryker and Shark are uncertain whether these differences in experimental design or some other factors are responsible for their failure to reproduce the results of Blakemore and others.

Some experiments with human beings provide evidence that visual acuity, and possibly orientation specificities of human cortical neurons, may be affected by early visual experiences. Most people see horizontal and vertical lines with greater acuity than oblique lines. Robert Annis and Barrie Frost of Queen's University in Kingston, Ontario, proposed that this effect may result from early exposure to environments that contain predominately horizontal and vertical lines. The Cree Indians, they noticed, do not grow up in such an environment but instead see a more heterogeneous array of contours. Their homes are conical, for example, and so they have a greater exposure to oblique lines than do most people. When Annis and Frost tested the visual acuity of Cree Indians, they found that these people did see oblique lines as well as horizontal or vertical lines; whereas a control group of Euro-Canadians did not.

Ralph Freeman of the University of California at Berkeley, together with Donald Mitchell of Dalhousie University in Halifax, Nova Scotia, and Michael Millodot of the University of Montreal studied the effects of astigmatism on visual acuity. A person with astigmatism has optical abnormalities that cause lines of certain orientations to appear blurred. For example, such a person might see all horizontal lines as blurs but vertical lines would be clear. Freeman, Mitchell, and Millodot found that reduced acuity to lines of certain orientations persists even when astigmatism is optically corrected with lenses. People with astigmatism consistently see horizontal lines with different acuity than they see vertical lines. Since this deficiency cannot be optically corrected, Freeman and his associates presume it is caused by a defect in the way visual information is decoded by the brain.

To test this hypothesis, Freeman and Pettigrew raised kittens with masks to simulate astigmatism and then removed the masks and probed the visual cortices of these animals. They report that the kittens' cortical neurons responded best when their eyes were stimulated by lines of orientations that were not blurred by the masks. Although analogous studies of cortical neurons cannot be performed with human beings, Freeman and Larry Thibos, also at the University of California at Berkeley, did find that subjects who, because of astigmatism, have reduced visual acuity when they view lines of a particular orientation, also have reduced electrical activity in their brains when they view such lines. Freeman suggests that, since there is some evidence that severe astigmatism is congenital, people with astigmatism had their visual perception restricted during a critical period of development. Thus they lost, or never developed, the ability to respond normally to lines of certain orientations.

In the 10 years since Wiesel and Hubel demonstrated effects of visual deprivation on the cortex of the cat, much evidence has been produced that confirms the hypothesis that early visual experience affects how and what animals see. At the very least, an animal prevented from seeing with one eye during a critical period loses vision in that eye. An animal prevented from seeing with both eyes at the same time (when first one eye, then the other, is covered) loses binocular vision.

Two explanations of these effects of environments on vision have been proposed. Hubel and Wiesel suggest that the neural connections necessary for normal responses in the visual cortex are genetically determined and consequently established at birth. Animals, however, go through critical periods when some of this information can be lost, through attrition, if it is not used. An alternate hypothesis, supported by Blakemore, John Pettigrew of the University of California at Berkeley, and others, is that genes code only for a rough outline of possible neural connections in the visual system. The final connections are established in response to environmental stimuli during critical periods of life.

Hubel and Wiesel proposed their attrition hypothesis when they found that some cells in the cortices of kittens with no visual experience respond specifically to lines of particular orientations. This result was questioned by Pettigrew, Blakemore, and others who argued that, since kittens have immature visual systems at birth, it is difficult to distinguish between orientation specificities that arise in response to environmental stimuli and orientation specificities that develop as directed by a genetic program. These investigators detected few, if any, orientation specific cells in the cortices of visually inexperienced kittens.

Hubel and Wiesel have now completed work with monkeys that supports their hypothesis of attrition. Monkeys are born with more mature visual cortices than are kittens and they appear to be able to see from the day of birth. Most cells in the visual cortices of newborn monkeys, they report, seem roughly normal even by adult standards. These cells have orientation specificities and are binocular—that is, they respond when appropriate receptive fields of both retinas are stimulated simultaneously. However, a monkey whose eyes were sewn shut at birth and not opened for 3 weeks had a great diminution of binocular cells. This, according to Hubel and Wiesel, is evidence that visual deprivation results in a deterioration of innate neural connections in the monkey.

In support of the hypothesis that neural connections in the visual system develop in response to environmental stimuli, Pettigrew cites the results of an experiment he and Freeman carried out. In this experiment, kittens were kept in the dark for the first 28 days of their lives. Then, for the next 13 days, the kittens spent 3 hours a day in an environment in which they saw only small, bright spots of light on a dark background and spent the remainder of those days in the dark. The kittens subsequently possessed cortical neurons that were highly responsive to spots of light, rather than the usual lines. Since these spot detectors were abnormal by ordinary standards, but were optimal cells for responding to these kittens' environment, Pettigrew suggests that these cells developed in response to the kittens' environment.

Additional arguments in favor of the developmental, as opposed to the attrition, hypothesis, are based on experiments with kittens and rabbits that indicate that many specific neural connections are not formed before visual experience occurs. Since there is evidence in support of both the attrition and the developmental hypothesis, the question of which is correct is still subject to debate.

Genes Affect Communication

The neural connections necessary for communication have not been identified. However, investigators have found that the ability to communicate, like the ability to see, is to a great extent genetically determined. But, like vision, communication can be affected by environmental stimuli during critical periods in animals' lives. It has been suggested that the ability to transmit information is, in many instances, genetically linked to the ability to receive information.

Peter Marler of Rockefeller University established that environmental stimuli normally play a key role when many species of birds learn to sing. When he raised certain birds with very different songs, such as red-winged blackbirds, white-crowned sparrows, and Arizona juncos, in isolation, the birds developed abnormal songs that were simpler than those of their wild counterparts, although the songs had some species specific characteristics.

Some birds need to hear the songs of their species in order to learn a normal repertoire of songs. Such species often have local song dialects. These birds, when reared in isolation, can learn appropriate songs by imitating recordings of songs of their own species. However, most of these species do not imitate recorded songs of different species.

Other bird species, which usually do not have local song dialects, can learn their songs without hearing songs sung by adults of their species. For these birds, the social stimulation provided by the presence of other young birds suffices to allow them to learn appropriate songs. Marler demonstrated this phenomenon by removing a group of five Arizona juncos from their nests when they were a week old and rearing them together. The young birds improvised songs and generally were socially stimulated to develop among them 21 song types, all of which would be acceptable as normal wild songs.

Birds need not only hear other birds in order to learn normal songs, but they must also hear themselves. Mark Konishi of the California Institute of Technology and Fernando Nottebohm of Rockefeller University found that deaf birds of different species produce similar grossly abnormal songs. These songs, Marler says, sound "noisy, scratchy, and unstructured." Marler had previously found that, for white-crowned sparrows, a critical period for song learning occurs before a bird learns to sing. Birds captured in the wild after this period and reared in isolation will develop normal songs. However, Konishi reports that birds taken from the nest and deafened after this period but before singing will produce the typically abnormal songs of birds deafened before the critical period.

Marler explains these results on song learning by means of a hypothetical auditory template. Many kinds of birds, he suggests, are genetically provided with only a rough outline, modifiable through experience, of what their songs should sound like. This outline is manifest when birds are reared in isolation and is usually used in guiding the bird in what model to imitate. The birds normally learn songs by matching their vocal output to some learned or innate concept of proper songs. According to Marler, the abolition of species differences by deafening early in life is consistent with the hypothesis that, during normal development, birds of different species rely on divergent instructions in their templates for selection of a model to copy.

Usually, only male birds sing; females recognize and respond to songs of the males of their species. This ability to respond, according to Konishi, may be a product of genes that are linked to genes that code for song production. The hypothesis that females also inherit a modifiable song template provides an explanation of the discovery that females have all the genetic information necessary to learn songs. Konishi injected females with the male sex hormone testosterone, which causes females to sing. He found that these females learned songs in the same way as males and that they had the same critical period for song learning.

Although a genetic link between song production and reception in birds is not established, a precedent for such a hypothesis exists with crickets. Ronald Hoy of Cornell University and David Bentley of the University of California at Berkeley showed that all the information necessary for transmitting and receiving cricket songs is genetically derived—environment plays no role—even though each cricket species, like each bird species, has its own song. Hoy and his associate Robert Paul of Cornell University report that, when crickets of two different species are mated, their male progeny produce a hybrid song (only males sing) that differs from the songs of males of either parental species. Moreover, the female progeny prefer the hybrid song of their brothers to the songs of males of either parental species, indicating that neural connections for song production and reception are inherited together.

Recently, Peter Eimas of Brown University and his associates discovered that human beings inherit, rather than learn, some abilities for perceiving speech sounds. Human infants that have not yet begun to speak are able to perceive contrasts in speech sounds and subsequently lose the ability to hear contrasts between speech sounds that are not differentiated in the language they eventually speak, in agreement with the attrition theory in vision.

People perceive speech sounds and nonspeech sounds differently. Nonspeech sounds that have continuously varying frequencies are heard as a continuum of sounds. Speech sounds that have continuously varying frequencies are heard as distinct segments of sound. For example, if a person listens to a continuum of sounds, produced by a machine, that vary from the sound [ba], as in bark, to [da], as in dark, the continuum will sound like two segments: one segment will sound like [ba] and the other like [da]. No sounds will be perceived as intermediate between [ba] and [da]. This tendency to segmentalize speech sounds, which is crucial to the comprehension of language, is manifest so early in life that some investigators think of it as inherited.

Kunito Miyawaki of the University of Tokyo, Alvin Lieberman of the Haskins Laboratory in New Haven, and their associates report that adult native speakers of Japanese cannot distinguish between the sounds [ra] and [la], whereas native speakers of English can. Eimas finds that the ability of English speakers to make this distinction is not learned, since American infants between 2 and 3 months of age distinguish between [ra] and [la]; the Japanese apparently lose this ability.

The critical period for retaining the ability to perceive phonetic contrasts such as that between [ra] and [la] is unknown. However, Eimas suggests it may include the first 16 years of life. Japanese who were exposed before the age of 16 to a language, such as English, in which [ra] and [la] are distinguished could later hear this phonetic contrast.

Bird and human communication, then, like vision, has some components influenced only by genes. Other components can be altered in response to environmental stimuli, although the range of modifiability seems also to be influenced by genetic constraints. The nature and extent of these constraints on the way in which environments produce these lasting changes in behavior promises to be a hotly debated question for future research.

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Foundations of Mathematics: Unsolvable Problems

Mathematicians have known since 1931 that some exotic mathematical problems must necessarily be unsolvable, but only within the last decade did they begin to discover examples of such problems in many parts of mathematics. Now hundreds of such problems have been proved to be unsolvable. Recently two rather famous problems—one proposed by the German mathematician David Hilbert in 1900 and the other proposed by the Russian mathematician Mikhail Souslin in 1920—have been added to the growing list.

Actually, there are two distinct types of "unsolvability" in mathematics. One kind, illustrated by the 19th-century result that the classical Greek problem of trisecting an angle is unsolvable, is really an instance of "impossibility." The other type, of far greater scientific and philosophic import, is really a judgment of "undecidability": the discovery of non-Euclidean geometry showed, for example, that Euclid's fifth (parallel) postulate could not be decided—that is, proved or refuted—on the basis of the other accepted axioms of plane geometry.

The possibility—indeed, the certainty—that some mathematical problems may actually be undecidable was first discovered by the logician Kurt Gödel, now at the Institute for Advanced Study in Princeton. He showed in 1931 that all axiomatic systems (except very simple ones) must contain assertions that can be neither proved nor refuted by logical deduction from the given axioms. This means that all of the famous unsolved problems of mathematics—the four color problem, Goldbach's conjecture, Fermat's last theorem, and so on—became candidates for the purgatory of perpetual undecidability, and that mathematicians will have to determine whether they are undecidable or merely very hard to solve.

The first major breakthrough in the search for specific undecidable propositions came in 1963. In that year Paul Cohen of Stanford University, extending work begun by Gödel in 1939, established the undecidability of a conjecture due to the 19th-century mathematician Georg Cantor concerning the relative sizes of subsets of the real number line. Cantor was trying to formulate a concept (now called cardinal number) that would permit comparative judgments about the sizes of infinite sets. He conjectured that every subset of the real numbers must have the same size either as the set of all integers or as the much larger set of all real numbers.

Cantor's so-called continuum hypothesis took nearly two-thirds of a century to resolve, and then Cohen found that the resolution was neither a proof of the conjecture nor a counterexample to it. It was, rather, a revolutionary analysis of the limitations of logical reasoning leading to the conclusion that Cantor's conjecture can be neither proved nor disproved on the basis of the accepted axioms of set theory.

Cohen's method of proof, the basis for most undecidability results, is a delicate chain of reasoning in which one very carefully forces into existence a mathematical