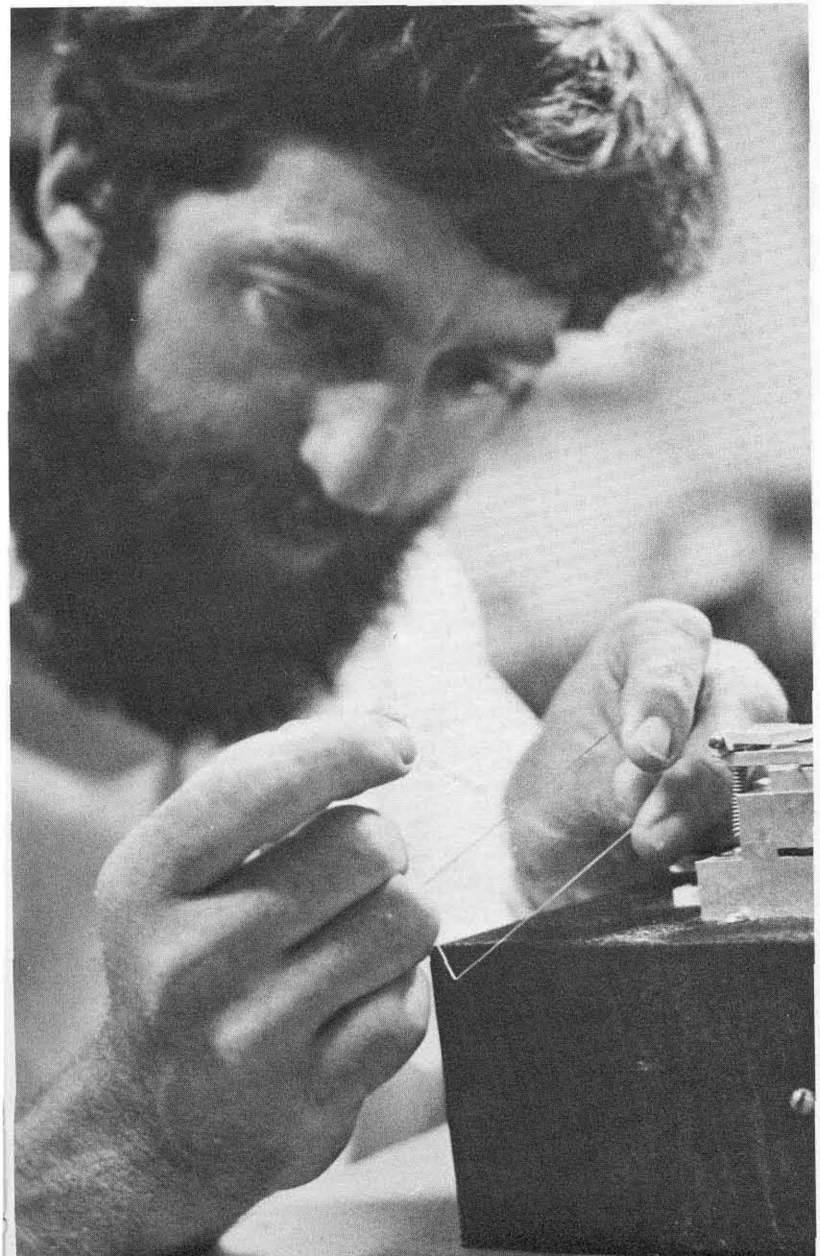
Line Detectors, Lion Detectors, and the Critical Period



John Pettigrew, assistant professor of biology, is investigating the importance of early experience in the development of visual perception in animals. The work has important applications to the study of visual problems in human beings and how these affect learning.

BY JOHN PETTIGREW

Some studies of the remarkable nature of the changes that can be wrought on the developing brain by environment

The five hundred million or so neurons in the visual cortex of a mammal permit him to estimate the statistical properties of the outside world. Each neuron has a specific "trigger feature" that will cause it to fire when this feature is present in the outside visual space. Such a feature will produce a certain sequential pattern of activation of the receptors in the eye; these ultimately send the information they received on to the cortex to activate the vision.

This discovery was made by David H. Hubel and Torsten N. Wiesel at the Harvard Medical School in the early 1960's when they discarded the use of high-intensity flashes of light and studied the response of single nerve cells in the visual cortex by projecting various patterns on a screen in front of a cat. They found that the trigger feature of the single cortical neuron was highly specific; the neuron would respond only if there was a contour or edge with a specific orientation in a specific part of the visual field. In addition, the line usually had to be moving, often in a specific direction at a specific velocity. Different neurons had different preferred orientations so that in a normal cortex there were cells that covered the full range of orientation around the clock.

Trigger features of cortical neurons can take a great variety of forms, and in the primary visual cortex at least five different stimulus dimensions are represented at each point in the visual field:

1. ORIENTATION.

2. BINOCULARITY. Every cell gets a separate input from each eye. This has two aspects: ocular dominance—there being some variation in the strength of activation from the two eyes; and disparity—there being variation in the precise positions of the two retinal areas, one in each retina, that activate the cells. (This variation in retinal disparity provides a cue to the distance of the trigger feature.)

3. CONTRAST. Some cells respond only if the stimulus is black on white, others respond if it is white on black;

some cells respond to an advancing dark edge, a receding light edge, and so on.

4. SPEED AND DIRECTION OF MOVEMENT. Many cells respond only when the required contour is moving, and for some cells, the movement must be sharply defined for both speed and direction.

5. SIZE. Some cells respond only to targets whose size does not exceed some optimal value.

Modifiability of the Trigger Feature

The discovery that single neurons have surprisingly specific trigger features has been succeeded by the discovery that the specific trigger features are dependent upon early visual experience. In the case of kittens, this means about two or three months after birth. During this time, when interconnections between cortical neurons are being formed and reformed at a rapid rate, subtle changes in stimulation cause long-lasting changes in organization; hence the term "critical period" in cortical development.

In the initial experiments it was shown that the second aspect of the trigger feature, binocularity, could be profoundly altered by closing one eye of a kitten during this critical period of cortical development. After such eye closure, neurons are preferentially activated by the eye that was open during early postnatal development.

A second vivid demonstration of the effect of early visual experience on specific cortical neuron properties was provided by H. V. B. Hirsch of the State University of New York at Albany. He raised kittens in total darkness except for a short time each day when they wore masks that restricted what they saw to contours of a specific orientation. Afterward, the kittens were found to have cortical neurons that responded preferentially to orientations present during the rearing; no neurons could be found that responded selectively to orientations the kittens had not seen.

Further confirmation of the plasticity of the orientation detection aspect of cortical neurons came from Colin Blakemore of Cambridge University, who raised kittens in long cylinders painted with stripes of different orientations. Afterward, the kittens had a striking deficit—both behavioral and physiological. This deficiency becomes obvious when two kittens—one raised in a vertical environment, with vertical stripes, and the other raised only with horizontal stripes—are put into a normal room for the first time. It is clear that they have visual capabilities, but when one tries to get them to play with a stick in their usual kittenish way, they will do so only one at a time. If you hold the stick vertically and move it, one kitten will come forward, follow it, and play with it, while the other looks about vacantly. The roles are reversed when you hold the stick horizontally. When they were examined physiologically with microelectrodes, both kittens had a striking absence of neurons that would respond selectively to the orientation the kitten had not seen during development. In other words, the kitten raised in the vertical-striped environment had an unusual number of neurons that responded selectively to vertical contours, but none that responded selectively to horizontal contours.

The discovery that single neurons have specific trigger features has been succeeded by the discovery that these features depend on early visual experience

A recent experiment underlines the remarkable nature of the changes that can be wrought on the developing brain by the environment. If a kitten is raised so that it never sees lines at all, then subsequently no neurons can be found that respond selectively to lines—whatever their orientation. This was discovered when we reared kittens in a planetarium-like environment—a big black sphere with little holes drilled in its roof so that the kittens' visual experience was confined to small pinpoint sources of light. When we examined the visual cortex of these kittens, we found a large number of cells with very unusual properties. Normally, in the visual cortex each cell has a specific requirement for a line or edge at a particular orientation. But in these kittens we found many cells that could be activated from a large part of the visual field by a tiny light spot. If the size of the spot was increased beyond about half a degree, the cell failed to respond. In a large sample of cells we could not find any that gave the usual vigorous and highly selective responses to elongated line stimuli

Implications for Humans

The finding that the specific orientation of single neurons to lines of that particular orientation is dependent upon the presence of contours of such orientation in the early visual environment led directly to the understanding of an effect in humans with astigmatism. This effect, called meridional amblyopia (partial blindness for orientations across a particular meridian) had been puzzling.

If a normal subject is tested for his ability to discern the lines in a grating of black and white stripes as a function of its orientation, he is able to see a much finer horizontal or vertical grating than one that is oblique. When the subject has ocular astigmatism (so that the lens of his eye is more powerful in one axis than another), the retinal image is blurred along one axis. However, even with perfect optical correction of the astigmatism, it is found that this subject will still have a deficiency in his ability to discern the lines of a grating whose orientation corresponds to the one that was blurred in his early life, before he was prescribed spectacles. Thus, even though there is now a sharp image on the subject's retina, the subject is still much poorer, because of a defect in the neural circuitry, at discriminating oriented lines having the same orientation as that blurred in his early childhood. Recent work suggests that if this optical abnormality is recognized and corrected early in childhood, the neural defect can be prevented.

One may even ask whether the normal subject's ability to discern horizontal and vertical contours more easily than oblique ones may not be the environmental result of the predominance of horizontal and vertical contours in Western architecture. A preliminary study on Cree Indians, who live within the sloping walls of wickiups, has failed to show a visual preference for horizontal and vertical over oblique, suggesting that Western architecture has in fact a mind-bending effect.

Nature and Nurture

While I have laid much stress on the plastic and modifiable properties of cortical neurons, let met also stress their limitations. First of all, a young kitten with *no* previous visual experience does have neurons with slight preferences for specific visual stimuli. These vague, initial preferences probably determine to some extent the direction of the shaping induced by environmental influences. For example, most visual neurons in a totally naive kitten have a specific sensitivity for movement, often in a specific direction. This movement sensitivity persists in an environment that is stroboscopically illuminated and therefore devoid of the stimulus of image motion.

Secondly, there appear to be marked individual variations in responses developed to visual stimulation during the critical growth period of kittens. In a number of cases I have observed quite different outcomes from identical visual stimulation in two kittens of comparable age. This becomes particularly striking in those cases where visual stimulation is potentially ambiguous or rivalrous and where the animal might have to make some choice about which aspect of the stimulus is important. For example, if one orientation is presented to one eye, and a different orientation is presented simultaneously to the other eye, it is possible to get two quite distinct types of resultant cortical organization in different kittens. In one type the cortex appears to be organized about the *particular eye* (ocular dominance) so that those neurons are grouped together which are driven only by one eye and only by the orientation to which that eye was exposed.

In the second type the cortical organization appears to be based primarily on orientation; one finds groups of neurons that respond to a particular orientation, but which may be driven by either—or both—of the eyes. This is surprising because it indicates that many cells are driven only by one eye, but by an orientation different from the one which that eye saw during the rearing.

In addition there appear to be marked species differences. The phenomena I have described for the kitten may not apply to the rabbit—a prototypical prey animal that does much information processing (including the processing for orientation) in its eye, which sends this information directly to the brainstem for action. In the cat, most of the neurons with highly specific trigger features are found in the visual cortex, which provides the most important input to the brainstem, where action patterns can be triggered. In contrast, the rabbit has large numbers of neurons with highly specific trigger features in the eye itself. These cells project directly to the brainstem, which is therefore much less dependent upon information relayed to it via the cortex. In the rabbit, then, one finds that rearing in an environment with a specific orientation has no effect on the development of the distribution of preferred orientations in the cortex, presumably because information about that orientation has been transmitted from the retina, where the connections were permanently established before visual experience.

Perhaps evolution provided an opportunity for a carnivorous animal to be partially freed from innate prewiring because of the long periods of dependence and protection afforded by parents. The need for a built-in "lion detector" is clearly not so great for the lion cub, protected as he is for so many months within the pride, as it is for the young zebra foal born on the veldt, who must be equipped for flight very soon after emerging from the uterus. Following this analogy, one would expect that environmental influences on cortical development will be of supreme importance in the most altricial (the most helpless at birth, that is) of all animals, the primate.

Perhaps the greatest hope for education lies in the possible definition of the time of onset, time course, and exact sequence of the critical periods for the development of "higher" cortical analytical processes, like those used for verbal, visual, and musical communication. Is it possible that everyone could have perfect pitch if we knew the precise time at which to expose the developing brain to the chromatic scale? □