The visual system of the cat

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So much of our current knowledge about the neurophysiology of vision has come from studying the visual system of the cat. Using microelectrode techniques, neurophysiologists have examined in great detail the spatial properties of receptive fields of neurons at various levels of the feline nervous system, and headway is now being made in discovering the patterns of neural connections which give rise to the remarkable degree of stimulus selectivity characteristic of these neurons. This paper reviews the major findings concerning the visual system of the normal adult cat, from optics to visual cortex, and summarizes the physiological consequences of early visual deprivation on the visual nervous system of the cat. The review concludes with remarks about the validity of generalizing from cat neurophysiology to human vision.

In the biological sciences, there exists a strong tendency for various research areas to adopt a methodological paradigm which concentrates on a particular animal species. For instance, in the case of genetics we immediately think of the fruit fly as a laboratory staple. Another classic example, familiar to students of animal learning, is the white rat which, in its heyday, enjoyed almost total domination in psychology laboratories. For a variety of reasons, including economy and methodological control, it makes sense for a discipline to focus its attention on a single species, although the onus is on those researchers interested in generalizing to the human species to demonstrate that the selection of their animal model involves considerations which go beyond those of simple convenience.

In the last couple of decades, the cat has emerged as the dominant species in the literature of visual neurophysiology. The cat's entry into the vision laboratory actually traces back to the early 1940s when Granit (1947) and colleagues first began using microelectrode techniques to record neural activity from cat retina. It wasn't until the 1950s, however, that the cat became the animal of choice, surpassing the frog as the most popular vertebrate for the study of visual neurophysiology. Since that time, the cat has been an extremely generous benefactor, contributing to our understanding of the functional organization of the vertebrate visual system, at least up to the level of the visual cortex. We now know

a great deal about the receptive field properties of neurons at several processing stages of the feline visual nervous system and we are beginning to learn how these physiological properties may be correlated with structural features such as morphology and sites of projection. These physiological and anatomical data, in turn, have stimulated a great deal of theorizing about the role of these neural mechanisms in the synthesis and perception of the complex visual world, a problem which traditionally has fallen within the domain of sensory psychology. It would be fair to state that cat neurophysiology currently represents the primary source of neural building blocks from which the majority of models of human vision are constructed (Sekuler, 1974).

In view of the profound influence of cat neurophysiology on current thinking about the neural basis of vision, it is useful to know some of the details of the visual system of the cat. This review seeks to provide these details on a stage-by-stage basis, going from optics to visual cortex. The scope of this review is limited to data which bears upon the spatial properties of receptive fields in normal, adult cat and to data dealing with the importance of early visual experience in determining these receptive field properties. No coverage is given to the meager work on the chromatic properties of cat visual neurons (e.g., Daw & Pearlman, 1969) or those studies of the effects of eye movements on the excitability of cat visual neurons (e.g., Adey & Noda, 1973). Also not included is the recent work on the visual system of the Siamese cat (e.g., Guillery & Casagrande, 1977).

This review is organized in the following manner. First, the paper proceeds stagewise through the visual nervous system, at each level describing major findings that pertain to the receptive field layout of neurons at that level. When available, information about possible underlying neural circuitry is included.

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Next, the paper contains a review of the effects of various forms of visual deprivation on cat visual neurons; included in this section is a summary of behavioral consequences of these various forms of visual deprivation. Finally, the review concludes with some comments about the extent to which generalizations from cat to human vision are justified.

OPTICS

Since the formation of a retinal image by the optics of the eye represents the initial stage in the process of seeing, the quality of this image, in terms of its intensity, size, and contrast, will necessarily set boundaries on the information available to subsequent processing stages of the visual system. So, naturally, an organism's ability to resolve spatial detail can never be greater than the fidelity with which this detail is represented in the image on the retina, and this fidelity is determined by the optical characteristics of the eye. In general, the development of any optical system, such as an eye, seems to involve some compromise between image intensity and image resolution, for the optical properties which favor one almost invariably detract from the other.

In the case of the cat, which is by nature a nocturnal animal, this compromise leans in favor of image intensity, at least according to human standards. Based on the schematic eye derived for the cat by Vakkur and Bishop (1963) and Vakkur, Bishop, and Kozak (1963), it is clear that the cat possesses a relatively large eyeball with a broadly curved cornea, a disproportionately large pupil and a globular shaped lens situated rather deep posteriorly within the eye. These structural adaptations endow the cat's eye with a great light-gathering capacity, and it is estimated that for a given object intensity, retinal illumination is 5.2 times greater in the cat than in the human (Vakkur & Bishop, 1963). Yet, at the same time, the size of the retinal image of any object is nearly 33% smaller in the cat's eye relative to the human's, by virtue of the more posterior location of the optical center of the cat's eye. This smaller image size would tend to reduce the cat's acuity, by involving fewer visual receptors. Moreover, at the back of the cat's eye, in the choroid just behind the retina, lies the tapetum lucidum which acts as a diffuse reflecting surface (Coles, 1971; Weale, 1953). This device further enhances the efficiency of the cat's eye for dim-light vision by reflecting light back through the visual receptors. But, again, this enhancement in sensitivity is purchased at the expense of image sharpness (Walls, 1942).

Both pupil size and accommodation are important ingredients in determining the optical quality of an image, and both of these have been studied in the cat. As everyone knows, the pupil of the cat assumes

an elliptical shape with increasing light intensities, and at modest photopic levels the pupil is reduced in shape to just a narrow slit. (Incidentally, Walls has pointed out that this slit pupil characteristic of many nocturnal animals such as the cat has nothing to do with seeing in dim light, but instead simply allows these animals, with their very sensitive eyes, to cope with daytime light levels without being blinded from glare.) Kappauf (1943) measured the dynamic range of pupillary response in the cat and found that over a 6 log-unit luminance range the diameter of the cat's pupil varied from 16 mm to less than .5 mm. More recently, Wilcox and Barlow (1975) obtained very similar results from pupil size measurements in cats lightly anesthetized with nitrous-oxide. It is interesting to note that the range of pupil areas in the cat is at least 10 times greater than in the human. The effects of such variations in pupil size on the image quality will be discussed shortly.

With respect to accommodation, Vakkur and Bishop (1963) have pointed out that changes in lens power could have only minimal influence on the refractive state of the cat's eye, because of the relatively large separation between the cornea and lens. As an alternative, they suggested that accommodation in the cat could be more effectively produced by the forward and backward movement of the principal planes of the lens. More recently, Hughes (1973) has confirmed that this is, indeed, the mechanism of accommodation in the cat. He found that as cats looked at objects placed at varying distances from the eyes, there was a noticeable change in the diameter of the bulge in the iris produced by the lens. This bulge, which outlines the lens resting just behind the very thin iris, increased when the cat shifted its gaze from a far to a near object, indicating that the lens was moving forward with accommodation. Vakkur and Bishop (1963) estimated the cat's range of accommodation to be only 4 diopters, a value which is in good agreement with the range measured by Hughes (1973) as well as with estimates based on behavioral data from the cat (Bloom & Berkley, 1977).

A number of investigators have attempted to determine the optical quality of the cat's eye by measuring in one way or another the light distribution in the retinal image produced by a particular optical stimulus. The most frequently employed method has involved photographing the retinal image of some object and then measuring the luminance distribution across the photograph with a densitometer (Bonds, Enroth-Cugell, & Pinto, 1972; Morris & Marriot, 1961; Wassle, 1971; Westheimer, 1962). With this technique, it is necessary to correct for the double passage of the image through the eye's dioptrics. Estimates of image quality derived in this manner

have varied somewhat, but the consensus seems to be that the optics of the cat are rather poor by human standards. Recently, however, Ikeda and Wright (1972) have questioned the efficacy of the double-passage technique, suggesting that it underestimates optical quality considerably. As an alternative, they photographed fine capillaries within the fundus of the cat (a technique which avoids the double-passage problem) and treated the resulting luminance profiles as line-spread functions. From their measurements, Ikeda and Wright concluded that the quality of the cat's optics was considerably better than previously estimated, though still somewhat inferior to human optics. Finally, Enroth-Cugell and Robson (1974) approached the problem even more directly by actually measuring the light distribution in the retinal image using a fiber-optic probe placed at the back of the eye of an anesthetized cat. Their results were in good agreement with those of Ikeda and Wright.

Regardless of the technique used, it has consistently been found that pupil size influences very significantly the quality of the image formed by the cat's optics. As would be anticipated on the basis of optical principles (e.g., Westheimer, 1972), the worst image in terms of contrast attenuation is obtained with the pupil fully dilated, the situation improving with increasingly smaller pupil diameters. It appears that optimal performance is achieved with a pupil 2-3 mm in diameter, which gives an optical resolution limit exceeding 20 cycles/deg (Bonds, 1974).

Finally, it is worth noting that this level of optical quality is not present from the time of natural eye opening around the end of the first postnatal week of life. Instead, the kitten's eye develops to adult optical standards over the 1½ months or so after birth (Bonds & Freeman, 1978). During this time, the extensive embryological vascular network is absorbed, leading to progressive clearing of the ocular media (Freeman & Lai, 1978), and the major refractive elements in the eye progressively grow to adult levels (Freeman, Wong, & Zezula, 1978; Thorn, Gollender, & Erickson, 1976). By the onset of the so-called critical period for neural development (discussed in the section on visual deprivation), the optics of the kitten's eye are more than sufficient to allow normal development of the neural pathways.

RETINA

Anatomy

Nearly a century ago, Chievitz (1891; in Walls, 1942) observed that in the retina of the cat rods predominate over cones even within the area centralis, the region of highest cone density. Not until quite recently, however, was there a systematic study of the distribution of rods and cones within the central and peripheral retina of the cat. By counting

rods and cones in photomicrographs of sections through the inner segment of the excised retina, Steinberg, Reid, and Lacy (1973) constructed detailed maps of receptor density over the entire cat retina. Their results show that cone density is highest within the area centralis but that even here rods are more than 10 times as numerous, confirming the observations of Chievitz. Maximum rod density occurs within an annular region 10-15 deg from the center of the area centralis and gradually tapers off with increasing retinal eccentricity. By comparing these receptor densities with the ganglion cell counts of Stone (1965), Steinberg et al. estimated the degree of receptor/ganglion cell convergence for different portions of the retina. Within the area centralis, the ratio of cones to ganglion cells is at a minimum, suggesting that this would be the region of maximum photopic acuity. On the other hand, the minimum rod/ganglion cell ratio occurs some 5 deg into the periphery, where optimum scotopic acuity would likely occur. These ratio estimates may vary, depending upon the meridian sampled, because of the horizontally elongated region of high ganglion cell density in the cat retina (Hughes, 1975; Stone, 1965).

This convergence of receptors onto ganglion cells is mediated by an elaborate network of neural connections within the outer and inner plexiform layers, and the details of these connections in the cat recently have been studied using the electron microscope. In the cat retina, cones synapse onto two types of bipolar cells, an invaginating type which connects with from 4 to 9 individual cones and a flat type which contacts 8-14 cones (Boycott & Kolb, 1973); there is no evidence for a bipolar which contacts just a single cone, such as the midget bipolar cells seen in primate retina. These cone bipolars in the cat, in turn, synapse directly onto ganglion cells (Kolb & Famiglietti, 1974). Rods, on the other hand, contact another type of bipolar, termed rod bipolars (Boycott & Kolb, 1973), and these do not synapse directly onto ganglion cells, but, instead, onto amacrine cells which then contact the ganglion cells (Kolb & Famiglietti, 1974). Also, in the cat retina, the receptors are interconnected by horizontal cells, the dendritic terminals of which synapse only with cones and the axon terminal only with rods (Kolb, 1974). Moreover, it appears that rods can have direct input to cones, perhaps via electrically passive gap junctions (Nelson, 1977). The exact significance of this synaptic arrangement between receptors is not clear, but it could be that the horizontal cells are somehow involved in the control of retinal sensitivity at different background illuminations (Enroth-Cugell & Lennie, 1975; Enroth-Cugell & Shapley, 1973).

Ganglion cells in the cat retina are not homogeneous with respect to morphology (Brown & Major, 1966; Honrubia & Elliot, 1970; Leicester & Stone, 1967).

Boycott and Wässle (1974) have described three types of ganglion cells which are distinguishable on the basis of axon thickness and dendritic field size. All three types, termed α , β , and γ cells, appear at all retinal eccentricities, but within the central region β cells are predominant. For each type, the spread of dendritic fields increases systematically with retinal eccentricity, but at any particular retinal locus the spread of α cells is usually greater than that of β cells. Moreover, the axon diameters of α cells are consistently larger than the diameters of β axons. As a rule, the γ cells display large dendritic fields but possess small axons. The significance of these morphological groups will be considered shortly.

Finally, at this point it perhaps should be mentioned that some evidence, both anatomical (Brooke, Downer, & Powell, 1965) and electrophysiological (Haft & Harman, 1967; Jacobson & Gestring, 1958), suggests the existence of centrifugal fibers from higher centers back to the retina of the cat. However, much of this evidence is open to rival interpretation, and the current attitude toward this possibility of centrifugal input to the retina seems to be one of skepticism (Brindley, 1970; Lin & Ingram, 1973, 1974).

Physiology

Not much is known about the photochemical and neural events which transpire prior to the ganglion cells, but surely a great deal of coding has taken place by then. Even in the dark, the ganglion cells in the cat retina generate frequent, irregularly timed spikes which some believe are of receptor origin (e.g., Barlow & Levick, 1969). Kuffler (1953) was the first to show how this spontaneous activity of the ganglion cells could be modulated by presentation of visual targets within a limited region of the retina. Kuffler found that in all light-adapted ganglion cells this region, the receptive field, could be subdivided into two zones, an approximately circular central region surrounded entirely by an annular area. Stimulation of one zone increased the cell's firing rate (ON response), while stimulation of the other caused a decrease in firing, followed by a burst of activity upon removal of the stimulus (OFF response). Some cells consisted of ON-centers and others of OFF-centers, but in each cell the center and surround always were arranged in an antagonistic fashion. It has been noted by many (e.g., Wiesel, 1960) that this center-surround organization seems particularly suited for the detection of spatial luminance gradients. Following Kuffler's discoveries, the spatial properties of cat ganglion cells have been studied in extensive detail. Most of this work has revolved around the hypothesis that the receptive field is composed of two distinct response mechanisms (center and surround) arranged concentrically, each with an approximately Gaussian sensitivity dis-

tribution; the response of the cell is determined by the subtractive interaction of these two mechanisms (Cleland & Enroth-Cugell, 1968; Enroth-Cugell & Robson, 1966; Rodieck, 1965; Rodieck & Stone, 1965). For the purposes of this review, a summary of some of the major findings will be sufficient.

The large majority of receptive fields which have been described for the cat ganglion cells conform to this antagonistic center-surround arrangement and display no selectivity for contour orientation or direction of movement. The receptive field centers of ganglion cells, whether ON or OFF type, vary in diameter from .5 to 8 deg visual angle (e.g., Wiesel, 1960) and are smallest within the area centralis. There have been several attempts to relate the sizes of these receptive field centers to the horizontal spreads of dendritic trees of retinal ganglion cells (e.g., Brown & Major, 1966; Leicester & Stone, 1967). The antagonistic surround portion of the field is several times larger than the field center, and there is evidence that the surround extends through the center (Cleland & Enroth-Cugell, 1968; Hammond, 1973; Rodieck & Stone, 1965). It has been suggested that amacrine cells are involved in the organization of the surround portion of the field (e.g., Rodieck, 1965). Barlow, Fitzhugh, and Kuffler (1957) showed that the inhibitory effect of this surround region on the center disappeared with dark adaptation, leaving only an ON or an OFF response throughout the field. Finally, McIlwain (1964) has reported that some ganglion cells exhibit weak excitatory effects to visual stimulation many degrees removed from the conventional receptive field center; others (e.g., Fischer, Kruger, & Droll, 1975) have examined this so-called shift effect in some greater detail.

While the distinction between ON-center and OFF-center cells has generally proved adequate for describing the spatial arrangement of receptive fields in the cat's retina, it becomes obvious that ganglion cells could also be classified along another dimension based on different response properties, independent of the center-surround organization. First to demonstrate this dichotomy were Enroth-Cugell and Robson (1966), who found that one class of ganglion cells, which they termed X cells, displayed approximately linear summation over the entire receptive field, while a second class, termed Y cells, was clearly nonlinear. Evidence for linear summation consisted of finding a "null position" within the receptive field, such that repetitive phase reversal of a bipartite field (e.g., one complete light/dark cycle of a grating) produced no net change in background activity. Using sinusoidal grating patterns to evoke discharges, Enroth-Cugell and Robson went on to determine the minimum contrast necessary to produce a noticeable modulation in a cell's maintained

discharge. By repeating this constant response maneuver at a number of spatial frequencies, they derived contrast sensitivity functions for a number of X cells. This family of functions all exhibited the same general shape, peaking near .5 cycles/deg and falling off gradually at lower frequencies and more steeply at higher frequencies. Varying the orientation of the grating had no effect, nor did changing the direction of movement. However, reducing the mean level of luminance produced an overall decrease in the cell's sensitivity, reduced the high-frequency cutoff point, and eliminated the low-frequency attenuation in sensitivity. They attributed this last result to the disappearance of the antagonistic surround portion of the field, which occurs with dark adaptation (Barlow, Fitzhugh, & Kuffler, 1957). For the nonlinear Y cells, Enroth-Cugell and Robson were unable to describe a single contrast sensitivity function, for the sensitivity of these cells depended on whether the gratings were flashed on and off or drifted across the receptive field.

This classification of retinal ganglion cells into two groups was independently established by Fukada and Saito (1971) and subsequently studied in greater detail by others (Cleland, Dubin, & Levick, 1971; Cleland & Levick, 1974a; Cleland, Levick, & Sanderson, 1973; Fukada, 1971; Hammond, 1975; Hochstein & Shapley, 1976a, 1976b; Ikeda & Wright, 1972; Rowe & Stone, 1976). The response properties which distinguish these two types of cells are detailed elsewhere (Cleland et al., 1973; Ikeda & Wright, 1972) and are given only in summary here, with references omitted. Cells categorized as type X typically display the following features: field centers more often on the ON type; field centers tend to be smaller than Y type; maintained activity usually higher than Y type; respond only to slow or moderate target speeds; show no periphery effect; predominate within the area centralis; surround portion of field smaller diameter; small stationary targets evoke sustained response; resolve higher spatial frequencies than Y type; possess slow conducting axons. Type Y cells, on the other hand: respond to very rapidly moved targets; show clear periphery effect; are insensitive to image defocusing; respond transiently to onset and offset of stimulus; possess fast conducting axons. On the basis of these contrasting properties,¹ several groups of workers (Cleland et al., 1971; Ikeda & Wright, 1972) have proposed that these two classes of retinal ganglion cells constitute separate neural channels which subserve different roles in visual perception. Presumably, X cells are involved in analyzing the spatial features of stimuli, while Y cells process information concerning movement and time varying stimulation. This duplex model in which X and Y cells constitute functionally distinct sets of neurons was rather promptly embraced

by visual psychophysics under the rubric of pattern vs. movement "channels." A great deal of work in the last few years has been directed at documenting the existence of these putative channels in human vision (Breitmeyer & Ganz, 1977; Frisby & Clatworthy, 1974; Keese, 1972; Kulikowski & Tolhurst, 1973; Legge, 1978; Spitzberg & Richards, 1975; Tolhurst, 1973, 1975).

More recently, there has been described a third category of retinal ganglion cells, the receptive fields of which depart considerably from the conventional center-surround organization (Stone & Fukada, 1974; Stone & Hoffmann, 1972). This new group of cells, which have been labeled W type, display field centers which are equivalent in size to Y cell centers (at a given retinal eccentricity), but the axons of the W cells conduct more slowly than either type X or type Y axons (Stone & Fukada, 1974). These W cells appear to comprise the bulk of the ganglion cells in the so-called visual streak of the cat retina (Rowe & Stone, 1976). The fact that this third category of cells projects heavily to the superior colliculus (Fukada & Stone, 1974) suggests that W cells may play some role in visuomotor behavior.

Some very compelling similarities exist between the physiological properties of the X, Y, and W ganglion cells and the morphological properties of the β , α , and γ cells described earlier (Boycott & Wässle, 1974). Recall that α cells are characterized by wide dendritic fields and thick axons; thus, by inference, these cells would possess large field centers and fast conducting axons. The β cells, on the other hand, have small dendritic fields and thin axons, implying small field centers and slow conduction axons. The remaining type, γ cells, display large dendritic fields but very thin axons, implying large field centers but very slow axons. These implied features of β , α , and γ cells all dovetail exactly with the known properties of X, Y, and W cells, respectively.

Projections

After exiting the eye at the optic disk, axons of the retinal ganglion cells partially cross at the optic chiasm. In general, fibers from the nasal retina of each eye cross to the contralateral side of the brain while fibers originating from the temporal retinae project ipsilaterally. However, this specificity is not absolute; in the cat there is a limited region around the area centralis which gives rise to bilateral projections comprised of crossed *and* uncrossed fibers (Stone & Fukada, 1974). Moreover, it has been shown that this composite strip of crossed-uncrossed axons is wider horizontally for Y cells than for X cells, when measured in terms of receptive field centers (Kirk, Levick, Cleland, & Wässle, 1976).

These optic fibers project to several subcortical sites in the brain (Garey & Powell, 1968; Laties &

Sprague, 1966). The majority of these ganglion cell axons innervate cells of the lateral geniculate nucleus (LGN), which actually consists of two anatomically distinct portions, the more prominent dorsal lateral geniculate and the smaller ventral lateral geniculate. The majority of cells in the dorsal LGN receive input from either X or Y cells (Wilson, Rowe, & Stone, 1976), while the ventral LGN innervation appears to be largely from W cells (Spear, Smith, & Williams, 1977). Because of their rather diffuse receptive-field properties and their projections to pretectal regions, it may be that cells of the ventral LGN are involved in the pupillary response to light and, perhaps, vestibular and oculomotor reflexes. Cells in the dorsal LGN, on the other hand, display more well-defined receptive field properties (described in the next section) and project to the visual cortex; in the remainder of this review, the abbreviation "LGN" will be used to refer to the dorsal LGN.

The remaining ganglion cell axons project to structures in the midbrain, the most prominent being the superior colliculus. It is often suggested that these midbrain structures are involved in visuomotor coordination while the geniculocortical pathways play the major role in spatial resolution and pattern recognition (see Stone & Freeman, 1973, for a summary of the evidence favoring this distinction). Since the major emphasis in this review is upon neural mechanisms in cat spatial vision, the remainder of this review will concentrate on the geniculocortical portion of the visual system.

LATERAL GENICULATE NUCLEUS

Anatomy

The most striking feature of the LGN of the cat is its well-defined laminar structure: cells of the geniculate are grouped into three major layers, with the optic tract fibers from the contralateral eye projecting exclusively to the dorsal and ventral layers while the ipsilateral fibers project to the middle layer (Garey & Powell, 1968; Guillery, 1966; Hayhow, 1958; Laties & Sprague, 1966; Stone & Hansen, 1966). Guillery (1970) has described an additional sublamina of the ventral layer which also receives an ipsilateral projection. The cells of the LGN also have been categorized (Guillery, 1966) on the basis of their morphology into several types, each of which displays a characteristic laminar distribution of cell dendrites (Guillery, 1966). Briefly, class 1 neurons exhibit large cell bodies and thick, rather straight dendrites punctuated by occasional spiny appendages. Class 2 neurons have somewhat smaller somata and rather thin, arching dendrites which terminate in clusters of spheroid appendages. Class 3 neurons have the smallest cell bodies and very thin, wavy dendrites along which appear complex arrays of

ovoid specializations. Class 4 cells are small in size and possess dendrites resembling class 1 cells. Class 1 and 2 cells are found in layers A, A1, and C, while class 4 cells are confined mainly to the C1 and C2 laminae. Intracellular staining procedures have demonstrated that class 1 and 2 cells are, indeed, relay cells, not interneurons (Ogawa, Takimori, & Takahashi, 1978). Some attempts have been made to study possible functional differences (X vs. Y) among these various morphologically distinct cell types (Wilson & Stone, 1975), and there is encouraging correlational evidence to indicate that the morphological/physiological correlations found in cat retina may hold true in the LGN, too (Garey & Blakemore, 1977a, 1977b; Garey & Powell, 1967; Gilbert & Kelly, 1975; LeVay & Ferster, 1977; Stone & Dreher, 1973). The most direct link between morphology and physiology has come from the work of Friedlander, Lin, and Sherman (1979), who have managed to inject physiologically identified X and Y cells with horseradish peroxidase. They found that class 1 (Guillery's scheme described earlier) morphological features were associated with Y cells while class 3 features were invariably of the X type; class 2 structural traits were exhibited by some X cells as well as by some Y cells. This structural-functional correlation differs somewhat from the scheme of LeVay and Ferster (1977), who proposed that class 1 neurons are Y cells, class 2 are X, and class 3 are interneurons. Part of this discrepancy stems from disagreement over the number of interneurons within the LGN of cat, a point that is considered below. Also open to question is the percentage of LGN relay cells which are Y type—recent estimates place this figure around 25% (LeVay & Ferster, 1977), which is considerably larger than the 3%-6% figure cited for Y-cell density in the retina (Stone, 1978; Wassle, Levick, & Cleland, 1975).

Cells of the cat LGN receive afferent input from several sources. The major excitatory input is supplied by the axons of retinal ganglion cells. Before terminating on geniculate cells, these axons divide into several branches (Guillery, 1966), suggesting that each individual optic fiber innervates several cells of the LGN. Still, the projection of the fibers onto geniculate cells is retinotopically organized in a very precise fashion (Stone & Hansen, 1966). In addition to this retinal input, the cells of the cat LGN also receive precise topographical projections from the visual cortex (Beresford, 1961; Guillery, 1967; Hollander, 1970; Kalil & Chase, 1970; Szentagothai, Harmori, & Tombol, 1966; Updyke, 1975), as well as a less organized projection from the superior colliculus (Altman, 1962). It seems likely that the LGN receives afferents from other nonvisual brain structures, too, since LGN activity can be modulated by stimulation of the midbrain reticular formation (Burke & Cole,

1978; Suzuki & Taira, 1961). Finally, besides this array of afferent inputs, the LGN of the cat also contains a rich network of interneurons, the axons of which remain within the LGN (Lin, Kratz, & Sherman, 1977; Szentagothai, Hamori, & Tombol, 1966; Tombol, 1969). There is some question concerning the approximate percentage of LGN cells that are interneurons, with estimates ranging from fewer than 10% (Lin, Kratz, & Sherman, 1977) to as many as 25% (LeVay & Ferster, 1979). Of these interneurons, one type possesses axons which are confined within a single lamina and which synapse on some 5-10 other neurons. The axons of the other type of interneuron cross the laminar borders while still remaining within the LGN. It is widely believed that both types of interneurons play a prominent role in lateral inhibitory interactions within the LGN (e.g., Fukada & Stone, 1976; Levick, Cleland, & Dubin, 1972; Singer, Poppel, & Creutzfeldt, 1972).

Physiology

Like the ganglion cells from which they derive their inputs, geniculate neurons in the cat possess receptive fields which are concentrically organized, with both ON-center and OFF-center types (Hubel & Wiesel, 1961). Moreover, the diameters of the receptive field centers of LGN cells are on the same order as ganglion cells; field sizes increase with retinal eccentricity (Hoffman, Stone, & Sherman, 1972; Hubel & Wiesel, 1961). And, like their retinal counterparts, LGN fields show virtually no specificity for orientation or direction of movement (e.g., Kozak, Rodieck, & Bishop, 1965), with rare exception (Daniels, Norman, & Pettigrew, 1977). There are, however, some notable differences between ganglion cell and geniculate fields. At the LGN level, the surround mechanism exerts a greater inhibitory influence on the center, in comparison to surrounds at the retinal level, thus enhancing the sensitivity of geniculate neurons to luminance gradients (Hammond, 1973; Hubel & Wiesel, 1961). Moreover, the surround portion of the geniculate field is responsive even at scotopic levels well below those at which the effects of ganglion cell surrounds disappear (Hammond, 1972; Maffei & Fiorentini, 1972). Unlike the retina, the LGN contains some cells which can be influenced via either eye, such that the cell is excited by stimulation of one eye and inhibited through the other (e.g., Sanderson, Bishop, & Darian-Smith, 1971). In view of the strict segregation of left- and right-eye afferents to the different laminae, it seems likely that interneurons supply the connections for these binocular inhibitory interactions. Finally, there is some evidence that the receptive fields of LGN cells include a third component not seen in retinal fields. For instance, Hammond (1973) has described an annular region, surrounding the conventional surround portion, which is of the same polarity (e.g., ON or OFF) as the field center; stimulation

of this outer surround reduces the effectiveness of the inner surround, thus disinhibiting the center. Similar observations were briefly mentioned by Maffei and Fiorentini (1972). However, an altogether different situation has been described by Cleland, Dubin, and Levick (1971). They, too, report finding an additional annular region encircling the familiar surround component, but in their work this outer surround always reduced or abolished the response of the center region and never produced excitation when stimulated alone. Cleland et al. are careful to point out that this third field component, called the suppressive field, is a feature peculiar to the LGN. It remains to be seen whether the conflicting results of Cleland et al. (1971) and Hammond (1973) can be reconciled.

By recording simultaneously from a geniculate neuron and the ganglion cell(s) providing the excitatory input, several investigators have demonstrated that most LGN neurons are innervated by just a few optic fibers and in some cases by only a single fiber (Cleland, Dubin, & Levick, 1971; Hammond, 1973; Hoffmann, Stone, & Sherman, 1972; Singer & Creutzfeldt, 1970). These simultaneous recordings also have demonstrated two important functional properties of the excitatory connections between retinal fibers and LGN cells. First, geniculate cells with ON-center fields receive excitatory input only from ON-center ganglion cells, and OFF-center geniculate cells are excited just by OFF-center ganglion cells (e.g., Cleland et al., 1971). This finding is consistent with the model of LGN synaptic organization proposed by Singer and Creutzfeldt (1970). Second, the X/Y grouping described for retinal cells is preserved at the LGN: X-type retinal cells innervate only X-type geniculate neurons and Y-retinal cells only Y-geniculate neurons (Cleland et al., 1971; Hoffmann et al., 1972). And, like their retinal counterparts, X-type geniculate neurons have slower conducting axons than the Y-type neurons. The LGN also contains a group of cells categorized as W type, and these are restricted to the ventral portion of layer C (Cleland, Levick, Morstyn, & Wagner, 1976); X and Y cells, in contrast, comprise almost exclusively the population of neurons in laminae A and A1 (Wilson, Rowe, & Stone, 1976). There is some evidence indicating that X cells in the LGN are more strongly subject to intrageniculate inhibition than are Y cells (Fukada & Stone, 1976), a physiological finding which may bear some relation to the morphological classes described by Guillery (1966). Finally, there appear to be a minority of LGN cells in the cat which exhibit some properties of both X and Y cells (Bullier & Norton, 1977). These may be counterparts to the mixed-type cells found in cat retina (Cleland & Levick, 1974b).

With respect to their spatial resolving power, geniculate neurons seem to respond over the same range of spatial frequencies as that handled by

retinal ganglion cells. Recall that Enroth-Cugell and Robson (1966) used a constant response technique to derive contrast sensitivity functions for X-type ganglion cells. Using nearly identical techniques, Campbell, Cooper, and Enroth-Cugell (1969) obtained similar functions for LGN neurons. Cutoff frequencies ranged up to about 4 cycles/deg, a value comparable to that measured for retinal cells. Others have performed similar analyses, measuring the frequency response of ganglion and geniculate cells using gratings, and have obtained similar results (Cleland et al., 1971; Maffei & Fiorentini, 1973). There is some evidence that X cells subserving the area centralis may actually be responsive to spatial frequencies near 8 cycles/deg (Ikeda & Wright, 1976), with the cutoff frequency for X cells dropping precipitously with retinal eccentricity. All in all, it appears that in relaying information from the retina to the cortex there is essentially no loss of resolving power at the LGN.

Besides the spatial layout of LGN receptive fields, it is clear also that time plays an equally important role in determining the response properties of geniculate cells and, by extension, other neurons in the visual pathways. These time domain effects have been examined in detail by Stevens and Gerstein (1976a, 1976b) using a so-called response plane plot. This analytical technique does not integrate neural response over space or time but, instead, expresses the effects of both space and time along orthogonal axes. The resulting plane consists of four components, or domains as they are called, which give rise to a fourfold classification scheme for LGN receptive fields. These results have been summarized by Stevens and Gerstein (1976a) in the form of a model of a cat LGN which assumes a novel pattern of innervation from retinal center and surround to LGN center and surround; the proposed network of innervations represents a departure from more conventional LGN organization schemes (e.g., Singer & Creutzfeldt, 1970). In general, this work serves to stress the importance of time, in addition to space, in determining the behavior of a visual receptive field.

Projections

In the cat, axons of geniculate neurons project to four visual areas of the cortex: areas 17, 18, 19, and the lateral wall of the suprasylvian gyrus (Garey & Powell, 1967; Niimi & Sprague, 1970). There is evidence that larger geniculate axons (hence faster conducting) project more heavily to area 18, while smaller axons (hence slower) terminate predominantly in areas 17 and 19 (Garey & Powell, 1967; Hollander & Vanegas, 1977). Keeping in mind that fast conducting LGN cells are generally Y type while the slower conducting cells are X type, this pattern of

projections to visual cortex suggests that areas 17 and 18 may subserve different visual functions in the cat. At the least, the termination of radiation fibers from the LGN upon several cortical areas suggests that some visual processing within the geniculocortical pathways occurs in parallel, not in series.

VISUAL CORTEX

Anatomy

In the cat, the visual cortex is divisible into three adjoining areas (17, 18, and 19), defined by cytoarchitectonic criteria (Otsuka & Hassler, 1962), and the visuotopic organization of these areas has been mapped using microelectrode techniques (Albus, 1975a; Bilge, Bingle, Seneviratne, & Whitteridge, 1967; Hubel & Wiesel, 1962, 1965a; Tusa, Palmer, & Rosenquist, 1978). In addition to these three contiguous areas there are other regions of the cortex which also are responsive to visual stimulation, the most notable being the lateral wall of the suprasylvian gyrus (Clare & Bishop, 1954; Hubel & Wiesel, 1969), an area which, in fact, consists of six retinotopically organized regions arranged in three mirror-symmetrical pairs (Palmer, Rosenquist, & Tusa, 1978). In each of these visual areas, the amount of cortex devoted to central vision is disproportionately large relative to more peripheral visual fields (e.g., see Whitteridge, 1973), with this exaggeration being the greatest in area 17 (Tusa et al., 1978). Besides receiving direct projections from the LGN, these visual areas are all interconnected, with area 17 sending projections to 18, 19, and the suprasylvian gyrus, and areas 18 and 19 projecting back onto 17 (Wilson, 1968). Finally, there also are projections from the visual areas of one hemisphere to those of the contralateral cortex via the corpus callosum (Ebner & Meyers, 1965; Hubel & Wiesel, 1967).

In his chapter in the *Handbook of Sensory Physiology*, Szentagothai (1973) has described the complicated structure of the visual cortex of the cat, especially in terms of its synaptic organization, and has provided a detailed picture of the constituent cell types and their laminar distribution. While these details will not be summarized here, it is worth noting that attempts are being made to relate the structural features of visual cortical cells to their functional properties determined physiologically (Van Essen & Kelly, 1973) as well as to the laminar patterns of the LGN (LeVay & Gilbert, 1976).

Physiology

Orientation. The concentric receptive field arrangement characteristic of retinal and geniculate levels gives way at the cortex to an altogether different layout of excitatory and inhibitory areas. For cortical

cells, these antagonistic areas are arranged in elongated strips so that the most effective stimulus is a straight contour (or a series of such contours) in a particular orientation. While there may be a small percentage of cortical cells with nonoriented receptive fields (e.g., see Spinelli & Barrett, 1969), it is generally recognized that orientation specificity is a fundamental property of neurons in the cat's visual cortex. Using receptive field mapping techniques, Hubel and Wiesel (1962, 1963) demonstrated how cells with the same preferred orientation are grouped into columns that are on the order of 73-100 μ in thickness. Neighboring columns have preferred orientations that are quite similar, within 10-15 deg or less, and a complete, orderly orientation sequence, i.e., 180 deg, is contained within a cortical column that is 300-700 μ m in thickness (Albus, 1975b). More recent work (Hubel & Wiesel, 1974; Stryker, Hubel, & Wiesel, 1977) has served further to elucidate this elegant layout of orientation specificity within visual cortex. In particular, it appears that the functional columns, in fact, take the form of sheets, or slabs, the walls of which are perpendicular to the cortical surface. The biological significance of such an arrangement has been discussed by Hubel and Wiesel (1974).

With respect to the selectivity of individual cells for orientation, there is wide cell-to-cell variation in the sharpness of tuning, with half-widths at half-amplitude ranging from as little as 5 deg up to at least 70 deg (e.g., Henry, Bishop, & Dreher, 1974). Not all cells display symmetrical tuning curves, with those exhibiting asymmetries tending to occur more frequently in area 18 (Hammond & Andrews, 1978). This lack of symmetry in tuning may arise from local irregularities in the layout of the orientation columns (Lee, Albus, Heggelund, Hulme, & Creutzfeldt, 1977). It has been noted in several laboratories that, although the responsiveness of a cortical cell may vary over time, the orientation preference and tuning of cells remains remarkably stable over time (Hammond, Andrews, & James, 1975; Henry, Bishop, Tupper, & Dreher, 1973); contradictory results (Donaldson & Nash, 1975) have been discounted by others as an artifact of depth of anesthesia. There is a growing body of evidence which implicates intracortical inhibitory connections in the orientation selectivity of cat cortical cells (Benevento, Creutzfeldt, & Kuhnt, 1972; Blakemore & Tobin, 1972; Daniels & Pettigrew, 1975; Nelson & Frost, 1978; Rose & Blakemore, 1974; Sillito, 1974). It is now generally believed that excitatory inputs from LGN to cortex establish a coarse orientation bias which is greatly refined by inhibitory connections between columns to yield the sharp tuning characteristic of cat cortical cells.

Although noted for their orientation selectivity, some cells in cat visual cortex are responsive to other

forms of visual stimulation. In particular, cortical cells will produce bursts of impulses when spots of light traverse their receptive fields (Pettigrew, 1974) and complex, but not simple, cells can be activated by movement of textured stimuli composed of random noise, i.e., a stochastically generated array of circular dots (Hammond & MacKay, 1977). It is tempting to speculate about the possible role of these noise-sensitive cells in the detection of motion in a textured environment (MacKay, 1965).

Cell types. Independent of their receptive field orientation, cells in cat visual cortex can be categorized into distinct groups (simple, complex, and hypercomplex) on the basis of other receptive field properties. (A very thorough review of these cortical cell classes has been given by Henry, 1977.) According to the scheme of Hubel and Wiesel, simple cells possess receptive fields composed of adjacent ON and OFF regions within which spatial summation occurs, and these regions can be mapped using stationary flashing targets. Other investigators (e.g., Sherman, Watkins, & Wilson, 1976; Pettigrew, Nikara, & Bishop, 1968a) have found it preferable to categorize cortical cells in terms of the cell's response to moving slits. Despite these differences in classification, there does appear to be substantial agreement concerning the receptive field properties which characterize simple vs. complex cells. In particular, simple cells display the following features: possess little or no spontaneous activity (Pettigrew, Nikara, & Bishop, 1968a); frequently respond more vigorously to one direction of movement than to the other (Bishop, Coombs, & Henry, 1971); prefer slowly moving stimuli (Movshon, 1975; Orban, Kennedy, & Maes, 1978; Pettigrew et al., 1968a); respond only within a rather narrow range of orientations (Hammond & Andrews, 1978; Henry, Bishop, & Dreher, 1974; Hubel & Wiesel, 1962; Watkins & Berkley, 1974); usually display linear spatial summation when tested with sinusoidal gratings (Movshon, Thompson, & Tolhurst, 1978a); possess small receptive fields, relative to the other cell types (Hubel & Wiesel, 1962); and are located predominantly in layer IV (Hubel & Wiesel, 1962; Kelly & Van Essen, 1974). In comparison, complex cells: respond very weakly to flashed stimuli anywhere within the receptive field and do not show spatial summation (Hubel & Wiesel, 1962) have comparatively large receptive fields (Hubel & Wiesel, 1962); respond over a somewhat broader range of orientations (Rose & Blakemore, 1974; Watkins & Berkley, 1974; Wilson & Sherman, 1976); are highly nonlinear in their response to sinusoidal gratings (Movshon, Thompson, & Tolhurst, 1978b); have a higher level of spontaneous activity (Kelly & Van Essen, 1974; Pettigrew et al., 1968a); prefer relatively high speeds of movement (Movshon, 1975; Pettigrew et al., 1968a; Pollen & Ronner, 1975); and are concentrated in the cortical layers on either side

of IV (Kelly & Van Essen, 1974). In general, both cell types have larger receptive fields, less orientation selectivity, and higher preferred speeds with increasing retinal eccentricity, but these variations are more pronounced in the complex cells (Wilson & Sherman, 1976). Finally, hypercomplex cells: are sensitive to the length of an oriented stimulus (Hubel & Wiesel, 1965a); have comparatively low spontaneous activity (Rose & Blakemore, 1974); vary widely in their degree of orientation tuning; and are encountered most often in areas 18 and 19, usually within layers II and III (Hubel & Wiesel, 1965a; Kelly & Van Essen, 1974).

While it is generally agreed that the properties of simple cells can be explained by assuming a direct input from geniculate fibers (Bishop, Coombs, & Henry, 1973; Hubel & Wiesel, 1962), there is active debate concerning the inputs which determine the properties of complex and hypercomplex cells. Hubel and Wiesel have proposed that complex cells receive their input from simple cells, and hypercomplex from complex. This hierarchical model has been challenged by others, principally the research group in Australia, who envision the complex cells working in parallel, not in series, with the simple cells. Certainly the survival of responsivity of area 18 neurons, which are mainly of the complex variety, following acute lesions of area 17 (e.g., Dreher & Cottee, 1975) and the maintained selectivity of area 18 neurons following cooling of area 17 (Sherk, 1978) are inconsistent with a strict hierarchical model. Moreover, several investigators have proposed that simple and complex cells represent the cortical terminations of the X and Y projections, respectively, from the LGN (Hoffmann & Stone, 1971; Maffei & Fiorentini, 1973; Stone, 1972). Consistent with this proposal is the tendency for fast-conducting axons (Y type) to project to area 18, in which complex cells predominate, and for slow-conducting axons to project to area 17, the cortical region in which simple cells are concentrated. Recent work by Movshon, Thompson, and Tolhurst (1978c) has convincingly documented that neurons in area 17 and in area 18 differ considerably in their spatial and temporal response properties, in a manner consistent with the notion that X cells project to area 17 while Y cells project predominantly to area 18. In particular, Movshon et al. found that area 17 neurons, whether simple or complex, preferred higher spatial frequencies and lower temporal frequencies relative to neurons in area 18. Within area 17, simple and complex cells (as distinguished by their linearity of summation) did not differ in terms of the distribution of their preferred spatial frequencies, but simple cells did tend to be more narrowly tuned for spatial frequency. In terms of the spatial resolving power of cortical neurons, there exist cells in area 17 which can respond to spatial frequencies as high as

7 cycles/deg while no cells in area 18 have been found to respond beyond 1.5 cycles/deg (Movshon et al., 1978c). It still remains to be determined just exactly how the simple/complex dichotomy maps onto the X/Y classification (Ikeda & Wright, 1975; Kelly & Van Essen, 1974; Maffei & Fiorentini, 1973). The existence of nonlinear complex cells in area 17 with X-like spatial and temporal properties (Movshon et al., 1978c) underscores the fact that classification criteria are crucial in categorizing these various cell types.

Besides the hierarchical and parallel models mentioned in the previous paragraph, there are also several hybrid models of visual cortical circuitry that place varying degrees of emphasis on inputs from the LGN as opposed to intracortical inhibition in the genesis of orientation selectivity (Bishop, Coombs, & Henry, 1973; Creutzfeldt, Kuhnt, & Benevento, 1974; Rose, 1979). These various models have been described and evaluated by Rose (1979).

Binocularity. Unlike cells in retina and LGN of the cat, most cortical neurons possess *two* receptive fields, one associated with each eye. Consequently, it is possible to activate these cortical cells through either eye (Hubel & Wiesel, 1962), and for many of these binocular cells simultaneous stimulation of both eyes yields a burst of activity which is greater than that produced by stimulation of either eye alone (e.g., Burns & Pritchard, 1968). Not all binocular cells are equally responsive through the two eyes; rather, different cells exhibit varying degrees of ocular dominance, with the extremes being cortical cells which can be activated through one eye only. As in the case of orientation, these binocular cells are arranged in ocular dominance columns which extend from pial surface to white matter: within a column, cells display much the same eye preference and the ocular dominance shifts systematically from column to column. The anatomical basis of these columns has been demonstrated using autoradiography (LeVay, Stryker, & Shatz, 1978; Shatz, Lindstrom, & Wiesel, 1977); this technique reveals that within layer IV (the terminal site of LGN afferents) of area 17 a complete cycle of ocular dominance occupies a band of tissue roughly .5 mm wide. There is some evidence that monocular cells predominate within the cortical projection area of central vision (Albus, 1975c), but this observation has yet to be firmly established.

With respect to their spatial properties, some binocular neurons have receptive fields which cover corresponding retinal areas; for others, however, there exists various degrees of retinal disparity between the pair of monocular receptive fields, and these disparities are typically more pronounced in the horizontal direction (Barlow, Blakemore, & Pettigrew, 1967; Nikara, Bishop, and Pettigrew, 1968). At one point there was some concern that these positional

disparities were artifacts of residual eye movements in the paralyzed preparation (Hubel & Wiesel, 1973), but now it is generally agreed that retinal disparity is a key ingredient in the layout of binocular receptive fields of cat cortical neurons. Some of these disparity-selective cells are very sharply tuned, such that shifts in positional disparity on the order of 6 min of arc can produce marked reductions in responsiveness in some cells (e.g., Pettigrew, Nikara, & Bishop, 1968b). Bishop (1973) has made a cogent case for the theory that these binocular neurons are involved in stereopsis.

Besides positional disparity, there are other ways in which the pair of receptive fields of binocular neurons may differ. For one, in area 17 of cat cortex the preferred orientation measured separately for the two eyes is not always identical (Blakemore, Fiorentini, & Maffei, 1972; Nelson, Kato, & Bishop, 1977). Even allowing for cyclorotational eye movements, some binocular neurons exhibit interocular orientation disparities as large as 15 deg. There is no trend, however, for these orientation disparities to be more pronounced for horizontal than for vertical, which militates against the notion that orientation disparity represents a neural mechanism for depth discrimination. In area 18 of the cat, there is a class of binocular cells which have different preferred directions of motion between the two eyes (Cynader & Regan, 1978; Pettigrew, 1973), and another class which has different preferred speeds of movement (Cynader & Regan, 1978). It has been speculated that such binocular neurons may encode information about objects moving in depth toward or away from the organism.

It should be pointed out that these differences in receptive field properties between the eyes are not necessarily the rule. It appears that for many binocular neurons the optimal stimulus, in terms of size, orientation, edge polarity, and direction of motion, is virtually identical for the two eyes.

Auxiliary visual areas. Compared to the work on cortical areas 17 and 18, there has been considerably less attention focused on the auxiliary visual areas in the cat cortex. Hubel and Wiesel (1969) reported that the receptive field properties of cells in the lateral supsylvian area were more or less similar to those of complex cells in areas 17 and 18. More recently, however, Spear and Baumann (1975) have pointed out some unique characteristics of lateral supsylvian cells, such as their lack of orientation selectivity, their extremely large receptive fields and a paucity of fields representing the upper visual field. These differences in receptive field properties between areas 17/18 and the lateral supsylvian region suggest that the latter may subserve a function other than simply higher level visual processing.

Visual evoked potentials. With single-unit recordings, there is always the possibility of overlooking

certain classes of neurons (e.g., those responsive to much higher spatial frequencies) because of limitations inherent in sampling procedure. To circumvent this possibility, some investigators have begun to employ evoked potential techniques for studying the spatial characteristics of the cat's visual system, on the assumption that the visual evoked potential reflects the combined activity from a large population of neurons. By determining the spatial frequency at which the evoked potential has fallen to zero, Berkley and Watkins (1971, 1973) estimated the acuity limit of the cat to be no greater than 6.5 cycles/deg. Using a similar strategy, Campbell, Maffei, and Piccolino (1973) derived a contrast sensitivity function for the cat by estimating the contrast level at which the evoked potential was zero. The resulting curve displayed both a low- and high-frequency fall-off in sensitivity, with the peak sensitivity occurring at approximately .2 cycles/deg. Campbell et al. repeated this procedure for several grating orientations, but found no meridional variations in contrast sensitivity.

VISUAL DEPRIVATION

At the same time the receptive field properties of visual neurons in normal, adult cats have been studied, neurophysiologists also have been exploring the extent to which these receptive field properties are influenced by visual deprivation. Besides providing important information on the genesis of neural specificity, this area of research has shed new light on the possible neural correlates of visual disorders, such as deprivation amblyopia. The general strategy has involved depriving cats of certain visual input for a limited period of time, and examining the resultant changes in morphology and/or response properties. A general conclusion from this research is that during the first 2-3 months of life, nonretinal portions of the visual system of the cat are quite vulnerable to certain types of visual deprivation (Wiesel & Hubel, 1963a, 1963b). Recent work has concentrated on the details of the time-course of this period of susceptibility (Blakemore & Van Sluyters, 1974; Hubel & Wiesel, 1970; Olson & Freeman, 1975; Van Sluyters & Freeman, 1977), and on possible differential influences of unilateral and bilateral deprivation upon X and Y mechanisms (Garey & Blakemore, 1977a; Sherman, Hoffmann, & Stone, 1972; Sherman & Stone, 1973; Hirsch & Leventhal, Note 1). More exotic forms of limited visual experience also have been explored (Blakemore & Cooper, 1970; Cynader, Berman, & Hein, 1975; Hirsch & Spinelli, 1970; Pettigrew & Freeman, 1973), but this set of findings is not without controversy (e.g., Stryker & Sherk, 1975).

The following sections provide a general overview of some of the work on visual deprivation in cats.

Monocular and Binocular Deprivation

Lateral geniculate nucleus. Form deprivation via eyelid suture during the first 3 months or so of a kitten's life appears to produce no major changes in the receptive field properties of retinal ganglion cells (Sherman & Stone, 1973), although abnormalities in the ERG have been described (e.g., Ganz, Fitch, & Satterberg, 1968). At the level of the lateral geniculate nucleus, however, monocular eyelid suture during early kittenhood leads to a failure of normal growth of cells in the laminae receiving projections from the deprived retina (Wiesel & Hubel, 1963a). Subsequent work (Guillery & Stelzner, 1970) has shown that this morphological effect of monocular deprivation is largely confined to the binocular portion of the lateral geniculate nucleus; cell size in the monocular crescent of the deprived lamina is more nearly normal. Other recent work (Dursteler, Garey, & Movshon, 1976; Hickey, Spear, & Kratz, 1977; Movshon & Dursteler, 1976; Wan & Cragg, 1976) has confirmed and extended these findings concerning the effects of monocular deprivation on LGN cell size. In contrast, binocular deprivation (via either bilateral lid suture or dark rearing) produces only a transitory retardation in LGN cell growth, with neurons eventually achieving almost normal size (Guillery, 1973; Hickey et al., 1977; Kalil, 1978).

With respect to the physiological effects of deprivation at the lateral geniculate nucleus, it was initially thought that the receptive fields of cells in the deprived laminae were normal (Wiesel & Hubel, 1963a). More recently, however, it has been found that monocular deprivation leads to a marked reduction in the proportion of Y cells sampled from the deprived laminae, while the proportion of X cells is relatively normal (Sherman et al., 1972; Sherman, Wilson, & Guillery, 1975). This selective loss in Y cells is found mainly in the binocular portion of the deprived laminae, and can be partially reversed with reverse lid suture (Hoffmann & Cynader, 1977). These physiological changes are accompanied by morphological effects which are relatively specific to the Y system (Garey & Blakemore, 1977a, 1977b; Lin & Sherman, 1978; Sherman, Guillery, Kaas, & Sanderson, 1974). The reduction in the encounter rate of Y cells from the deprived laminae following monocular deprivation may be due, in part, to electrode sampling bias. Recent work (Eysel, Grusser, & Hoffmann, 1979) has shown that within the optic radiation, which is central to the LGN, there is a *normal* complement of Y neurons following monocular deprivation; at the same time, it was found that Y cells were less frequently sampled when recording from the LGN. Eysel et al. speculate that this apparent paradox may arise from a greater reduction in the size of somas of Y cells, compared to X cells, as the result of deprivation.

While the proportion of recordable X cells is normal throughout all laminae, both deprived and normal, there is some question as to the normality of their receptive field properties. Sherman and his colleagues found that most recordable cells within the deprived laminae displayed normal receptive field layouts. Others (Hoffman & Sireteanu, 1977; Maffei & Fiorentini, 1976), though, have found that cells in the deprived laminae (irrespective of X or Y class) have lower spatial frequency resolution, compared to units innervated by the nondeprived eye. These two sets of results are not necessarily contradictory, for Sherman and his colleagues made no attempt to measure spatial selectivity but, instead, concentrated on qualitative descriptions of field size and measurements of response latencies. Binocular deprivation produces a less severe, though still significant, reduction in Y-cell frequency throughout the entire lateral geniculate nucleus, monocular crescent included (Sherman et al., 1972). Again, X-cell frequency is relatively normal.

Visual cortex. At the level of visual cortex, the effects of deprivation are well established. Numerous researchers (Blakemore & Van Sluyters, 1974a, 1975; Hubel & Wiesel, 1970; Movshon, 1976a; Olson & Freeman, 1975; Peck & Blakemore, 1975; Pettigrew, 1974; Schectel & Murphy, 1976; Wiesel & Hubel, 1963b) have documented the shift in ocular dominance of cortical cells following monocular deprivation and have worked out the time-course of this shift. In general, even brief periods of monocular eyelid suture destroy the normal degree of binocularity; most neurons in the binocular segment of the visual cortex can be activated through the nondeprived eye. Accompanying this physiological change in ocular dominance is an unmistakable shrinkage in the anatomically identified band of cells in cortical layer IV innervated by the deprived eye (Shatz & Stryker, 1978). This shift in cortical binocularity can be juggled between the two eyes by reverse suturing during the first 2 or 3 months following birth, but after this period most neurons become fixed in terms of their eye preference. After deprivation there does seem to remain some residual plasticity which allows a modicum of recovery with usage of a previously deprived eye (Mitchell, Cynader, & Movshon, 1977; Olson & Freeman, 1978); the success of this recovery technique may be related to the amount of normal binocular visual experience prior to deprivation (Blasdel & Pettigrew, 1978; Van Sluyters, 1978).

The effects of monocular deprivation are not uniformly distributed spatially. In more peripheral portions of the visual field, the incidence of cortical cells responsive through the deprived eye increases, although many of these cells, both simple and complex, display abnormal receptive field properties (Wilson & Sherman, 1977). Interestingly, simple cells in the deprived monocular segment of visual

cortex appear normal in all respects while many complex cells in this region display abnormal fields (Wilson & Sherman, 1977). Also, there is an unusually large percentage of cells driven by the nondeprived eye which display abnormal receptive fields, and these units are encountered only within the binocular segment of visual cortex (Wilson & Sherman, 1977). Finally, it is noteworthy that the physiological effects of monocular deprivation are found in both areas 17 and 18, but that in area 18 the contralateral pathway (i.e., the hemisphere contralateral to the deprived eye) is much more resistant to the effects of monocular deprivation than is the ipsilateral pathway (Singer, 1978); this asymmetry between crossed and uncrossed projections is not observed in area 17. This finding, like those of Eysel et al., suggests that the Y-cell system may be less affected by monocular deprivation than previously thought.

The loss of cortical binocularity which characterizes monocular deprivation actually can be created by other manipulations, including induced strabismus and alternating monocular occlusion (Blake & Hirsch, 1975; Blakemore, 1976; Hubel & Wiesel, 1965b). In general, it appears that any rearing procedure which precludes congruent binocular stimulation reduces the degree of binocularity (e.g., Blakemore, 1976). It would be interesting to know more about the degree of dissimilarity in stimulation, spatially and temporally, which can be tolerated before binocular connections begin to suffer.

With binocular deprivation, the effects at the cortex are somewhat different from those produced by monocular deprivation. The loss of binocularity is somewhat less severe, but there is a large increase in the number of visually unresponsive cells (Blakemore & Van Sluyters, 1975; Imbert & Buisseret, 1975; Pettigrew, 1974) compared to the normal case. Among those cells which are visually responsive, there is a tendency for cells to respond over a wider range of orientations (e.g., Wiesel & Hubel, 1965a) and retinal disparities (Pettigrew, 1974). Also, in binocularly deprived cats there are fewer directionally selective cortical cells (Singer & Tretter, 1976a) and an unusual number of cells with exceedingly large receptive fields which appear to lack inhibitory sidebands (Singer & Tretter, 1976b). There is some reason to believe that the precise nature of these cortical deficits depends on whether binocular deprivation results from lid suture as opposed to dark-rearing (Kratz & Spear, 1976). Of intriguing significance are the findings of Blakemore and Van Sluyters (1975) and of Leventhal and Hirsch (1977): In binocularly deprived cats, those cortical cells which are orientation selective tend to be of the simple type. This raises the possibility that the normal array of X cells in the LGN (Sherman et al., 1972) of binocularly deprived cats is projecting to simple cells in layer IV of visual cortex, thereby providing some substrate for orientation selectivity.

On the other hand, Y cells at the LGN are more susceptible to the effects of deprivation, so their cortical target cells (the complex cells—Hoffman & Stone, 1971) are more abnormal.

Recovery. It now appears that some of the deleterious effects of monocular deprivation on cortical cells may be reversible. Duffy, Snodgrass, Burchfiel, and Conway (1976) reported that binocularity in some cells could be temporarily restored following prolonged monocular deprivation by intravenous administration of bicuculline, an antagonist of the putative inhibitory neurotransmitter gamma-aminobutyric acid (GABA). Following cessation of bicuculline infusion, the deprived eye soon returned to its unresponsive state. This finding suggests that the deprived eye maintains some synaptic contact with cortical cells but that the nondeprived eye exerts some form of chronic inhibition over its deprived partner.

Another, somewhat more gross manipulation which has the same reversing effect is enucleation of the nondeprived eye (Kratz, Spear, & Smith, 1976). Almost immediately following removal of the normal eye, there is a significant increase in the percentage of units which respond to stimulation of the deprived eye. Kratz et al. stressed, however, that the receptive field properties of these resurrected cells are quite abnormal. This finding has been replicated by some (Hoffman & Cynader, 1977; Smith, Spear, & Kratz, 1978) but questioned by others (Harris & Stryker, 1977). The effectiveness of enucleation in reversing the actions of monocular deprivation may depend on the age of onset of deprivation (Van Sluyters, 1978) and on the integrity of the afferent pathways from the extraocular muscles (Crewther, Crewther, & Pettigrew, 1978). Certainly the reversibility of deprivation with enucleation could be interpreted within the framework of chronic interocular inhibition.

It should be pointed out that neither of these post-deprivation maneuvers, enucleation or bicuculline, yielded near full recovery by the deprived eye: the proportion of responsive cells still remains below normal levels. This failure of recovery makes sense in view of the convincing anatomical demonstrations that the distribution of axons from the deprived eye (via the deprived LGN lamina) is much reduced (Stryker & Shatz, 1976; Thorpe & Blakemore, 1975).

Finally, some very recent work by Kasamatsu and Pettigrew (1976) and Pettigrew and Kasamatsu (1978) indicates that catecholamine neurohormones play a critical role in promoting the cortical plasticity indicated by the effects of monocular deprivation. These workers found that intraventricular injection (Kasamatsu & Pettigrew, 1976) or local perfusion (Pettigrew & Kasamatsu, 1978) of 6-hydroxydopamine (6-OHDA) prevented the usual loss of binocularity following monocular deprivation. They attributed this action to the depletion of catecholamines (either dopamine or norepinephrine) produced by the neurotoxin 6-OHDA.

This suggests that brain catecholamines serve to maintain cortical plasticity. Pettigrew and Kasamatsu went on to demonstrate that local perfusion of catecholamine can induce plasticity, as evidenced by an effect of monocular deprivation, in the visual cortex of cats which would otherwise be immune to deprivation. In general, these exciting findings provide an important first step in understanding the vexing mechanism which controls the timing of the so-called critical period.

Strabismus

Although less severe than lid suture in terms of altering visual input, induced squint (misalignment of the two eyes via section of an eye muscle) can produce physiological consequences which rival those of deprivation, in terms of altering the visual nervous system. Hubel and Wiesel (1965b) were the first to show that artificial squint in young kittens leads to a marked reduction in the number of binocularly innervated cortical cells: virtually all neurons sampled could be activated only through one eye or the other. In other respects, the receptive field properties of cortical cells in squint kittens appeared qualitatively normal, although no systematic study of tuning properties was performed by Hubel and Wiesel. These findings of reduced binocularity following induced squint have been confirmed by others (Gordon & Gummow, 1975; Wickelgren-Gordon, 1972; Yinon, Averbach, Blank, & Friesenhausen, 1975), and the period of susceptibility to squint has been studied for both esotropia and exotropia (Yinon, 1976a). Moreover, it has been found that comparable losses in binocularity can be produced by optically induced squint, wherein a kitten wears prisms which simulate eye misalignment without disrupting the eye muscles (Levitt & Van Sluyter, 1979; Smith, Bennett, Harwerth, & Crawford, 1979). This means, of course, that asymmetrical, conflicting visual input alone can lead to a breakdown in cortical binocularity in the absence of impaired ocular motility, such as that produced by section of an eye muscle. More surprising is the finding that cortical binocularity is disrupted in kittens reared in total darkness with one of the extraocular muscles cut (Maffei & Bisti, 1976). This startling finding would mean that asymmetrical ocular motility alone is sufficient to reduce binocularity independent of visual input. There is some evidence to support the notion that extraocular afferents can play a role in visual deprivation (Crewther, Crewther, & Pettigrew, 1978), but clearly the situation in the case of dark-reared, strabismic kittens deserves further study, because the conclusions of Maffei and Bisti (1976) represent a radical departure from conventional thinking about the nature and consequences of strabismus (von Noorden, 1977).

Ikeda and Wright (1976) have examined the effects of induced convergent squint (i.e., esotropia) on the receptive field properties of LGN neurons in kittens. They found a reduction in the spatial resolving power of cells receiving innervation from the area centralis of the deviating eye; no such loss was observed in cells receiving input from the normal eye. In addition, geniculate receptive fields in the periphery of the deviating eyes were normal. In a later paper, Ikeda, Tremain, and Einon (1978) showed that the severity of the loss in spatial resolving power of LGN cells was directly related to the age at which squint was induced. Moreover, they (Ikeda, Plant, & Tremain, 1977) found that the severity of squint (i.e., degree of eye misalignment) determined the extent of loss of nasal field representation in the LGN lamina innervated by the deviated eye. Comparable morphological changes were observed in the form of cell size shrinkage in the squint-innervated lamina of the LGN (Ikeda & Wright, 1976). In none of their work have Ikeda and Wright studied the effects of divergent squint (exotropia).

In a couple of experiments, more unusual forms of eye deviation have been produced in cats, the aim being to investigate possible changes in receptive field layout. Shlaer (1971) reared kittens wearing prismatic lenses that induced a vertical disparity between the two eyes (a situation which mimics hypertropia). Rather than disrupting cortical binocularity, this condition led to a remapping of retinal correspondence, such that binocular receptive fields were shifted, relative to the normal topography, to maintain the fields in binocular register. Others (Smith et al., 1979; Van Sluyters, Note 2) have failed however, to replicate this remarkable finding. Shinkman and Bruce (1977) rotated the images to the two eyes of kittens in opposite directions, using prisms. They, too, found that binocularity was maintained in the face of these discrepant inputs and the interocular differences in preferred orientation matched the prism rotation experienced during rearing.

The most unusual form of eye deviation to be studied involves wholesale rotation of one eye of a kitten. This rearing procedure, not surprisingly, greatly reduces the proportion of binocularly activated cortical cells; the retinotopic mapping from the rotated eye remains normal, unlike in the case of Shlaer's (1971) kittens; and the binocular cells which can be driven by the rotated eye have stimulus specificities (orientation, direction selectivity) which remain faithful to the true retinal coordinates, with no compensation for rotation (Blakemore, Van Sluyters, Peck, & Hein, 1975; Yinon, 1976b, 1977).

Unusual Visual Environments

In the deprivation experiments described up to

this point, kittens have been raised in more or less ordinary environments which presumably are rich in visual stimulation: the deprivation effects were induced by manipulating the input via lid suture or by disrupting binocular coordination via eye deviation. The experiments included in this section have employed a rather different tactic to examine plasticity and deprivation: Animals were raised in visual environments which restricted visual stimulation to just a limited set of features, and the effects of this restriction on the receptive field properties of cortical neurons were then assessed.

Orientation. Perhaps the most striking group of experiments in this category involves the changes in orientation specificity of cat cortical neurons following exposure to stripes of a single orientation. In one paradigm (Hirsch & Spinelli, 1970, 1971), kittens were reared wearing goggles which carried a few stripes seen by each eye, vertical to one eye but horizontal to the other. Of the minority of neurons which retained any orientation selectivity, there was a clear trend for a cortical cell driven by one eye to prefer the orientation experienced by that eye. This finding has subsequently been replicated by others (Blakemore, 1976; Gordon, Presson, Packwood, & Scheer, 1979; Pettigrew, Olson, & Hirsch, 1973; Stryker & Sherk, 1975; Stryker, Sherk, Leventhal, & Hirsch, 1978).

Another technique employed to limit visual experience has been to rear kittens for several hours a day inside tall cylinders, the walls of which contain contours of a single orientation (Blakemore & Cooper, 1970). This strategy also produces shifts in preferred orientation toward that experienced, and the effects reported initially (Blakemore & Cooper, 1970; Blakemore & Mitchell, 1973) were even more striking than those produced by the goggle technique. There then ensued some controversy about the replicability of the effects of rearing in a cylinder (Stryker & Sherk, 1975), but the balance of evidence strongly favors the outcome originally described (Blakemore, 1977; Blakemore, Movshon, & Van Sluyters, 1978; Blakemore & Van Sluyters, 1975; Blasdel, Mitchell, Muir, & Pettigrew, 1977). Furthermore, there is one report (Daniels, Norman, & Pettigrew, 1977) that stripe-rearing in cylinders can induce weak orientation biases in neurons in the LGN, although this effect appears limited to cells that respond in a transient fashion. This geniculate modification was attributed to corticogeniculate influences.

A third technique which proves effective in altering cortical orientation selectivity has been to rear kittens with cylindrical lenses in front of the eyes, a maneuver which restricts clear focus to a single orientation. Cortical cells in cats reared in this fashion displayed orientation preferences which clustered around the focused meridian (Freeman & Pettigrew,

1973). A somewhat similar effect has been reported for unilateral induced astigmatism (Cynader & Mitchell, 1977). If, in front of one eye, the kitten wears a lens that defocuses the entire image, in all meridians, the number of cortical neurons driven by that eye is reduced and those which can be activated through the originally defocused eye exhibit an overall depression in contrast sensitivity (Eggers & Blakemore, 1978). This latter finding may represent the neural basis of anisometropic amblyopia.

There are a few experiments in which kittens were reared in environments totally devoid of straight contours. In those experiments, the environment consisted only of randomly scattered spots of light and subsequent cortical recordings revealed a high degree of selectivity for circular targets matched in size to those seen during rearing and a very low proportion of neurons preferentially responsive to contours (Blakemore & Van Sluyters, 1975; Pettigrew & Freeman, 1973; Van Sluyters & Blakemore, 1973).

Finally, there is some evidence that exposing kittens to a single orientation *and* spatial frequency can produce a *loss* in responsiveness to gratings of spatial frequency similar to that experienced during early rearing (Maffei & Fiorentini, 1974). Moreover, this type of neural plasticity, wherein exposure leads to a loss of neural responsivity, has been reported in the case of adult cats too (Creutzfeldt & Heggelund, 1975). These findings have not been replicated, however (Blakemore, Movshon, & Van Sluyters, 1978), and therefore must be interpreted with caution.

Directional selectivity. Many cortical cells in the normal cat respond more vigorously to movement of a contour in one direction as opposed to other directions (e.g., Pettigrew, Nikara, & Bishop, 1968a), and this direction selectivity appears to be an innate property seen even in the inexperienced visual cortex of young kittens (Pettigrew, 1974). Despite its primacy, though, this receptive field property also is susceptible to restrictions in early visual experience. Kittens have been reared in environments containing contours moving in just one direction, and the effects on cortical physiology are analogous to those found in the case of stripe rearing: For kittens which view, say, only leftward motion, the cortical receptive fields were strongly biased toward leftward-moving contours (Berman & Daw, 1977; Cynader, Berman, & Hein, 1975; Daw, Berman, & Ariel, 1978; Daw & Wyatt, 1976; Tretter, Cynader, & Singer, 1975). In some of these studies, it was noted that preferred velocity, unlike direction of motion, was not matched to that experienced during rearing. Besides the shift in direction preference, cortical cells of the simple, but not complex, type in these kittens also exhibited a bias for vertically oriented contours, even in cases where the environment contained only irregularly shaped patches (Cynader et al., 1975). Moreover, an unusually high percentage of

cortical cells in directionally deprived cats are exclusively monocular (e.g., Berman & Daw, 1977). This reduction in binocularity is rather curious in view of the fact that both eyes were open during rearing and presumably received congruent input.

As in the cases of other forms of special rearing, there exists a critical period for the manufacture of this cortical bias in direction selectivity. Interestingly, this critical period does not exactly coincide with that for monocular deprivation, but, rather, terminates earlier (Berman & Daw, 1977). In a clever set of experiments, Daw, Berman, and Ariel (1978) capitalized on the disparity between these two critical periods, one for direction and the other for eyelid suture, to create a visual cortex with many cells responsive to stimulus situations (e.g., leftward motion viewed by the right eye) which were never seen. Clearly, the neural connections subserving binocularity and direction selectivity involve at least some different synapses which follow different time courses during development.

Another rearing manipulation which very effectively changes direction selectivity involves raising cats in stroboscopic illumination (Cynader, Berman, & Hein, 1973; Cynader & Chernenko, 1976; Olson & Pettigrew, 1974; Orban, Kennedy, Maes, & Amblard, 1978). This procedure, which permits patterned visual stimulation without the experience of movement, leads to an irreversible reduction in the proportion of cortical cells displaying direction selectivity. By varying the temporal frequency of illumination, Cynader and Chernenko (1976) were able to produce a visual cortex with normal orientation selectivity but grossly abnormal direction selectivity. Again, the implications of this result, in terms of the independence of the mechanisms responsible for these two properties, are obvious.

Remarks

The deprivation paradigm has proved to be a goldmine for those interested in studying visual development and cortical plasticity. It seems clear that, for at least a portion of time, the visual system of the cat is extremely vulnerable to environmental influences (including experimenters skilled in eye surgery). Moreover, this deprivation paradigm has furnished a possible strategy for relating underlying neural mechanisms to visual capacities assessed behaviorally. To the extent that a particular receptive field property provides the neural machinery for some discriminative ability, we would expect animals lacking cells with this property to exhibit deficits on such a discrimination. There has not been an overwhelming amount of behavioral work exploring this question, but to date the correlations between behavior and physiology have ranged from very robust (e.g., Blake & Hirsch 1975) to very weak (e.g., Hirsch,

1972). Table 1 gives a rather complete listing of those papers which contain behavioral observations on the visual capacities of deprived cats; these are listed according to the form of deprivation and include a very brief summary of the findings.

GENERALIZATIONS FROM CAT TO HUMAN

As indicated by the volume of studies reviewed here, the visual nervous system of the cat has been dissected in great detail. For the neuroscientist primarily interested in understanding neural function in terms of structure, this abundance of findings represents a self-contained feast sufficient for the largest appetite. The fact is, however, that many of us wish to know to what extent these neurophysiological findings in cat reflect the events occurring within our own visual systems. Questions of this sort involve jumping several rungs on the evolutionary ladder, but several considerations indicate that this jump may be a relatively safe one.

For one thing, the receptive field properties characteristic of cat visual neurons are similar in most respects to those found in the visual systems of our closer relatives, the primates. Consider the visual system of the monkey. At the level of the retina (e.g., Hubel & Wiesel, 1960) and LGN (e.g., Wiesel & Hubel, 1966), receptive fields are concentrically arranged in antagonistic fashion, and the X/Y classification worked out in the cat has been successfully extended to the retina (Monasterio, Gouras, & Tolhurst, 1976) and LGN (Dreher, Fukada, & Rodieck, 1976) of the monkey. At the cortical level in monkey, the same array of cell types, i.e., simple, complex, and so on, is present (e.g., Hubel & Wiesel, 1968; Schiller, Finlay, & Volman, 1976); many of these neurons are binocular and, just as in cat, some are specific for retinal disparity (e.g., Poggio & Fischer, 1977). Moreover, it is well established that the visual system of the monkey is susceptible to many of the same deprivation effects (e.g., Hubel, Wiesel, & LeVay, 1977) which have been shown in cat. There are some notable differences between the species, such as the more detailed chromatic selectivity of monkey neurons and the projection of monkey LGN afferents exclusively to area 17, but, on the balance, the visual system of cat and monkey are remarkably analogous in terms of their receptive field properties.

Another consideration which provides some foundation for generalizing from cat to human comes from comparisons of human and cat visual psychophysics; these comparisons have been discussed in some detail elsewhere (Berkley, 1976; Blake, 1978). The only major qualitative difference between human and cat vision seems to emerge in the case of color discrimination, and some very recent findings

Table 1
Summary of Behavioral Studies and Observations of the Visual Capacities of Deprived Cats,
Organized According to Rearing Procedure and Behavioral Test(s)

Rearing Condition and Study	Outcome
Monocular Deprivation	
Wiesel & Hubel (1963b) Wiesel & Hubel (1965b) Sherman (1973) Blakemore & Van Sluylers (1974a) Movshon (1976b) Van Hof-Van Duin (1976a)	Absence of normal visually guided behavior using deprived eye, with some recovery over time especially following reverse lid suture. Tasks have included visual placing, tracking, startle reaction, visual cliff.
Ganz & Fitch (1968) Dews & Wiesel (1970) Rizzolatti & Tradardi (1971) Chow & Stewart (1972) Ganz, Hirsch, & Tieman (1972) Ganz & Haffner (1974) Spear & Ganz (1975) Loop & Sherman (1977) Van Hof-Van Duin (1976b)	Although requiring extensive training, monocularly deprived cats can learn brightness, form, and pattern discriminations. Performance is less reliable, shows only marginal interocular transfer; training is hastened with reverse lid suture and impaired by large-scale lesions of visual cortex. Cats can learn brightness discrimination with deprived eye still closed.
Giffin & Mitchell (1978) Mitchell, Cynader, & Movshon (1977)	Visual acuity in deprived eye is reduced by an amount related to duration of deprivation.
Sherman (1973, 1974) Sherman, Guillery, Kaas, & Sanderson (1974) Sherman & Guillery (1976) Van Hof-Van Duin (1977) Heitlander & Hoffman (1978)	Perimetry testing reveals a reduction in the visual field of the deprived eye; the spatial extent of this deficit is controversial.
Binocular Deprivation*	
Wiesel & Hubel (1965b) Baxter (1966) Chow & Stewart (1972) Sherman (1973) Van Hof-Van Duin (1976b) Kalil (1978) Vital-Durand & Jeannerod (1975)	Cats appear blind when first tested on conventional visuomotor tasks but recover to normal within a few months or less.
Vital-Durand & Jeannerod (1974) Berthoz, Jeannerod, Vital-Durand, & Oliveras (1975) Van Hof-Van Duin (1976a)	Optokinetic nystagmus can be elicited immediately following deprivation but lacks certain normal components.
Chow & Stewart (1972) Zablocka, Konorski, & Zernicki (1975) Zablocka (1975) Timney, Mitchell, & Giffin (1978) Blake (1978)	Cats display considerable difficulty on pattern discrimination; visual acuity and contrast thresholds are impaired but can improve.
Sherman (1973, 1974) Kalil (1978)	Visual perimetry indicates blindness of the temporal hemiretinae.
Blake & Hirsch (1975) Packwood & Gordon (1975)	Alternating monocular occlusion yields deficits in stereopsis but not in visual acuity.
Strabismus	
Hubel & Wiesel (1965b) Blakemore & Van Sluylers (1974b) Franklin, Ikeda, Jacobson, & McDonald (1975) Ikeda & Jacobson (1977a) Ikeda & Jacobson (1977b)	Induced exotropia yields no apparent deficits in visual behavior. Esotropia leads to acuity losses and nasal visual field blindness.
Blakemore, Van Sluylers, Peck & Hein (1975) Peck & Crewther (1975) Mitchell, Giffin, & Muir (1976)	Using an eye which was surgically rotated shortly after birth, cats display normal visuomotor behavior, with some errors, and can learn pattern discriminations.
Orientation	
Hirsch (1972) Muir & Mitchell (1973, 1975) Blasdel, Mitchell, Muir, & Pettigrew (1977)	Stripe-reared cats show modest deficits in visual acuity for nonexperienced orientations but only marginal deficits in orientation discrimination.

*Lid suture or dark rearing; alternating occlusion.

(Loop & Bruce, 1978; Ringo, Wolbarsht, Wagner, Crocker, & Amthor, 1977) may even force us to abandon this notion. In many other respects, cat and human vision are comparable. For instance, the cat (like man): shows a rod/cone discontinuity during dark adaptation as well as a Purkinje shift (LaMotte & Brown, 1970), suffers a falloff in visual acuity with retinal eccentricity (Blake & Bellhorn, 1978), handles about a 5-octave range of spatial frequencies (Blake, Cool, & Crawford, 1974), shows a tradeoff in sensitivity between spatial and temporal resolution (Blake & Camisa, 1977), and possesses stereopsis (Fox & Blake, 1971). Now, it is true that in the case of some of the acuities (e.g., spatial frequency) cat and man differ in terms of absolute values. The important consideration, though, is that for both species these acuities vary in the same manner with various stimulus manipulations (e.g., light adaptation level). This sort of equivalence argues for comparable underlying neural mechanisms which are simply scaled differently (e.g., receptive field size) in the two. In this respect, we might think of the differences between cat and human as analogous to those between a violin and viola, two instruments which are constructed according to identical principles but are scaled, or tuned, to different frequencies.

Finally, from clinical evidence we know that disturbances in human vision are frequently associated with disorders early in life which closely resemble those artificially induced in cats. In many instances, the perceptual deficits in humans and cats are directly comparable (e.g., Freeman, Mitchell, & Millodot, 1972; Muir & Mitchell, 1975). Indeed, in clinical ophthalmology the visual deprivation findings in cat and monkey now provide the basis for thinking about the etiology of various forms of amblyopia (e.g., von Noorden, 1977).

All in all, these kinds of considerations strengthen confidence that the feline visual nervous system represents a reasonable model of the neural mechanisms involved in human vision. Of course, when it comes to understanding just how these neural mechanisms are involved in the business of perceiving our complex visual world, we are dealing with an entirely different set of problems which entail other considerations, both experimental and philosophical. Nevertheless, visual science is indebted to the cat for bringing us to this stage where it is feasible to talk about the neural basis of vision.

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NOTE

1. The extent to which these various tests for X vs. Y actually distinguish the two cell-types is a debatable point. Some workers

(e.g., Friedlander, Lin, & Sherman, 1979) place great faith in these various criteria, while others (e.g., Hochstein & Shapley, 1976a) have placed the primary emphasis on the linear/nonlinear classification scheme. Certainly, the sustained vs. transient nature of the time course of the response of retinal ganglion cells is an inadequate index of whether a cell is X or Y, for this property varies greatly depending on adaptation level (Jakiela & Enroth-Cugell, 1976). In fact, there is some skepticism as to whether there genuinely exists distinct, nonoverlapping cell types, as opposed to a continuum of receptive-field properties (Enroth-Cugell, Note 3). Clearly, the time is ripe for a critical evaluation of the various classification schemes which have been proposed and for the adoption of some uniform scheme. More sophisticated Fourier analyses of the neural response of cat retinal ganglion cells may offer the most plausible quantitative means for classifying retinal cells (Shapley & Victor, 1978).

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