--
--

Perceptual Development and Learning: From Behavioral, Neurophysiological, and Morphological Evidence To Computational Models

delim $$

Vasant Honavar
Computer Sciences Department
University of Wisconsin-Madison

Abstract

An intelligent system has to be capable of adapting to a constantly changing environment. It therefore, ought to be capable of learning from its perceptual interactions with its surroundings. This requires a certain amount of plasticity in its structure. Any attempt to model the perceptual capabilities of a living system or, for that matter, to construct a synthetic system of comparable abilities, must therefore, account for such plasticity through a variety of developmental and learning mechanisms. This paper examines some results from neuroanatomical, morphological, as well as behavioral studies of the development of visual perception; integrates them into a computational framework; and suggests several interesting experiments with computational models that can yield insights into the development of visual perception.

Role of Environmental Experience in Development and Learning

In order to understand the development of information processing structures in the brain, one needs knowledge of changes it undergoes from birth to maturity in the context of a normal environment. However, knowledge of its development in aberrant settings is also extremely useful, because it reveals the extent to which the development is a function of environmental experience (as opposed to genetically determined pre-wiring). Accordingly, we consider development of the visual system under both normal and restricted rearing conditions.

The role of experience in the early development of the sensory systems in general, and the visual system in particular, has been widely studied through a variety of experiments involving carefully controlled manipulation of the environment presented to an animal. Extensive reviews of such results can be found in (Mitchell, 1984; Movshon, 1981; Hirsch, 1986; Boothe, 1986; Singer, 1986). Some examples of manipulation of visual experience are total pattern deprivation (e.g., dark rearing), selective deprivation of a certain class of patterns (e.g., vertical lines), monocular deprivation in animals with binocular vision, etc. Extensive studies involving behavioral deficits resulting from total visual pattern deprivation indicate that the deficits arise primarily as a result of impairment of visual information processing in the brain. The results of these experiments suggest specific developmental or learning mechanisms that may be operating at various stages of development, and at different levels in the system. We will discuss some of these

---

This is a working draft. All comments, especially constructive criticism and suggestions for improvement, will be appreciated. I am indebted to Prof. James Dannemiller for introducing me to some of the literature in infant development; to Prof. Leonard Uhr for his helpful comments on an initial draft of the paper; and to numerous researchers whose experimental work has provided the basis for the model outlined in this paper. This research was partially supported by grants from the National Science Foundation and the University of Wisconsin Graduate School.

results and their implications.

Although experiments involving visual deprivation can provide useful insights into the mechanisms of plasticity in the developing visual system, one ought to be somewhat cautious in extrapolating from these studies to the situation in normal development. This is necessitated by the fact that some of the manipulations of the visual environment used in the experiments are rather gross. Further, there is a risk that some of these manipulations may depart too much from the range of environmental variability that the visual cortex has evolved to cope with.

That learning involves the modification of the basic structure of connections between neurons in the brain, throughout life, shaped by experience, is a hypothesis that has attracted a number of workers in neuroscience and psychology, as well as artificial intelligence. Ramon y Cajal (1893) proposed that formation of new synapses was a likely neural basis for learning. Tanzi (1893) suggested that the changes in the efficacy of previously existing synapses could incorporate new patterns into the organization of the brain. Hebb (1949) hypothesized that the increase in the efficacy of a synapse between two neurons that fire simultaneously was the basis of forming associations and therefore, of learning. We will examine the experimental evidence available in support of both the hypotheses.

A great deal of experimental work involving behavioral and morphological studies of the brain has provided insights into the mechanisms of perceptual learning in adult animals (i.e., beyond the so-called *critical period*). A survey of some of the experiments that examine the role of experience in the development of different perceptual modalities beyond the critical period can be found in (Greenough, 1976; Greenough, 1987). Most of the experiments involve comparison among animals reared in environments of differing complexity. This kind of experiment was first performed by Hebb who found that rats reared in complex environments (e.g., homes) were better at learning a series of complex maze patterns than those reared in the laboratory in cages. It has been suggested that the observed effects might be the result of differences in the amounts of acquired knowledge that animals reared in different environments can draw upon when presented with a novel situation (Greenough, 1987). It is interesting to ask in what ways, if any, the mechanisms of plasticity in the adult brain differ from those in the developing infant's brain. We will summarize the results from experimental studies of visual development in animals beyond the critical period and attempt to address this question.

Perceptual studies of infants of different ages have attempted to throw some light on the development of various aspects of perceptual abilities. The body of literature in this field is enormous and a detailed review is beyond the scope of this paper. The interested reader is refered to (Banks, 1983) for a broad review. We will selectively examine some of the studies concerning the development of pattern discrimination abilities (mainly through experiments involving preferential fixation), principles of perceptual organization, generalization of shapes.

The results of behavioral, neurophysiological, and morphological studies of perceptual development and learning offer many insights into the underlying computational mechanisms involved in the emergence of the information structures and processes that enable an animal to successfully learn from its interactions with the environment. We will sketch out a general computational framework that is useful for studying perceptual development and learning; to suggest experiments designed to fill the gaps in our understanding of these phenomena; and to build synthetic systems of comparable perceptual and cognitive abilities.

Development of the Visual System

This section summarizes known results from studies of visual development in several animals (cats, monkeys, and human infants) in normal as well as experimentally manipulated settings. It is beyond the scope of this paper to describe in detail the known anatomy and physiology of the visual system. The reader is refered to (Van Essen, 1985; Crick, 1986; Uhr, 1986; Zeki, 1988; DeYoe, 1988; Livingstone, 1988) for review of such material. A general understanding of the anatomy and physiology of the visual system is assumed in the discussion that follows.

Development of the Retina

The anatomical development of the human retina has been investigated at two levels: the microstructural level concerning the fine structure of neurons and synaptic contacts; and the macrostructural level concerning the gross morphology of the retina (its layering, distribution of neuron types, etc.). In spite of the differences across different species in the degree of retinal development at the time of birth, similarities in the sequences of retinal development among different species (cats, dogs, rats and primates) have been noted (Dunn, 1972) - e.g., the peripheral retina is in many respects, more mature than the central retina (Abramov, 1982).

No new cones and retinal neurons differentiate in the foveal region postnatally (Hendrikson, 1976). The density of cones in the fovea is significantly higher in the adult than that in an infant. The increasing density of foveal cones accompanied by a decrease in the density of ganglion cells and inner nuclear layers (bipolars, amacrines, and horizontals) suggests a migration of cones from the periphery towards the center of the retina and that of gangion and inner nuclear cells, from the fovea towards the periphery of the retina. A given set of ganglion cells respond to different visual features at different ages (e.g., a set of cells that respond to a straight edge may later respond to a curve). It has been suggested that the mapping between environmental features and their representations in the retina may therefore demand continuous recalibration (Banks, 1983).

Physiological studies have shown that the ganglion cells in kittens respond fairly briskly to visual stimuli by 3 weeks although the contour enhancement and gain control effects of lateral inhibition may not be present until about 2 months of age (Hamasaki, 1977; Rusoff, 1977). However, one has to be cautious in extrapolating from these data to humans or even primates because the retina in kittens is much less mature anatomically than that in human or primate infants.

Monocular and binocular deprivation has no obvious impact on either the number (Sherman, 1973) or the spatial and temporal response properties (Kratz, 1979), and by inference, on the peripheral retinal neurons in cats. Thus, it is unlikely that the deprivation effects observed at higher levels of the visual pathway (LGN and visual cortex) are caused by changes in the retinal mechanisms.

Development of the LGN

There is a great deal of similarity in prenatal as well as postnatal development of the LGN in monkeys and humans (Hitchcock, 1980; Rakic, 1977). The LGN of the newborn human infant has many characteristics of the mature adult structure (Hickey, 1977). 6 layers, 2 magnocellular and 4 parvocellular, are readily distinguishable; but the cell bodies in each layer are smaller than in adults. Neurons in the parvocellular layer grow rather rapidly from birth to about 6 months and then at a slower pace until about 12 months, when their size approaches that in the adult. Neurons in the magnocellular layers grow much more slowly, and do not reach the adult size until about 24 months. Development of the LGN in the monkey is quite similar, although more rapid than that in humans (Rakic, 1977). Geniculate cells in very young monkeys respond quite sluggishly and fatigue rather easily (Blakemore, 1980). In newborn monkeys, the acuity of geniculate cells supplied by the fovea is slightly higher than that supplied by the periphery; and the visual acuity of foveal geniculate cells improves with age much more dramatically than that of peripheral geniculate cells. The geniculate cells of the newborn monkey can be classified into X and Y cells based on tests of spatial summation; but not tests involving response duration (Blakemore, 1980). Thus several properties leading to the distinction between X and Y cells in the adult monkey develop postnatally.

The development of the LGN in cats appears to be different from that in the monkey. The retinotopic arrangement of receptive fields across the geniculate is adultlike; but the individual cells are very slow to respond, fatigue rather easily, have abnormally large receptive fields, and the inhibitory region (surround) of the center-surround receptive field is less pronounced (Daniels, 1978; Norman, 1977). Several *silent* areas are encountered during physiological recording, suggesting that some cells are simply not responsive to visual stimulation. Also, the distinction between X and Y cells is much less apparent in the young kitten as compared to the adult cat (Daniels, 1978; Norman, 1977). Postnatal development of X cells is more rapid (with the receptive fields attaining their adult-like center-surround antagonism by 4-5 weeks after birth) than that of Y cells (which take a few weeks longer to attain their adult-like receptive fields). There is some evidence that the physiological immaturities observed in the LGN are more marked than among the ganglion cells (Daniels, 1978), suggesting that the time courses of development of the retina and the LGN may be different. There is strong evidence that the anatomical development in the LGN of the kitten is more susceptible to disruption by monocular deprivation (which leads to marked cell shrinkage) than by binocular deprivation (Shapley, 1980; Sherman, 1972). This has led to the suggestion that some sort of binocular competition modulates cell growth in the LGN (Guillery, 1972).

Quantitative measurements reveal a fourfold increase in synaptic density in the cat LGN during the first postnatal month (Cragg, 1975a). These synapses can be divided into two main groups, asymmetric and symmetric; asymmetric synapses are thought to be excitatory, symmetric ones inhibitory. Most of the synapses formed during the first 3 postnatal weeks are asymmetric (Winfield, 1980). The proportion of symmetric synapses and, by inference, inhibitory connectivity increases dramatically (to about 30% of the total) shortly after the beginning of the 4th postnatal week (Winfield, 1980). The LGN cells in the cat acquire their adult size and morphology by the 6th to the 8th postnatal week (Kalil, 1978; Mason, 1983). During this time, the LGN volume increases to its adult size and the adult complement of large cells develops in the paracentral portion of the lamina A (Kalil, 1978). Further, the proportion of symmetric synapses continues to increase till the adult level of 45% is reached by about the 15th postnatal week (Winfield, 1980). Consistent with this, the cat LGN cells continue to increase their sensitivity to higher spatial frequencies and their spatial resolving power until the adult levels are reached by about the 16th postnatal week.

Development of Visual Cortex

The full complement of prospective cortical neurons is produced well before birth. The lamination characteristics of the adult cortex are apparent in the cortex of the newborn infant. Individual neurons in the cortex of the monkey undergo marked morphological changes after birth (Boothe, 1979; Lund, 1977). All neurons in area 17 appear to go through a common developmental sequence at very similar times: Just before birth, axons and dendrites are easily recognized, but dendrites are short and poorly arborized. All neurons then grow a large number of dendritic spines, the greatest occuring at about 2 months after birth. Thereafter, the number of spines gradually diminishes, until adult levels are reached several months later. Neurons in cortical layers that receive primarily a parvocellular geniculate input (layer 4C$beta$) approach adult spine densities sooner than cells in layers receiving primarily a magnocellular geniculate input (layer 4C$alpha$). For some neuronal populations, the spine frequency is still above adult levels as late as 9 months after birth (Boothe, 1979). Similar morphological changes have been observed in humans (Conel, 1939-1963). The general proliferation of dendrites takes place more gradually in humans than in monkeys, reaching its peak at roughly 6 months of age. The vertical organization of dendritic trees, presumably underlying the columnar organization of function, is present at birth. It is known that in primates, the afferent fibers from the LGN reach cortical layer 4 before birth, but it is not known when they form connections with the cortical cells (Rakic, 1981). These afferent fibers are not initially segregated according to ocular dominance; but instead, in monkeys, a gradual segregation takes place until the adult pattern is achieved by about 1 month after birth (Hubel, 1977).

In the cat, afferents from the LGN reach area 17 about 12 days before birth (Anker, 1977). Their distribution within area 17 changes significantly during the first 3 postnatal weeks: During the 1st postnatal week the LGN afferents project more heavily into the upper cortical layers (especially layer 1) than in the adult (Anker, 1977; LeVay, 1978; Kato, 1983). At this stage, projections to layer 4 are wider than those in the adult cat and the projections to layer 5 are much denser than those in the adult (LeVay, 1978). The LGN afferents to area 17 approach the adult distribution with the highest density of projections restricted to layer 4 and the segregation of afferents into ocular dominance patches appears by the end of the 3rd postnatal week (LeVay, 1978; Kato, 1983).

Dendritic spines are sites of synaptic contacts (LeVay, 1973), and developmental changes in spine numbers reflect changes in the numbers of synapses (Mates, 1983a; Mates, 1983b; Mates, 1983c). Quantitative measurements of synapses have demonstrated an overshoot in the number of synapses in monkey striate cortex with an excess of neural connections made between birth and 6 months of age, followed by a decrease to the adult value (O’Kusky, 1982). It has been estimated that that the total number of synapses increase from approximately 389 billion at birth to 741 billion at six months and then decrease to about 381 billion in the adult.

In kittens, the formation of synapses begins before birth but by the time the eyes open, less than 2% of the normal adult complement of cortical synapses is present. Between 1 and 5 weeks, a burst of synaptogenesis occurs (Cragg, 1975a). This phase is at least partially dependent on visual input and is followed by a partial loss of synapses until adult levels are reached at about 3 months (Cragg, 1975b). Winfield (1981) examined kittens at several different postnatal ages to specify the time course of the overshoot. Synaptic density reached a peak at about 10 weeks of age. After this age, the density decreased to about 83% of the peak value at about 16 weeks of age, and the cortical synaptic density in the adults was about 70% of the peak value.

Unlike cells in the retina and the LGN, visual cortical neurons exhibit binocularity, disparity selectivity, orientation selectivity, and direction selectivity. The role of visual experience on each of these properties has been studied by a variety of environmental manipulations.

At birth, kittens' eyes are closed. When the eyes open (at about 1-2 weeks of age), the optics of the eyes are noticeably cloudy (Bonds, 1978). This makes it difficult to assess the receptive field properties of cortical neurons until about 3 weeks of age. However, several researchers have measured the receptive field properties of the area 17 neurons in very young kittens (e.g., Blakemore, 1975; Bonds, 1979; Hubel, 1963; Pettigrew, 1974; Beckmann, 1982; Albus, 1984). There are similarities and dissimilarities in the reported observations. They all agree that these cells exhibit, at the youngest testable ages, some properties of adult cells: retinotopy (topographic mapping of the visual field onto the cortex), direction selectivity, and to some extent, binocularity. They disagree on properties such as orientation selectivity. The reported observations in this case range from "all cells exhibit clear orientation preferences" (Hubel, 1963) to "very few, if any, exhibit orientation selectivity" (Pettigrew, 1974). When an attempt is made to distinguish orientation from direction selectivity, only about 20% of the neurons in the visual cortex of the kitten are truly orientation selective and less than 50% show selective response to orientation or direction of movement at the time the eyes open (Blakemore, 1975). The few cells that are orientation selective at 2-3 weeks of age tend to be monocular and are found primarily in cortical layer 4 and 6 where the bulk of the LGN afferents terminate (Blakemore, 1975; Albus, 1984). There is some evidence based on latency to electrical stimulation of afferent pathways (Beckmann, 1982) that these cells are *first order neurons*, activated monosynaptically by LGN afferents. In addition, the first orientation selective cells in area 17 have receptive field characteristics (Blakemore, 1975; Beckmann, 1982; Albus, 1984) associated with *simple cells* in area 17 of adult cats, and simple cells are good candidates for first order neurons (Hubel, 1962; Singer, 1975). The nonselective cells are more like *complex cells* (Blakemore, 1975) in the area 17 of the adult cat and thus many of them may be *second order cells* (Hubel, 1962; Singer, 1975). It has been suggested that the orientation selectivity of area 17 cells is at least partly produced by the intracortical GABA-mediated inhibitory inputs (Sato, 1984). Under normal rearing conditions, the proportion of orientation selective cells increases dramatically after the 3rd postnatal week (Blakemore, 1975; Bonds, 1979; Albus, 1984) reaching the adult level between 4-5 weeks of age. Further, the *tuning width* of cortical cells continues to become narrower after 5 weeks of age, their selectivity approaching the adult levels by 6-8 weeks of age (Derrington, 1981).

There is some evidence (based on the proportions of orientation selective cells present at 6 weeks of age) that the maturation of the layers 2/3 and lower 6 lags behind the maturation of the other layers in the area 17 of the cat (Tsumoto, 1982). It has been suggested (Hirsch, 1986) that the development of orientation selectivity may continue beyond 6 weeks of age in those layers (2/3) of area 17 that provide the bulk of the efferent projection to other cortical areas. The spatial frequency tuning continues to increase between 6 and 8 weeks of age (Derrington, 1981), and this is consistent with an increase in inhibitory input to area 17 cells during this period.

The development and maintenance of orientation and spatial frequency selectivity in kittens during the first 3 postnatal weeks (involving mostly the first order cells, those that receive monosynaptic excitatory inputs from LGN X cells) is not affected by dark-rearing (Bonds, 1979). However, the development and/or maintenance of orientation selectivity (Blakemore, 1975; Pettigrew, 1974; Bonds, 1979) and spatial frequency selectivity (Derrington, 1984) among the bulk of the area 17 cells (including many that receive their excitatory inputs from other area 17 cells and/or LGN Y or W cells) does require visual stimulation.

Unlike kittens, monkeys are born with their eyes open and with clear optics. According to one study (Wiesel, 1974), most cortical neurons in the new born monkey exhibit preference to narrow bands of orientations, and either simple or complex receptive fields. Ocular dominance and prefered orientation change systematically as the recording electrode is advanced, suggesting the presence of columnar organization. However, the disagreements in the reported results from studies of cortical neurons in kittens call for caution in the interpretation of this account.

Disparity selectivity, an important property of mature cortical neurons, is strikingly imprecise in very young kittens: the binocular disparity of an otherwise optimal stimulus could be varied by several degrees of visual angle without influencing the response rate. Disparity tuning improved rapidly thereafter, approaching adult values by 6 weeks of age (Pettigrew, 1974).

In cats altogether deprived of visual stimulation since birth, many cells do not respond to visual input, and those that do are erratic in their response (Blakemore, 1975). Few cells exhibit orientation selectivity, but most are binocular and have direction selectivity. The abnormality of the binocularly deprived cortex relative to the normal cortex does not emerge until 4 to 5 weeks of age: Before 4 weeks, the cortical neurons of binocularly deprived kittens are essentially indistinguishable from normally reared kittens (Blakemore, 1975). After 4 weeks, the cells in deprived animals become less and less responsive and selective as compared to the normally reared kittens, and continued deprivation causes the receptive field characteristics of the cortical neurons to regress to neonatal status or worse. One can infer from these results that there is little, if any, passive (experience-independent) maturation of the cortical neurons in the kitten beyond 4 weeks of age. Early binocular deprivation severely disrupts the selectivity of cortical neurons in monkeys (Crawford, 1975). Thus, it is evident that visual experience plays a major role in the development of visual cortex in cats as well as monkeys.

Monocular deprivation causes severe loss in responsiveness through the deprived eye in both cats and monkeys (Blakemore, 1978; Blakemore, 1974; Crawford, 1975; Wiesel, 1965). Very few binocular cells are observed in monocularly deprived animals. In the visual cortex of a normal adult monkey, the inputs from the two eyes terminate in alternating bands (columns). If one eye is deprived of input during development, the columns corresponding to that eye are much narrower than the other eye, the one not deprived of its normal input. LeVay, Wiesel and Hubel found that, in the initial stage of development, the inputs from the two eyes overlap and no distinct organization of ocular dominance columns is present. During normal development, the input fibers from both the eyes regress simultaneously and gradually such that the sharply defined occular dominance columns found in the adult emerge. When one eye is deprived of its input, its connections to the cortex regress more than that in the case of the other eye receiving normal input, resulting in alternating bands of narrow and wide columns (LeVay, 1980). Although the exact mechanisms involved are subject to debate, it appears likely that the connections *compete* to *represent* the input, and the actively firing synapses are the ones that win the competition or that synchronous firing of the presynaptic terminal and the postsynaptic neuron may contribute to the sustenance of a synapse (Singer, 1986).

The nature of binocular experience necessary for maintenance of binocularity has been investigated through experiments that introduced an interocular imbalance between either the overall intensities or the clarity of the patterns in the two retinal images (Blakemore, 1976). Imbalance in pattern clarity alone disrupted binocularity while imbalance in overall intensities of retinal images did not. Thus, one can conclude that presentation of *similar* pattern information to the two eyes is necessary to preserve binocularity. Experiments with kittens and monkeys raised with their visual axes artificially misaligned (Blakemore, 1976; Van Sluyters, 1980; Baker, 1974) have suggested that lack of registration between two retinal images leads to loss of binocularity. Cortical binocularity is disrupted by alternately depriving kitten's eyes day by day (Blakemore, 1976). Thus, binocular visual experience has to be both concordant as well as synchronous to ensure normal visual development.

In kittens reared in environments composed of small, randomly arrayed spots (i.e., devoid of extended contours), most cortical neurons failed to develop normal orientation selectivity; instead, they prefered spots rather than bars or edges, in sharp contrast with cells in normally reared cats (Pettigrew, 1973). Neurophysiological studies on animals reared in an environment that restricts their visual experience to a certain class of patterns (e.g., vertical or horizontal lines) show that the neurons in the visual cortex of such animals respond strongly when the animal sees stimuli close to the rearing stimuli and poorly otherwise (Hirsch, 1970). Behavioral studies similarly indicate that such animals perform better at resolving lines at orientations close to the ones present in the rearing environment (Blasdell, 1977; Corrigan, 1979). Experiments with animals deprived of visual motion perception have been shown to have similar effects on cortical neurons that selectively respond to the direction of movement (Cynader, 1976).

Morphological studies have shown that total pattern deprivation has pronounced effects on the structure of the visual cortex. The neurons of visually deprived animals make fewer connections than those found in normal animals. This is suggested by the fewer numbers of dendrites, fewer spines (the primary site of connections) per dendrite, and, as expected, fewer synapses on the average per neuron in the visual cortex of such animals (Fifkova, 1968; Valverde, 1971; Rothblat, 1979; Coleman, 1968; Globus, 1973; Cragg, 1975b; Winfield, 1981). Similar results have been reported even in the case of subcortical visual structures following pattern deprivation (Fifkova, 1979; Globus, 1975). On the other hand, overstimulation of the visual system has been shown to have the opposite effect, i.e., greater than normal numbers of spines per dendrite on an average in the visual cortex (Parnavelas, 1976) of the rat.

An important question concerning the role of experience in the development of cortex is: When is the appropriate visual experience required? The answer to this question varies as depending on particular environmental inputs as well as particular cortical cell properties (Cynader, 1976). The longer the duration of visual deprivation, the less irreversible is the resulting deficit, even if suitable visual experience is made available at a later time. This has been demonstrated through behavioral studies (Crabtree, 1979), neurophysiological studies (Cynader, 1976), as well as morphological studies (Valverde, 1971). In cats and monkeys, the so-called sensitive period extends from 2 to 14 weeks (Hubel, 1970; Crawford, 1975) and appears to be substantially longer in humans.

Greenough has suggested that the quality of early experience may play a role in regulating the duration for which the developing nervous system remains plastic or sensitive to such experience (Greenough, 1987). This is supported by the experiments of Cynader and Mitchell, who found that kittens dark reared until 6 to 10 months remained highly sensitive to monocular deprivation effects (Cynader, 1980). This contrasts with the light reared kittens, in which the sensitivity to monocular deprivation peaks within the first 2 months of life. If monocular deprivation begins after the first 3 or 4 months, it has little effect on kittens reared in normal lighting (Hubel, 1970; Olson, 1978). Thus, the duration of the so called critical period and the quantity and quality of the sensory input to the system seem to be intricately linked. Further, once a critical amount of experience has tuned the neural circuitry involved, the system becomes insensitive to later disruptive influences (i.e., it shuts off its plasticity at least in the corresponding areas of the brain).

Based on studies of development across different species, Schuz has suggested that the timing of overproduction of synapses may be tied with the physical ability of the animal to begin to actively explore its environment (Schuz, 1978).

The experimental results reviewed in this section so far underline the importance of appropriate sensory experience to ensure the normal development of visual cortex. It is interesting to ask: To what extent, if any, is the nature of plasticity and developmental processes in the visual cortex different from that in the cortices involved in other sensory modalities? In a recent study, Sur and coworkers surgically rerouted the outputs of the retinal neurons in newborn ferrets so that the visual information went to auditory cortex instead of visual cortex (Sur, 1988). They studied the response of cells in the auditory cortex while the animals were being presented visual patterns. They found that the cells in the auditory cortex had developed oriented receptive fields similar to those seen in the visual cortex of normal animals. This finding suggests that the auditory and visual cortices are essentially similar in their intrinsic properties and developmental processes; and whatever detailed differences that may exist between visual, auditory, and other cortical operations are learned as a result of specific neural wiring patterns somehow programmed by early sensory inputs. This is consistent with the striking capacity of the young brain for recovery of function in response to damage (Finger, 1982; Marshall, 1985).

Development and Learning Beyond Early Infancy

Most of the experiments reviewed in the section on visual development above have concentrated on the role of environmental experience during early development. It is natural to ask: What are mechanisms of plasticity that form the basis of perceptual learning in adults? Given some of the experimental evidence presented earlier, it is unlikely that the mechanisms underlying plasticity in the adult brain are exactly the same as those present during early development.

Neural Basis of Learning and Memory: Use-Dependent Changes in Synaptic Efficacies Versus Generation of New Synapses

One of the oldest (Tanzi, 1893; Hebb, 1949) and perhaps, the most popular idea holds that the modification of weights or efficacies associated with pre-existing synapses is the primary neural mechanism of learning in the adult brain (See Brown, 1989a for a review). Theoretical studies have shown that networks of neuron-like units with modifiable interconnections can exhibit simple associative learning and self-organizational capabilities (Anderson, 1981; Edelman, 1987; Kohonen, 1987; Barto, 1981; Cooper, 1985; Linsker, 1988; Rumelhart, 1986; Rosenblatt, 1962). Neurobiological studies of learning in higher invertebrates have provided significant evidence that certain forms of Pavlovian conditioning result from activity dependent changes in synaptic strengths (e.g., Kandel, 1987; Bailey, 1985). There is some morphological as well as neurophysiological data that suggests that learning in vertebrates involves such modification of weights associated with connections between neurons (see Greenough, 1988 for a review).

If the use-dependent modification of synaptic efficacies were to be the only neural mechanism for learning, the brain has to start out with a sufficient number of appropriately linked connections. This seems implausible, given the complexity and variety of the environments encountered by an individual during his/her life time. This suggests the possibility that new associations may be learned by selectively generating new connections in response to the environmental input. Ramon y Cajal (1893) proposed that such growth of new connections may form a neural basis for learning. We will examine some evidence in support of this hypothesis.

Long-term synaptic potentiation (LTP) is a leading candidate as a synaptic mechanism for rapid learning in mammals (Brown, 1988b). LTP is a persistent increase in synaptic efficacy (Bliss, 1973; Bliss, 1988; Baxter, 1985) that can be quickly induced. The biophysical process that controls one type of LTP is formally similar to the synaptic weight change mechanism postulated by Hebb (Hebb, 1949). LTP can be induced by brief (lasting 10-100 msec) stimulation of an afferent input (usually at 100 to 400 Hz). It outlasts all other known forms of synaptic enhancement (e.g., facilitation, augmentation, and posttetanic potentiation). Although LTP was first observed in rabbit hippocampus (Bliss, 1973), it is not unique to hippocampus (Baxter, 1985; Briggs, 1985). However, it has only been reported at excitatory synapses (Bliss, 1988; Brown, 1988a).

LTP is measured as the increase in the amplitude of the excitatory postsynaptic potential (EPSP) or current (EPSC) produced by a single pulse stimulation of the afferent input using intracellular recording techniques. Using field potential recording techniques, LTP is measured as the increase in the amplitude or slope of some component of the field potential produced by stimulating the afferent input. Field potential recordings suggest that LTP can last in vivo for weeks, and possibly months (Racine, 1988). Several forms of LTP have been identified on the basis of a number of different criteria, e.g., decay time constants (Racine, 1988), associative versus non-associative (Brown, 1988a; Brown, 1989b; Johnston, 1988).

The Hebbian interpretation of the associative LTP mechanism has been rather thoroughly tested in the hippocampus (Kelso, 1986; Malinov, 1986; Sastry, 1986): Neither postsynaptic activity alone nor synaptic stimulation while applying voltage clamp to the soma of the postsynaptic cell produced LTP. However, LTP was induced when presynaptic stimulation was paired with simultaneous postsynaptic depolarization. Further, the associative enhancement appears to be specific to just those synapses that are active in the same region at about the same time (Brown, 1989; Kelso, 1986; Levy, 1979).

Spine stem widening and shortening has been suggested as a mechanism underlying LTP (Fifkova, 1981). However, the evidence supporting this hypothesis is limited to the dentate gyrus in mammals (Desmond, 1988) and Sirevaag and Greenough (1985) found no evidence for cerebral cortical spine stem changes in rats reared in an enriched environment. However, they found an increase in sizes of synaptic contacts in occipetal cortical layer 4 in such rats. An increase in the so called *subsynaptic plate perforations* (SSPP) has been reported in the visual cortex of rabbits trained on a visual discrimination task (Vrensen, 1981) as well as in several other situations potentially involving plastic changes in the synapses (See Greenough, 1988 for a review). LTP induction has been reported to increase the number of vesicles near the presynaptic membrane (e.g., Desmond, 1988). The size of the *active zones* at the number and density of Ca^{2+} *channels* at the nerve terminals have been reported to be correlated with synaptic efficacies (Greenough, 1988; Atwood, 1986). Studies with higher invertebrates such as Aplesia (Bailey, 1985; Kandel, 1987) have demonstrated that long-term memory is accompanied by an increase in the number, size, and vesicle complement of sensory neuron active zones in sensitized animals and a corresponding decrease in habituated animals.

The molecular mechanisms underlying LTP (e.g., a suspected sequence of events: the conjunction of transmitter binding and postsynaptic depolarization; opening of Ca^{2+} channels; increase in intracellular Ca^{2+} concentrations; activation of protein kinases; phosphorylation of a substrate that ultimately causes synaptic enhancement) are only beginning to be understood (See Brown, 1989a for a review). Induction, expression, and maintenance of LTP are being investigated in an attempt to link it with learning, using pharmacological and physiological techniques. It has been shown, for example, that blocking the induction of LTP using pharmacological agents (e.g., AP5) prevents learning a new spatial memory task without affecting the retention of previously learned behaviors (Morris, 1986). Yet, the evidence linking LTP to learning is not conclusive (Barnes, 1988; Skelton, 1987; Berger, 1988).

Bennet et al. (1964) found that cerebral cortex in rats reared in enriched environments (EC) was thicker as compared to the rats reared in individual cages (IC). Rosenzweig et al. (1964) found that a fixed sample of occipetal cortex of rats placed in groups in a large, toy-filled cage was heavier than that in rats reared individually or in groups in standard cages, irrespective of age at which the exposure to an enriched environment occured. Diamond and coworkers found that the cerebral cortex of the EC rats had neurons with larger cell bodies as well as a larger number of glial cells (Diamond, 1967). The findings of Rosenzweig et al. (1964) were confirmed and elaborated upon by Diamond et al. (1972) in a study that compared rats reared in enriched (EC), standard colony (SC), and impoverished (IC) environments starting at 2 different ages (25 days and 60 days) for 30 days. They found statistically significant weight increases in EC rats as compared to IC rats, in both occipetal cortex (by about 6% to 16%) as well as somesthetic cortex (by 2% to 8%). Further, the total cortical weight and the ratio of cortical to total brain weight was significantly higher in EC rats. The increase in the weight of cortex was accompanied by an increase in cortical thickness. The cortical weight as well as the thickness measures for the SC rats fell between those of EC and IC rats. Greenough and colleagues found that the EC rats had about 20 percent more dendrites than the IC rats (Greenough, 1973). Turner and Greenough have provided direct evidence that EC rats had 20% to 25% more synapses per neuron in the upper visual cortex than the IC rats (Turner, 1985). (Similar differences between EC and IC animals have been found in rat hippocampus as well as in the cerebellum in monkeys and rats (Greenough, 1979; Juraska, 1985; Pysh, 1979).

Statistically significant increases in the mean number of dendritic branches per neuron (by 5% to 25%), as well as the mean total dendritic length per neuron (by 30% to 50%), in the cortex of young-adult (e.g., 112 to 142 days of age - Juraska, 1980; Uylings, 1978), as well as middle-aged (e.g., 450 to 495 days of age - Green, 1983) EC rats over IC rats have been reported. In normal adult humans (between 51 and 80 years of age), a net growth of dendrites has been revealed by a Golgi study of pyramidal neurons in parahippocampal gyrus whereas such a growth was absent in subjects suffering from senile dementia (Buell, 1981). Greenough et al. (1979) have found that the dendritic fields of pyramidal neurons in visual cortex (layers 4 and 5) were significantly larger, and the degree of branching of apical dendrites in distal regions (beyond 250 mum from the cell body) significantly higher, in adult rats given extensive training on multiple maze patterns than in control animals. Direct measurements of synapses per neuron are yet to be reported in adult animals. However, the close correlation between the dendritic field sizes and the number of synapses per neuron in younger animals suggests a similar relationship in adults as well (Greenough, 1987).

It appears likely that the neural mechanisms underlying learning are more complex than those suggested by the simple categorization into synaptic weight changes and generation of new synapses. However, these two mechanisms seem to offer a first approximation of the processes involved for the purposes of computational modeling.

Given the fairly substantial evidence that the cerebral cortex retains its ability to generate new synapses well into adulthood, at least two hypotheses have been proposed as to the nature of the processes involved (Greenough, 1987):

[a] The process of synapse generation during later development and adulthood is similar to the one that takes place during early post-natal sensory system development; that is, excess synapses are generated in a somewhat random manner throughout the part of the brain that remains plastic; among the synapses so generated, only those that get reinforced through experience survive, and the rest get eliminated.

[b] The generation of new synapses during later development and adulthood is a consequence of the activity of neurons as they perform their information processing or neuromodulatory functions; in this case, the newly generated synapses are localized in cortical regions involved in the specific activity that led to their generation.

The hypothesis of local activity triggered generation of synapses appears attractive for a number of reasons: the metabolic resources necessary are smaller in this case than that required to sustain a certain rate of excess synapse production over the entire system; in the long run, the amount of *noise* injected into the system is much lower, and the *stability* of the information processing structures much higher, if fewer synapses are generated and their effect is local, as opposed to the chronic generation and degeneration of synapses over the entire system. On the other hand, the hypothesis of rather nonsystematic, chronic overproduction of synapses (a significant proportion of which degenerate due to inactivity) appears attractive for reasons of evolutionary parsimony, because it reflects a continuation of the processes found during early sensory development into adulthood.

Role of Neuromodulators in the Governance of Neural Plasticity

Diffusely acting neurotransmitters such as norepinephrine and acetylcholine and possibly some neuropeptides and other hormones seem to play a role in regulating (initiating, maintaining, and perhaps terminating) the plasticity of visual cortex during development and learning. A detailed discussion of evidence supporting such a role for neurotransmitters is beyond the scope of this paper. The interested reader is refered to (Lauder, 1986; Miller, 1981; Fink, 1985) for such reviews. It suffices here to point out that there is evidence that the chemical neurotransmitter norepinephrine regulates sensitivity to monocular deprivation (Kasamatsu, 1976). Treatment with 6-hydroxydopamine, which reduces brain norepinephrine prevents the shift in control of the visual cortex neurons from the deprived eye in cats monocularly deprived during the critical period. Replacing norepinephrine by local administration into visual cortex results in the occurence of ocular dominance shift in such animals (Pettigrew, 1978). More recent work (Bear, 1986) has suggested that two neurotransmitters, norepinephrine and acetylcholine may be involved in regulating developmental sensitivity of the visual cortex. Reports of regulation of adult memory storage processes by norepinephrine systems (e.g., Gold, 1984) suggests the possibility of a quite general role for such neuromodulatory systems in the governance of plastic neural processes.

Development of Visual Pattern Perception

The ability to recognize, classify, and identify objects on the basis of the information in the image formed on the retina is perhaps one of the most complex of our visual abilities. This section summarizes some of the results from the studies of various aspects of pattern perception in infants. The amount of literature in this field is enormous and a detailed review is beyond the scope of this paper. We will concentrate on only a few aspects of pattern vision during infancy. The interested reader is refered to (Banks, 1983) for a broader review.

One of the basic empirical questions that has generated a lot of interest, especially since Fantz' refinement of the *pattern preference paradigm* is this: What evidence is there to suggest that infants can perceive patterns? Fantz (1961, 1963) measured relative preferences in human infants from birth to about 6 months of age for different patterns (e.g., a schematic face, a bull's eye, newsprint, and three discs of different colors). Infants of all ages exhibited differential fixation times among most of these patterns. This was interpreted as suggesting that even young infants have at least primitive pattern discrimination abilities.

Fantz' findings set the stage for asking further questions, for e.g.: What features or properties of patterned stimuli allow infants at different ages to discriminate them? What features, if any, are prefered at different ages? Fantz and Nevis (1967) compared infant pattern preferences to a grating relative to bull's eye. They found that before 1 month of age, the grating was strongly prefered over the bull's eye. By 2 months of age, a strong preference emerged for the bull's eye and it persisted until 6 months of age, the oldest age tested. The two patterns were similar in a number of respects: overall size, brightness, contrast, element width, and the amount of contour. The two patterns differ in a number of ways, for e.g.: bull's eye is made of connected curved lines, while the grating is made of a number of disconnected straight lines; bull's eye has a number of concentric circles; gratings do not. Pattern variables that contributed to discrimination among these two patterns have been investigated by a number of researchers. Fantz and colleagues partialled out the concentricity and connectedness dimensions in a series of experiments with infants of ages ranging from 2 to 5 months. They found that in spite of wide variations in the types of patterns presented, the infants almost always prefered the most curvilinear member of the pair (Fantz, 1975). Ruff and Birch (1974) explored 3 variables (concentricity, number of different variations, and curvilinearity) in 3 month olds. They found that infants prefered curvilinear patterns over linear ones when other variables were held constant. Similarly, concentric patterns were prefered over non-concentric ones, and multiple orientations over single orientation, when the other variables were equated.

The relationship between *pattern complexity* and pattern preference as well as discrimination has been investigated by a number of researchers. One critical problem with this line of research has to do with the definition of pattern complexity. There seems to be little concurrence among different investigators on an adequate definition of complexity. Some definitions that have been used include such measures as the number of elements (Brennan, 1966; Greenberg, 1972; Hershenson, 1964), number of angles (Hershenson, 1965; McCall, 1967; Munsinger, 1967). Brennan and coworkers (1966) presented infants of various ages checkerboards differing in the number of elements (2x2, 4x4, 8x8, 24x24). They found that 1 month olds fixated on the 2x2 checkerboards longer than on the others; 2 and 4 month olds prefered 8x8 and 24x24 checkerboards, respectively. Since the number of squares and their size were inversely related in these patterns, it could be infered that the prefered number of elements increased with age; or that the prefered size decreased with age. An extrapolation of this result would be that the infants prefered increasingly higher spatial detail with age. Hershenson et al. (1965) and Munsinger and Weir (1967), using random polygons that differed in number of angles, concluded that older infants prefered patterns with a larger number of angles. Miranda and Fantz (1971) and Fagan (1975), through a series of carefully conducted experiments, showed that the size and number of elements are important determinants of pattern preferences. In general, there is a great deal of difficulty in interpreting the results of the pattern preference experiments with infants, especially the negative results: For example, if an infant does not exhibit a differential preference, can one assume an inability to discriminate? It has been demonstrated that infants often do exhibit evidence for discrimination in habituation experiments although they don't show any differential preferences (McGurk, 1970). Further, because of a lack of a widely applicable characterization of pattern complexity, the results of these experiments do not carry over easily, (if at all they do), to untried pattern sets.

The *linear systems analysis model* (Banks, 1981; Gayl, 1983; Ginsburg, 1983) claims that infant pattern preferences are governed by pattern information available to the various decision centers in the central nervous system. It is assumed that pattern information available to the decision centers is only a small fraction of the information impinging on the infant's eye. Some information is lost through the filtering process that takes place at every stage of processing in the visual system. The *contrast sensitivity function (CSF)* was assumed to be a good model of the filtering properties. (CSF relates the minimal contrast required to detect a sine wave grating to the grating's spatial frequency and CSF of infants at various ages have been studied by several researchers e.g., Banks, 1978; Fiorentini, 1978). The linear systems model has been used to predict the pattern preferences of infants from 1 to 3 months of age for a large variety of patterns (Banks, 1981) although it fails to offer a theory for explaining pattern preferences or discrimination abilities in older infants.

One hypothesis that has been proposed to explain the results of the pattern preference experiments discussed above suggests that an infant's information processing capacity grows with age and, consequently, that different levels of stimulus complexity provide optimal stimulation at different ages. Some have argued that patterns with more elements, e.g., angles or contours, are more complex; some others have sought to define complexity in terms of the interactions between the stimulus and the infant's previous experience. Perhaps a more reasonable view of complexity has to take into account not simply the number of elements, but the spatial interactions among them. The infant's previous experience or genetic predisposition determines what the basic *elements* are. In this context, it is interesting to consider the results of experiments on the perception of angular relations by infants.

In 8 different experiments, Schwartz and Day (1979) habituated 2 to 4 month old infants to a single angle or shape and then tested them with variations of the habituation stimulus. One test item was the same shape in the original orientation, another was the same shape but in a new orientation, and others were new shapes in different orientations. In almost all instances, the infants generalized better to the original habituation shape, regardless of orientation, than to any of the new shapes. Schwartz and Day went on to conclude that their findings supported the Gestalt view that infants have the innate ability to perceive simple shapes and angles as wholes.

Cohen and Younger (1984) have reported the results of two experiments, one with 3 month old infants and the other with 6 week old infants. They used a set of habituation stimuli that contained two different shapes: a 45^{o} angle and a 135^{o} angle. Note that both the stimuli consisted of line elements at the same orientation. The test stimuli included the habituation stimuli and 3 different rotated versions of each of the habituation stimuli. Thus the stimuli were designed to differentiate the infants' responses based on the orientation of individual line segments making up a stimulus from those based on angular relations between the line segments. Cohen and Younger found that the 3 month old infants responded to change in the angular relationships between line segments (i.e., the angles per se). Thus, the 3 month old infants could tell the difference between a 45^{o} angle and a 135^{o} angle, even though both consisted of the individual line segments at the same orientations. When the same experiment was repeated with 6 week old infants, Cohen and Younger found that the 6 week olds, unlike the 3 month olds, showed no evidence of processing angular relations between line segments. Thus, the response of the 6 week olds did not appear to be able to tell the difference between a 45^{o} angle and a 135^{o} angle, both containing individual line segments at the same orientations.

Two simple experiments with perception of angular relations by infants cannot be considered as conclusive tests of competing hypotheses of perceptual development. However, the results obtained by Cohen and Younger seem to support the constructivist view (Hebb, 1949; Piaget, 1952) that infants first perceive line segments in particular orientations and only later, through experience and/or development, attain the ability to integrate the line segments into entire angles and by extrapolation, more complex shapes (as opposed to the Gestalt view). Additional studies such as those summarized here with other shapes, of differing degrees of complexity, can help determine the (logically rather compelling) generality of developmental change from processing parts to processing wholes.

Development of Mechanisms for Perceptual Organization

Everyday scenes can be rather complex, consisting of a rich mosaic of contours, colors, textures, etc. But our perceptual experience is not necessarily that of an unordered bunch of image features; We seem to be capable of segregating the scene into its constituent objects. This process of segregation is called *perceptual organization* or, *image segmentation*.

The underlying principles of perceptual organization are not very well understood. The proponents of the Gestalt view studied the phenomenon with abstract, 2-dimensional patterns (Koffka, 1935; Kohler, 1959). They failed to come up with a convincing explanation of the perceptual organization process. They did discover however, several principles of organization that the visual system appears to use:

[1] *Good Continuation*: Elements that appear to follow in the same direction, such as along a straight line or along a smooth curve, tend to be grouped together,

[2] *Proximity*: Elements that are relatively close together tend to be grouped together,

[3] *Similarity*: Elements that are similar in brightness, hue, and texture tend to be grouped together,

[4] *Symmetry*: Elements that are mirror images of one another tend to be grouped together, and

[5] *Common fate*: Elements that move in the same direction tend to be grouped together.

The above list is not exhaustive; a more complete enumeration of Gestalt principles is given in (Hochberg, 1971). The Gestaltists believed that all the principles of perceptual organization reflected a tendency for organization to yield perceptual outcomes that were *good* or *simplest possible*. Ginsburg (1978) has presented a series of demonstrations that suggest that most of the Gestalt principles can be viewed as the natural byproducts of low frequency filtering mechanisms. Given that the Gestalt principles generally yield good groupings of features in an image, it is natural to ask as to what extent these principles are learned through experience. Some have suggested (e.g., Brunswick, 1956) that the Gestalt principles are probably learned because they manifest themselves in everyday scenes. Others have argued that they must be innate because, without some ability to segregate the contours properly, perceptual development could not commence (e.g., Zuckerman, 1957; Kohler, 1956). The controversy is far from being resolved, since only a few developmental studies have been conducted to examine the two alternatives.

Bower (1965) investigated the principles of proximity, common fate, and good continuation in 1 to 9 month old infants. He presented stimuli that were either consistent or inconsistent with one of these principles and measured the sucking rate when each stimulus was presented. A decrease in sucking rate was interpreted as indicating surprise in response to the stimulus presented. He found that infants did not exhibit surprise to transformations inconsistent with good continuation or proximity until about 7 months of age but the infants exhibited surprise when common fate principle was violated as early as 1 month of age. In a subsequent study by the same author (Bower, 1967), 1 month old infants exhibited surprise in response to a stimulus that violated good continuation, thereby contradicting one of his earlier results, but his other two results were in agreement with those obtained by his previous study.

Kellman and Spelke (1980) found evidence for the principle of common fate early in life, but failed to see any evidence for good continuation. They habituated 4 month old infants to a partially occluded object (a rod hidden behind a block). Then they examined the infants' response to the rod alone, and to a broken rod. The infants did not preferentially fixate on either stimulus, suggesting that good continuation was not operating. When the rod was moved back and forth during habituation, the infants subsequently fixated on the complete rod over the broken rod.

Bertenthal et al. (1980) habituated 5 and 7 month olds to either a subjective contour pattern (i.e., a Kanizsa square - 4 angles of aligned to form a square, but no sides) or a pattern that had the 4 angles, but in arrangements that did not form a square. Once habituated, the infants were presented with either the subjective contour pattern or one of the other patterns. 7 month olds dishabituated to a change from one to the other; 5 month olds did not. This suggested that perception of subjective contours did not develop until about 7 months of age.

Salapatek (1975) investigated the principle of similarity by embedding a small matrix of one kind of elements (say small squares) in an otherwise uniform matrix of another kind of elements (say short line segments). When adults and pre-school children viewed the stimuli, they fixated on the matrix of discrepant elements; and 2 month old infants on regions of high density of contours irrespective of the elements present. One interpretation of this result is that the organization principle of similarity is absent at 2 months of age.

Bornstein et al. (1981) and Fisher et al. (1981), working with 4 month old infants found that symmetry about the vertical axis facilitated encoding and discrimination of patterns early in life.

Although the experiments summarized above suggest that some of the perceptual organization principles may be functional fairly early in life, evidence is not conclusive that these principles are innate. If these principles are learned through experience, the exact mechanisms that facilitate such learning are of interest.

Development of Form Discrimination, Generalization and Object Centered Representations

The mature visual system is quite adept at recognizing complex objects without regard to variations in size, position, context, and to some extent, rotation. *Form* is usually thought of as that aspect of a pattern that remains constant in spite of changes in low order variables such as brightness, contrast, color, size, position, etc. An ability to extract form information is a prerequisite for object recognition. It is interesting therefore, to investigate the mechanisms involved in the development of structures that extract form information from the scene. It is generally difficult to study form perception in pre-verbal human infants because many lower order variable can confound the experimental process and several studies, some as recent as 1980 suffered from this problem. We will summarize the results from a few experiments that controlled the contamination from low order variables quite well.

Milkewski (1979) used a habituation-dishabituation paradigm to study form discrimination in 3 month old infants. The stimuli were two configurations of 3 dots on an otherwise uniform field. One configuration formed a vertical straight line and the other formed a triangle. The two configurations were identical in form as well as overall brightness. The dots were not connected in either stimulus. The size and the position of the two configurations were randomly varied during habituation, so the discrimination based on size, position, and local features could be ruled out. Milkewski found that the infants dishabituated significantly when a novel configuration was introduced but not when a familiar configuration with a novel size and position was introduced. This showed that 3 month olds are capable of at least simple form discrimination.

Ruff (1978) habituated 6 and 9 month olds to objects constant in form but differing in color, size and orientation. She then presented the infants with a familiar form and a novel form, both with novel color, size and orientation. She found that 9 month olds dishabituated to the novel form, only when it was quite dissimilar from the familiar form. Thus, 9 month olds were capable of responding on the basis of at least forms that were quite dissimilar. On the other hand, 6 month olds did not demonstrate such an ability, even for the more dissimilar forms.

The retinal image of an object changes as the viewer moves about in an environment. If an object is to be identified in spite of changes in viewpoint, the visual system needs a stable representation of the object that is *object-centered* as opposed to *viewer centered*. Most of the data available to date from the studies of size-invariance suggest that some form of size constancy (ability to generalize across different sizes of the same object shape) is present at about 6 months of age in human infants (e.g., McKenzie, 1980). It is however unclear whether size constancy is operative in younger infants. It has been noted that several skills develop between 4 to 6 months of age that could contribute to the emergence of size constancy, e.g., visually guided reaching, several depth cues, linear perspective, etc. (Banks, 1983). Studies such as (Bower, 1972; Day, 1973; Caron, 1979) are consistent with the statement that shape constancy is operative at 3 months of age. This suggests that at least some ability to encode objects in an object-centered representation rather than a viewer centered representation is present before locomotion and visually guided reaching are possible.

Suggested Mechanisms for a Computational Model of Visual Development and Learning

Most of the attempts at modeling perceptual development and learning (e.g., the *connectionist* models) to date use activity-dependent reweighting of links between neuron-like units, that may or may not be guided by external feedback. A unit computes some simple function, usually a sum, over its inputs and applies a threshold or a sigmoid, before firing out the result. The sum computed is typically assumed to mimic the *frequency* of firing of a biological neuron.

What do the experimental results from the behavioral, neurophysiological, and morphological studies of developing visual systems tell us about the underlying computational processes that result in the appropriate information processing structures for perception? The structure of the visual system is at best *underspecified* at the time of birth. There is an overproduction of connections during the early phase of post-natal development. The exact mechanisms that trigger such production are not well-understood; However, the fact that the timing of synaptogenesis coincides with the availability of environmental input (i.e., the opening of the eyes) suggests that the latter may, at least in part, act as a trigger for the production of connections. It cannot be ruled out however that it may be an intrinsic (pre-programmed) process. The basic mechanisms of development (learning) at this stage involve:

[a] growth of connections at a rapid rate, perhaps as a function of the availability of the environmental input and possibly activity of neurons in response to such input;

[b] activity dependent pruning of connections, which can be viewed as a result of competition among the connections to transduce, transform, and transmit the environmental input to successively deeper regions of the brain;

[c] activity dependent fine-tuning of the synaptic efficacies through mechanisms along the lines of those proposed by Hebb (Hebb, 1949).

The growth of connections provides the system with the necessary components to build appropriate information processing structures. The activity-dependent pruning of connections sharpens the pre-disposition of the neurons by getting their firing to become increasingly better correlated with a pattern in the input. It is interesting that the sensitivity of the system to external input, i.e., its plasticity in the retina, the LGN, as well as lower layers of the cortex, is turned off once a certain amount of tuning of the system has taken place. Although the exact mechanisms involved are not clear, it seems safe to guess that the quantity and quality of the input at least partially determine the rate of decrease in plasticity. Some possibilities are: mechanisms internal to individual neurons which shut off plasticity of its connections once the firing rate reaches an optimal value; mechanisms, possibly mediated by neuromodulators, that monitor activities of groups of neurons and turn off the plasticity as the connectivity and the firing frequencies of the neurons change. Several such regulatory mechanisms can be compared and evaluated through computational simulations.

Early post-natal development, if allowed to proceed normally, provides the system with a set of well-tuned primitives on which further development or learning can be based. Behavioral, neurophysiological as well as morphological evidence from studies of visual development beyond the *critical period* suggests that increased environmental input leads to a higher number of connections among neurons in the cortex. Evidence is not conclusive as to the exact nature of the process: It may be that the connections are generated locally, in the cortex, in response to the activity of neurons in the neighborhood; or that the increased number of connections simply reflects a greater percentage of connections sustained through activity, out of a chronically and somewhat randomly generated pool of connections. Both these possibilities lend themselves to experimental comparisons through simulation of the corresponding computational models. The basic mechanisms of learning at this stage involve:

[a] activity-dependent fine-tuning of synaptic weights in the subnetworks that are plastic, possibly as a function of feedback either from the environment or from other sensory modalities,

[b] generation of new connections, either continually, throughout the network, in a random fashion, or when triggered by activity, locally and selectively, in the affected subnetworks, and

[c] elimination of excess connections through a variety of mechanisms, most of which are likely to be activity-dependent (e.g., local competition, re-weighting, etc.)

It is worth pointing out that generation of a new synapse does not always correspond to the generation of a new connection between two units in the corresponding computational model. For example, new synapses generated between two neurons that already have synaptic contact can be interpreted as the strengthening of an existing link between the two units. However, synapses formed between neurons that previously did not have such interaction corresponds to the generation of a new link in the corresponding computational model.

It is known that the full complement of neurons - the basic computational units of the brain, as well as the layered, topographically mapped structure of the visual system, are present at birth, well before the environmental input becomes available. It is also clear from the results of morphological, neuroanatomical, as well as behavioral studies summarized in this paper that the development of visual perceptual abilities relies heavily on the availability of certain kinds of input at certain stages in development. The studies of the development of perceptual abilities in infants offer what is certainly suggestive, although not conclusive evidence for the hypothesis that the emergence of certain abilities (e.g., form discrimination) occurs only after the development of certain other requisite abilities (e.g., discrimination of line segments at different orientations). Studies involving visual deprivation in animals suggest that certain kinds of experience are necessary during certain critical periods to ensure normal development. Thus, all of the visual system does not stay plastic to the same extent throughout the animal's life time. Plasticity can, and seems to be, initiated, regulated and terminated by an intricate interplay between the structure of the developing system, the quality as well as the quantity of the environmental input, and perhaps influences mediated by attentional and motivational mechanisms. Interactions between these processes can be quite complex, and computational models incorporating several of these mechanisms can offer interesting insights into their operational principles. Such models also provide an attractive test-bed for a controlled manipulation of the component processes individually or collectively to study the effects on development.

Several questions can be formulated in terms of comparison of appropriate computational models. The results of such comparison might shed light on the developmental significance of particular processes. On the other hand, the mechanisms found in living systems can provide suggestions for incorporating such mechanisms in synthetic systems designed to attain comparable perceptual abilities by exploring the environment. We will present some examples to illustrate this idea in what follows.

As noted earlier, there is evidence for activity-dependent generation of connections in the cortex. This model can be compared with a model that incorporates rather unsystematic, chronic generation of new connections. Empirical studies of both the models on several aspects of visual perception, at various rates of generation of new connections are of interest. Such studies can suggest further behavioral as well as neuroanatomical and morphological experiments. They can also provide insights into relative speed of development or learning, relative performance (say, at a pattern classification task), relative stability of the resulting information structures, and so on. Activity dependent, possibly feedback-aided reweighting of existing connections has been proposed (and implemented in several computational models) as a mechanism for learning. It is clear that if a network had to learn by reweighting of its links alone, it has to start with the sufficient number of appropriate connections between its units. Given the complexity of, and the variability in the environment, this is far from feasible. A system that can judiciously generate new connections, on the other hand, can acquire the necessary connectivity through experience. The relative rates of reweighting of existing connections and generation and possibly, degeneration of links as a function of experience are of crucial importance to the perceptual learning abilities of the system. There is some evidence for competition among units to transform, and transmit environmental input to successively deeper cortical regions (e.g., in the development of ocular dominance columns). Some of these issues can be explored using appropriate computational models.

There is some evidence for the Gestalt principles of organization (e.g., proximity, similarity, etc.) in very young infants. Incorporation of one or more of these principles as topological or processing constraints in a computational model can provide useful insights into their functional significance in development and learning. For example, Honavar and Uhr have found that building in proximity or locality as a constraint in a multi-layered connectionist learning network can substantially improve learning speed as well as accuracy of recognition at simple pattern perception tasks (Honavar, 1988b; Honavar, 1989); Qian and Sejnowski (1988) have reported that the locality constraint enables a network to learn stereo correspondence while a random connectivity does not.

Initiating plasticity in a controlled manner in a layered network enable the network to discover successively more complex spatial and temporal relationships between features in the input. For example, the development of oriented edge detectors facilitates the learning of oriented lines, which in turn, enables the system to learn angles by discovering the spatial relations between lines, and so on. Such mechanisms are of interest given the results from the studies of perception of angles by infants. A simple version of such experience induced learning of visual patterns though generation and modification of links in a network of neuron-like units, under guidance from environmental feedback has been implemented in a computational model described in (Honavar, 1987; Honavar, 1988a; Honavar, 1988b; Honavar, 1989).

Biological systems seem to utilize a variety of learning/developmental mechanisms (e.g., reweighting of connections, activity dependent generation and degeneration of links) whose interactions with each other, and the network structures that emerge as a result, are controlled by a layer of largely chemical control (in the form of slowly diffusing neuromodulators) that has been largely ignored by most computational models of perceptual development and learning. Especially since very little is known about the exact nature of such modulatory mechanisms, computational models can provide an interesting testbed for exploring their potential roles (e.g., inducing generation of new links between units as opposed to reweighting; controlling the rate of learning; protecting certain crucial knowledge structures from unwelcome environmental disruption) in biological as well as synthetic systems. Organizational principles such as proximity, similarity, etc. seem to assist the brain considerably in learning useful relations present in the environmental input. Initiation, regulation, and termination of plasticity is well regulated to yield a stable, yet flexible system. Such mechanisms appear to enable learning to proceed in carefully controlled phases - using simpler structures to construct more complex ones, in a hierarchical fashion, which greatly contributes to a reduction in the complexity of the task of learning. Attempts at modeling natural systems cannot afford to ignore this rich mosaic of processes found in biological systems.

The variety of mechanisms and the intricate interplay among them in biological systems is a rich source of suggestions for the design of synthetic systems of comparable abilities. Even rather simple additions (e.g., locality, activity dependent, feedback-aided generation of new connections) to the basic connectionist models of perceptual learning can yield large improvements in learning (Honavar, 1988b; Honavar, 1989). We can therefore expect a closer examination of development and learning in biological systems and a judicious use of mechanisms suggested by such an examination (the details of which have to be worked out through systematic experimental as well as theoretical comparisons of the corresponding computational models) to yield synthetic systems that can learn to perceive, through their interaction with complex environments.

Computational Models and the Explanation of Perceptual Development and Learning

One of the goals of neuroscience is to account for perceptual, cognitive, and behavioral phenomena in terms of known circuits of neurons, the known mechanisms of changes in such circuitry (e.g., generation and modification of synapses), the sensory input impinging at the time, and of the innate or acquired knowledge encoded in memory. However, the more complex the behavior to be explained, and the more complex the living system exhibiting such behavior, the less likely it is to be amenable to a complete analysis by the experimental tools of neuroscience. An explanation in the form of a logical procedure consistent with the known facts about the brain, perhaps a computer program that implements a computational model, seems indicated in such a case. Computational models of perceptual development and learning offer such a framework for explanation and experimentation, for exploring competing hypotheses, and for suggesting experiments designed to fill the gaps in our understanding of these phenomena.

References

Abramov, I., Gordon, J., Hendrickson, A., Hainline, L., Dobson, L., and LaBoissiere, E., ‘‘The retina of the newborn human infant,’’ *Science*, vol. 217, pp. 265-267, 1982.

Albus, K. and Wolf, W., ‘‘Early postnatal development of neuronal function in the kitten’s visual cortex: A laminar analysis,’’ *Journal of Physiology*, vol. 348, pp. 153-185, 1984.

Anderson, J. A. and Hinton, G., ‘‘---,’’ in *Parallel Models of Associative Memory*, ed. G. Hinton and J. A. Anderson, Erlbaum, Hillsdale, NJ, 1981.

Anker, R. L., ‘‘The prenatal development of some of the visual pathways in the cat,’’ *Journal of Comparative Neurology*, vol. 173, pp. 185-204, 1977.

Bailey, C. H. and Kandel, E. R., ‘‘Molecular approaches to the study of short-term and long-term memory,’’ in *Functions of the Brain*, ed. C. W. Coen, Oxford University Press, Oxford, UK, 1985.

Baker, F. H., Grigg, P., and von Noorden, G. K., ‘‘Effects of visual deprivation and strabismus on the responses of neurons in the visual cortex of the monkey, including studies on the striate and prestriate cortex in the normal animal,’’ *Brain Research*, vol. 66, pp. 185-208, 1974.

Banks, M. S. and Salapatek, P., ‘‘Infant pattern vision: A new approach based on the contrast sensitivity function,’’ *Journal of Experimental Child Psychology*, vol. 31, pp. 1-45, 1981.

Banks, M. S. and Salapatek, P., ‘‘Infant visual development,’’ in *Handbook of Child Psychology*, Wiley, New York, NY, 1983.

Barnes, C. A., ‘‘---,’’ *Trends in Neuroscience*, vol. 11, pp. 163-, 1988.

Barto, A. G., Sutton, R. S., and Brouwer, P., ‘‘Associative network: A reinforcement learning associative memory,’’ *Biological Cybernetics*, vol. 40, pp. 201-211, 1981.

Baxter, D. A., Bittner, G. D., and Brown, T. H., ‘‘---,’’ *Proceedings of the National Academy of Sciences, U. S. A.,* vol. 82, pp. 5978-, 1985.

Bear, M. F. and Singer, W., ‘‘Modulation of visual cortical plasticity by acetylcholine and noradrenaline,’’ *Nature*, vol. 320, pp. 172-176, 1986.

Beckmann, R. and Albus, K., ‘‘The geniculocortical system in the early postnatal kitten: An electrophysiological investigation,’’ *Experimental Brain Research*, vol. 47, pp. 49-56, 1982.

Berger, T. W. and Sclabassi, R. J., ‘‘---,’’ in *Long-Term Potentiation: From Biophysics to Behavior*, ed. P. W. Landfield and S. A. Deadwyler, Liss, New York, NY, 1988.

Bertenthal, B. I., Campos, J. J., and Haith, M. M., ‘‘Development of visual organization: The perception of subjective contours,’’ *Child Development*, vol. 51, pp. 1072-1080, 1980.

Blakemore, C. and Van Sluyters, R. C., ‘‘Reversal of the physiological effects of monocular deprivation in kittens: Further evidence for a sensitive period,’’ *Journal of Physiology*, vol. 237, pp. 195-216, 1974.

Blakemore, C. and Van Sluyters, R. C., ‘‘Innate and environmental factors in the development of the kitten’s visual cortex,’’ *Journal of Physiology*, vol. 248, pp. 663-716, 1975.

Blakemore, C., ‘‘The conditions required for the maintenance of binocularity in the kitten’s visual cortex,’’ *Journal of Neurophysiology*, vol. 261, pp. 423-444, 1976.

Blakemore, C., Garey, L. J., and Vital-Durand, F., ‘‘The physiological effects of monocular deprivation and their reversal in the monkey’s visual cortex,’’ *Journal of Physiology*, vol. 283, pp. 223-262, 1978.

Blakemore, C. and Vital-Durand, F., ‘‘Development of the neural basis of visual acuity in monkeys: speculation on the origin of deprivation amblyopia,’’ *Transactions of the Ophthalmological Societies of the United Kingdom*, vol. 99, pp. 363-368, 1980.

Blasdel, G. G., Mitchell, D. E., Muir, D. W., and Pettigrew, J. D., ‘‘A physiological and behavioral study in cats of the effect of early visual experience with contours of a single orientation,’’ *Journal of Physiology*, vol. 265, pp. 615-636, 1977.

Bliss, T. W. P. and Lomo, T., ‘‘---,’’ *Journal of Physiology*, vol. 232, pp. 331-, 1973.

Bonds, A. B. and Freeman, R. D., ‘‘Development of optical quality in the kitten eye,’’ *Vision Research*, vol. 18, pp. 391-398, 1978.

Bonds, A. B., ‘‘Development of orientation tuning in the visual cortex of kittens,’’ in *Developmental Neurobiology of Vision*, ed. R. D. Freeman, Plenum Press, New York, NY, 1979.

Boothe, R. G., Greenough, W. T., Lund, J. S., and Wrege, K., ‘‘A quantitative investigation of spine and dendrite development of neurons in visual cortex (area 17) of macaca nemestrina monkeys,’’ *Journal of Comparative Neurology*, vol. 186, pp. 473-490, 1979.

Bornstein, M. H., Ferdinandsen, K., and Gross, C. G., ‘‘Perception of symmetry in infancy,’’ *Developmental Psychology*, vol. 17, pp. 82-86, 1981.

Bower, T. G. R., ‘‘The determinants of perceptual unity in infancy,’’ *Psychonomic Science*, vol. 3, pp. 323-324, 1965.

Bower, T. G. R., ‘‘Phenomenal identity and form perception in an infant,’’ *Perception and Psychophysics*, vol. 2, pp. 74-76, 1967.

Bower, T. G. R., ‘‘Object perception in infants,’’ *Perception*, vol. 1, pp. 15-30, 1972.

Brennan, W. M., Ames, E. W., and Moore, R. W., ‘‘Age differences in infants’ attention patterns of different complexity,’’ *Science*, vol. 151, pp. 354-356, 1966.

Briggs, C. A., Brown, T. H., and McAfee, D. A., ‘‘---,’’ *Journal of Physiology*, vol. 359, pp. 503-, 1985.

Brown, T. H., Chang, V. C., Ganong, A. H. , Keenan, C. L. , and Kelso, S. R., ‘‘Long-term synaptic potentiation,’’ in , vol. 242, pp. 724-728, 1988a.

Brown, T. H., Chapman, P. F., Kairiss, E. W., and Keenan, C. L., ‘‘Long-term synaptic potentiation,’’ *Science*, vol. 242, pp. 724-728, 1988b.

Brown, T. H., Ganong, A. H., Kairiss, E. W., and Keenan, C. L., ‘‘---,’’ in *Annual Review of Neuroscience*, 1989a.

Brown, T. H., Ganong, A. H., Kairiss, E. W., Keenan, C. L., and Kelso, S. R., ‘‘---,’’ in *Neural Models of Plasticity*, ed. J. H. Byrne and W. O. Berry, Academic Press, New York, NY, 1989b.

Brunswik, E., *Perception and the design of psychological experiments*, University of California Press, Berkeley, CA, 1956.

Buell, S. J., Colemann, P. D., ‘‘Quantitative evidence for selective dendritic growth in normal human aging but not in senile dementia,’’ *Brain Research*, vol. 214, pp. 23-41, 1981.

Caron, A. J., Caron, R. F., and Carlson, V. R., ‘‘Infant perception of the invariant shapes of objects varying in slant,’’ *Child Development*, vol. 50, pp. 716-721, 1979.

Cohen, L. B. and Younger, B. A., ‘‘Infant perception of angular relations,’’ *Human Behavior and Development*, vol. 7, pp. 37-47, 1984.

Conel, J. L., *The Postnatal Development of the Human Cerebral Cortex (Vols 1-7)*, Harvard University Press, Cambridge, MA, 1939-1963.

Cooper, L. N., Munro, P., and Schofield, C., ‘‘---,’’ in

Synaptic Modification, Neuron Selectivity, and Nervous System Organization, ed. W. B. Levy, J. A. Anderson, S. Lehmkuhle, Erlbaum, Hillsdale, NJ, 1985.

Corrigan, J. G. and Carpenter, D. L., ''Early selective visual experience and pattern discrimination in hooded rats,'' *Developmental Psychobiology*, vol. 12, pp. 67-72, 1979.

Cragg, B. G., ''The development of synapses in the kitten visual cortex during visual deprivation,'' *Experimental Neurology*, vol. 45, pp. 445-451, 1975a.

Cragg, B. G., ''The development of synapses in the visual system of the cat,'' *Journal of Comparative Neurology*, vol. 160, pp. 147-166, 1975b.

Crawford, M. L. J., Blake, R., J., Cool S., and von Noorden, G. K., ''Physiological consequences of unilateral and bilateral eye closure in macaque monkeys: Some further observations,'' *Brain Research*, vol. 84, pp. 150-154, 1975.

Cynader, M. and Chernenko, G., ''Abolition of direction selectivity in the visual cortex of the cat,'' *Science*, vol. 193, pp. 504-505, 1976.

Cynader, M. and Mitchell, D. E., ''Prolonged sensitivity to monocular deprivation in dark-reared cats,'' *Journal of Neurophysiology*, vol. 43, pp. 1026-1040, 1980.

Daniels, J. D., Pettigrew, J. D., and Norman, J. L., ''Development of single-neuron responses in kitten's lateral geniculate nucleus,'' *Journal of Neurophysiology*, vol. 41, pp. 1373-1393, 1978.

Day, R. H. and McKenzie, B. E., ''Perceptual shape constancy in early infancy,'' *Perception*, vol. 2, pp. 315-320, 1973.

Derrington, A. M. and Fuchs, A. F., ''Development of spatial frequency selectivity in the kitten striate cortex,'' *Journal of Physiology*, vol. 316, pp. 1-10, 1981.

Derrington, A. M., ''Development of orientation selectivity in striate cortex of vision-deprived cats,'' *Experimental Brain Research*, vol. 55, pp. 431-437, 1984.

Desmond, N. L. and Levy, W. B., ''---,'' in *Long-Term Potentiation: From Biophysics to Behavior*, ed. P. W. Landfield and S. A. Deadwyler, Liss, New York, NY, 1988.

DeYoe, E. A. and Van Essen, D. C., ''Concurrent processing streams in monkey visual cortex,'' *Trends in Neuroscience*, 1988.

Diamond, M. C., ''Extensive cortical depth measurements and neuron size increases in the cortex of the environmentally enriched rats,'' *Journal of Comparative Neurology*, vol. 131, pp. 357-364, 1967.

Diamond, M. C., Rosenzweig, M. R., Bennett, E. L., Lindner, B., and Lyon, L., ''Effects of environmental enrichment and impoverishment on rat cerebral cortex,'' *Journal of Neurobiology*, vol. 3, pp. 47-64, 1972.

Dunn, J. S., ''Development of the human neural retina,'' *Journal of Anatomy*, vol. 111, pp. 510-512, 1972.

Edelman, G. M., *Neural Darvinism*, Basic Books, New York, NY, 1987.

Fagan, R. L. and Fantz, J. F. III, ''Visual attention to number and size of pattern details by term and preterm infants during the first six months,'' *Child Development*, vol. 16, pp. 3-18, 1975.

Fantz, R. L., ''The origin of form perception,'' *Scientific American*, vol. 204, pp. 66-72, 1962.

Fantz, R. L. and Nevis, S., ''Pattern preferences and perceptual-cognitive development in early infancy,'' *Merrill-Palmer Quarterly*, vol. 13, pp. 77-108, 1967.

Fantz, R. L., Fagan, J. F. III, and Miranda, S. B., ''Early visual selectivity as a function of pattern variables, previous exposure, age from birth and conception, and expected cognitive deficit,'' in *Infant Perception: From Sensation to Cognition (Basic Visual Processes)*, ed. L. B. Cohen and P. Salapatek, Academic Press, New York, NY, 1975.

Fifkova, E., ''Changes in the visual cortex of the rats after unilateral deprivation,'' *Nature*, vol. 220, pp. 379-381, 1968.

Fifkova, E. and Anderson, C. L., ''---,'' *Experimental Neurology*, vol. 74, pp. 621-627, 1981.

Finger, S., and Stein, D. G., ''Brain damage and recovery,'' in *Research and Clinical Perspectives*, Academic Press, New York, NY, 1982.

Fink, G., ''Homeostasis and hormonal regulation (neuroendocrine reflections of the brain),'' in *Functions of the Brain*, ed. C. W. Coen, Oxford University Press, Oxford, UK, 1985.

Fiorentini, A. and Maffei, L., ''Spatial contrast sensitivity of myopic subjects,'' *Vision Research*, vol. 16, pp. 437-438, 1976.

Fisher, C. B., Ferdinandsen, K., and Bornstein, M. H., ''The role of symmetry in infant form discrimination,'' *Child development*, vol. 52, pp. 457-462, 1981.

Gayl, I. E., Roberts, J. O., and Werner, J. S., ''Linear systems analysis of infant visual pattern preferences,'' *Journal of Experimental and Theoretical Psychology*, vol. 35, pp. 30-45, 1983.

Ginsburg, A. P., ''Visual Information Processing Based on Spatial Filters Constrained by Biological Data,'' *Doctoral dissertation*, University of Cambridge, Cambridge, UK, 1978.

Globus, A., Rosenzweig, M. R., Bennett, E. L., and Diamond, M. C., ''Effects of differential experience on dendritic spine counts in rat cerebral cortex,'' *Journal of Comparative and Physiological Psychology*, vol. 82, pp. 175-181, 1973.

-- --

Globus, A., ''Brain morphology as a function of presynaptic morphology and activity,'' in *The Developmental Neuropsychology of sensory deprivation*, ed. A. H. Riesen, Academic Press, New York, NY, 1975.

Gold, P. E., ''Memory modulation: Neurobiological contexts,'' in *Neurobiology of Learning and Memory*, ed. G. Lynch, J. L. McGaugh and N. M. Weinberger, Guilford, New York, NY, 1984.

Green, E. J., Greenough, W. T., and Schlumpf, B. E., ''Effects of complex or isolated environments on cortical dendrites of middle-aged rats,'' *Brain Research*, vol. 264, pp. 233-240, 1983.

Greenberg, D. J. and O'Donnell, W. J., ''Infancy and optimal level of stimulation,'' *Child Development*, vol. 43, pp. 639-645, 1972.

Greenough, W. T. and Volkmar, F. R., ''Pattern of dendritic branching in occipetal cortex of rats reared in complex environments,'' *Experimental Neurology*, vol. 40, pp. 491-504, 1973.

Greenough, W. T., Juraska, J. M., and Volkmar, F. R., ''Maze training effects on dendritic branching in occipetal cortex of adult rats,'' *Behavioral and Neural Biology*, vol. 26, pp. 287-297, 1979.

Greenough, W. T., ''Thoughts on the bases of experience-sensitive synaptic plasticity,'' *Developmental Psychobiology*, pp. 387-407, Academic Press, New York, NY., 1986.

Greenough, W. T., Black, J. E., and Wallace, C. S., ''Experience and Brain Development,'' *Child Development*, vol. 58, pp. 539-559, 1987.

Greenough, W. T. and Bailey, C. H., ''The anatomy of a memory: convergence of results across a diversity of tests,'' *Trends in Neuroscience*, vol. 11, pp. 142-147, 1988.

Guillery, R. W., ''Binocular competition in the control of geniculate cell growth,'' *Journal of Comparative Neurology*, vol. 144, pp. 117-129, 1972.

Hamasaki, D. I. and Flynn, J. T., ''Physiological properties of retinal ganglion cells of 3-week-old kittens,'' *Vision Research*, vol. 17, pp. 275-284, 1977.

Hebb, D. O., *The Organization of Behavior*, John Wiley and Sons, New York, NY., 1949.

Hendrickson, A. and Kupfer, C., ''The histogenesis of the fovea in the macaque monkey,'' *Investigative Ophthalmology*, vol. 15, pp. 746-756, 1976.

Hershenson, M., ''Visual discrimination in the human newborn,'' *Journal of Comparative Physiological Psychology*, vol. 58, pp. 270-276, 1964.

Hershenson, M., Munsinger, H., and Kessen, W., ''Preferences for shapes of intermediate variability in the newborn human,'' *Science*, vol. 147, pp. 630-631, 1965.

Hickey, T. L., ''Postnatal development of the human lateral geniculate nucleus: relationship to a critical period for the visual system,'' *Science*, vol. 198, pp. 836-838, 1977.

Hirsch, H. V. B. and Spinelli, D. N., ''Visual experience modifies horizontally and vertically oriented receptive fields in cats,'' *Science*, vol. 168, pp. 869-871, 1970.

Hirsch, H. V. B., ''The Tunable Seer: Activity dependent development of vision,'' in *Handbook of Behavioural Neurobiology, Vol. 8, Developmental Psychobiology and Developmental Neurobiology*, ed. E. M. Blass, Plenum Press, New York, NY, 1986.

Hitchcock, P. F. and Hickey, T. L., ''Prenatal development of the human lateral geniculate nucleus,'' *Journal of Comparative Neurology*, vol. 194, pp. 395-411, 1980.

Hochberg, J., *Perception*, Prentice Hall, Englewood Cliffs, NJ, 1978.

Honavar, V. and Uhr, L., ''Recognition Cones: A neuronal architecture for perception and learning,'' *Computer Sciences Technical Report #717*, University of Wisconsin-Madison, Madison, WI, September 1987.

Honavar, V. and Uhr, L., ''Experimental results indicate that generation, local receptive fields, and global convergence improve perceptual learning in connectionist networks,'' *Computer Sciences Technical Report #805*, University of Wisconsin-Madison, Madison, WI, November 1988.

Honavar, V. and Uhr, L., ''A network of neuron-like units that learns to perceive by generation as well as reweighting of its links,'' in *Proceedings of the 1988 Connectionist Models Summer School*, ed. D. S. Touretzky, G. E. Hinton and T. J. Sejnowski, Morgan Kaufmann, San Mateo, CA, 1988.

Honavar, V. and Uhr, L., ''Generation, local receptive fields, and global convergence improve perceptual learning in connectionist networks,'' in *Proceedings of the 1989 International Joint Conference on Artificial Intelligence*, Morgan Kaufmann, San Mateo, CA, 1989.

Hubel, D. H. and Wiesel, T. N., ''Receptive fields, binocular interaction, and functional architecture in the cat's striate cortex,'' *Journal of Physiology*, vol. 160, pp. 106-154, 1962.

Hubel, D. H. and Wiesel, T. N., ''Receptive fields of cells in striate cortex of very young, visually inexperienced kittens,'' *Journal of neurophysiology*, vol. 26, pp. 994-1002, 1963.

Hubel, D. H. and Wiesel, T. N., ''The period of susceptibility to the physiological effects of unilateral eye closure in kittens,'' *Journal of Physiology*, vol. 206, pp. 419-436, 1970.

Hubel, D. H., Wiesel, T. N., and LeVay, S., ''Plasticity of ocular dominance columns in monkey striate cortex,'' *Philosophical Transactions of the Royal Society*, vol. B 278, pp. 377-409, 1977.

Johnston, D., Hopkins, W. F., and Gray, R., ''---,'' in *Long-Term Potentiation: From Biophysics to Behavior*, ed. P. W. Landfield and S. A. Deadwyler, Liss, New York, NY, 1988.

Juraska, J. M., Greenough, W. T., Elliott, C., Mack, K. J., and Berkovitz, R., ''Plasticity in adult rat visual cortex: An examination of several cell populations after differential rearing,'' *Behavioral and Neural Biology*, vol. 29, pp. 157-167, 1980.

Kalil, R. E., ''Development of the dorsal lateral geniculate nucleus in the cat,'' *Journal of Comparative Neurology*, vol. 178, pp. 265-292, 1978.

Kandel, E. R., Klein, M., Hochner, B., Schuster, M., and Siegelbaum, S. A., ''---,'' in *Synaptic Function*, ed. G. M. Edelman, W. E. Gall, W. M. Cowan, Wiley, New York, NY, 1987.

Kasamatsu, T. and Pettigrew, J. D., ''Depletion of brain catecholamines: Failure of ocular dominance shift after monocular occlusion in kittens,'' *Science*, vol. 194, pp. 206-209, 1976.

Kato, N., Kawaguchi, S., Yamamoto, T., Samejima, A., and Miyata, H., ''Postnatal development of the geniculocortical projection in the cat: Electrophysiological and morphological studies,'' *Experimental Brain Research*, vol. 45, pp. 254-266, 1981.

Kellman, P. J. and Spelke, E. S., *Infant's perception of partly occluded objects: Sensitivity to movement and configuration,* Presented at the Society for Research in Child Development meeting, Boston, MA, 1981.

Kelso, S. R., Ganong, A. H., and Brown, T. H., ''---,'' *Proceedings of the National Academy of Sciences, U. S. A.*, vol. 83, pp. 5326-, 1986.

Koffka, K., *Principles of Gestalt Psychology,* Harcourt, Brace, New York, NY, 1935.

Kohler, W., *Gestalt Psychology,* Mentor, New York, NY, 1959.

Kohonen, T., *Content-Addressable Memories,* Springer-Verlag, New York, NY, 1987.

Kratz, K. E., Mangel, S. C., Lehmkuhle, S., and Sherman, S. M., ''Retinal X and Y cells in monocularly lid-sutured cats: normality of spatial and temporal properties,'' *Brain Research*, vol. 172, pp. 545-551, 1979.

Lauder, J. M. and Krebs, H., ''Do Neurotransmitters, neurohumors, and hormones specify critical periods?,'' in *Developmental Neuropsychology*, ed. W. T. Greenough and J. M. Juraska, Academic Press, New York, NY, 1986.

LeVay, S., ''---,'' *Journal of Comparative Neurology*, vol. 150, pp. 53-86, 1973.

LeVay, S., Stryker, M. P., and Shatz, C. J., ''Ocular dominance columns and their development in layer IV of the cat's visual cortex: A quantitative study,'' *Journal of Comparative Neurology*, vol. 179, pp. 223-244, 1978.

LeVay, S., Wiesel, T. N., and Hubel, D. H., ''The development of ocular dominance columns in normal and visually deprived monkeys,'' *Journal of Comparative Neurology*, vol. 191, pp. 1-51, 1980.

Linsker, R., ''Self-organization in a perceptual network,'' *IEEE Computer*, pp. 105-116, March 1988.

Livingstone, M. and Hubel, D., ''Segregation of form, color, movement, and depth: anatomy, physiology, and perception,'' *Science*, vol. 240, pp. 740-749, 1988.

Lund, J. S., Boothe, R. G., and Lund, R. D., ''Development of neurons in the visual cortex (area 17) of the monkey (macaca nemestrina: A Golgi study from fetal day 127 to postnatal maturity,'' *Journal of Comparative Neurology*, vol. 176, pp. 149-188, 1977.

Malinow, R. and Miller, J. P., ''---,'' *Nature*, vol. 320, pp. 529-, 1986.

Marshall, J. F., ''Neural plasticity and recovery of function after brain injury,'' *International Review of Neurobiology*, vol. 26, pp. 201-247, 1985.

Mason, C. A., ''Postnatal maturation of neurons in the cat's lateral geniculate nucleus,'' *Journal of Comparative Neurology*, vol. 217, pp. 458-469, 1983.

Mates, S. and Lund, J., ''--- ,'' *Journal of Comparative Neurology*, vol. 221, pp. 60-90, 1983a.

Mates, S. and Lund, J., ''--- ,'' *Journal of Comparative Neurology*, vol. 221, pp. 98-105, 1983b.

Mates, S. and Lund, J., ''--- ,'' *Journal of Comparative Neurology*, vol. 221, pp. 91-97, 1983c.

McCall, R. B. and Kagan, J., ''Attention in the infant: Effects of complexity, contour, perimeter, and familiarity,'' *Child Development*, vol. 38, pp. 939-952, 1967.

McGurk, H., ''The role of object orientation in infant perception,'' *Journal of Experimental Child Psychology*, vol. 9, pp. 363-373, 1970.

McKenzie, B. E., Tootell, H. E., and Day, R. H., ''Development of visual size constancy during the first year of human infancy,'' *Developmental Psychology*, vol. 16, pp. 163-174, 1980.

Milkewski, A. E., ''Visual discrimination and detection of configurational invariance in 3-month-old infants,'' *Developmental Psychology*, vol. 15, pp. 357-363, 1979.

Miller, R., *Meaning and Purpose in the Intact Brain,* pp. 121-143, Oxford University Press, Oxford, UK, 1981.

Miranda, S. B. and Fantz, R. L., ''Distribution of visual attention by newborn infants among patterns varying in size and number of details,'' in *Proceedings of the Annual Convention of the American Psychological Association*, vol. 6, pp. 181-182, 1971.

Mitchell, D. E. and Timney, B., ''Postnatal development of function in the mammalian nervous system,'' in *Handbook of Physiology, Section 1: The Nervous System*, ed. J. M. Brookhart and V. M. Mountcastle, vol. 3, pp. 507-555, American Physiological Society, Bethesda, MD., 1984.

Morris, R. G. M., Anderson, E., Lynch, G. S., and Baudry, M., ''---,'' *Nature*, vol. 319, pp. 774-, 1986.

Movshon, J. A. and Van Sluyters, R. C., ''Visual Neuronal Development,'' *Annual Review of Psychology*, vol. 32, pp. 477-522, 1981.

Munsinger, H. and Weir, M. W., ''Infants' and young children's preference for complexity,'' *Journal of Experimental Child Psychology*, vol. 5, pp. 69-73, 1967.

Norman, J. L., Pettigrew, J. D., and Daniells, J. D., ''Early development of X-cells in kitten lateral geniculate nucleus,'' *Science*, vol. 198, pp. 202-204, 1977.

O'Kusky, J. and Colonnier, M., ''---,'' *Journal of Comparative Neurology*, vol. 210, pp. 291-306, 1982.

Olson, C. R. and Freeman, R. D., ''Monocular depravation and recovery during sensitive period in kittens,'' *Journal of Neurophysiology*, vol. 41, pp. 65-74, 1978.

Parnavelas, J. G. and Globus, A., ''The effect of continuous illumination on the development of cortical neurons in the rat: A Golgi study,'' *Experimental Neurology*, vol. 51, pp. 637-647, 1976.

Pettigrew, J. D. and Freeman, R. D., ''Visual experience without lines,'' *Science*, vol. 182, pp. 599-601, 1973.

Pettigrew, J. D., ''The effect of visual experience on the development of stimulus specificity by kitten cortical neurons,'' *Journal of Physiology*, vol. 237, pp. 49-74, 1974.

Pettigrew, J. D. and Kasamatsu, T., ''Local perfusion of noradrenaline maintains visual cortical plasticity,'' *Nature*, vol. 271, pp. 761-763, 1978.

Piaget, J., *The Origins of Intelligence in Children,* Norton, New York, NY, 1952.

Pysh, J. J. and Weiss, M., ''Exercise during development induces an increase in Purkinge cell dendritic tree size,'' *Science*, vol. 206, pp. 230-232, 1979.

Qian, N.Sejnowski, T. J., in *Proceedings of the 1988 Connectionist Models Summer School*, ed. D. S. Touretzky, G. E. Hinton, and T. J. Sejnowski, Morgan Kaufmann, San Mateo, CA, 1988.

Racine, R. J. and deJonge, M., ''---,'' in *Long-Term Potentiation: From Biophysics to Behavior*, ed. P. W. Landfield and S. A. Deadwyler, Liss, New York, NY, 1988.

Rakic, P., ''Prenatal development of the visual system in the rhesus monkey,'' *Philosophical Transactions of the Royal Society*, vol. B 278, pp. 245-260, 1977.

Rakic, P., ''Developmental events leading to laminar and areal organization of the neocortex,'' in *The Organization of Cerebral Cortex*, ed. F. O. Schmitt, F. G. Worden, G. Adelman and S. G. Dennis, MIT Press, Cambridge, MA, 1981.

Ramon y Cajal, S., ''New findings about the histological structure of the central nervous system,'' *Archiv fur Anatomie und Physiologie (Anatomie)*, vol. 17, pp. 319-428, 1893.

Rosenblatt, F., *Principles of Neurodynamics*, Spartan Books, New York, NY, 1962.

Rosenzweig, M. R., Bennett, E. L., and Krech, D., ''---,'' *Journal of Comparative Physiological Psychology*, vol. 57, pp. 438-439, 1964.

Rothblat, L. A. and Schwartz, M., ''The effect of monocular deprivation on dendritic spines in visual cortex of young and adult albino rats: evidence for a sensitive period,'' *Brain Research*, vol. 161, pp. 156-161, 1979.

Ruff, H. A. and Birch, H. G., ''Infant visual fixation: The effect of concentricity, curvilinearity, and the number of directions,'' *Journal of Experimental Psychology*, vol. 17, pp. 460-473, 1973.

Ruff, H. A., ''Infant recognition of invariant form of objects,'' *Child Development*, vol. 49, pp. 293-306, 1978.

Rumelhart, D. E., Hinton, G. E., and Williams, R. J., ''Learning internal representations by error propagation,'' in *Parallel Distributed Processing: Explorations in the Microstructure of Cognition*, MIT Press/Bradford Books, Cambridge, MA, 1986.

Rusoff, A. C. and Dubin, M. W., ''Development of receptive field properties in retinal ganglion cells of kittens,'' *Journal of Neurophysiology*, vol. 40, pp. 1188-1198, 1977.

Salapatek, P., ''Pattern perception in early infancy,'' in *Infant Perception: From Sensation to Cognition (Basic Visual Processes)*, ed. L. B. Cohen and P. Salapatek, Academic Press, New York, NY, 1975.

Sastry, B. R., Goh, J. W., and Auyeung, A., ''---,'' *Science*, vol. 232, pp. 988-, 1986.

Sato, H. and Tsumoto, T., ''GABAergic inhibition already operates on a group of neurons in the kitten visual cortex at the time of eye opening,'' *Developmental Brain Research*, vol. 12, pp. 311-315, 1984.

Schuz, A., ''Some facts and hypotheses concerning dendritic spines and learning,'' in *Architectonics of the cerebral cortex*, ed. M. A. B. Brazier and H. Petsche, Raven Publishers, New York, NY, 1978.

Schwartz, M. and Day, R. H., ''Visual Shape Perception in Early Infancy,'' *Monographs of the Society for Research in*

Child Development, vol. 44 (No. 7), 1979.

Shapley, R. M. and So, Y. T., ‘‘Is there an effect of monocular deprivation on the proportion of X and Y cells in the cat geniculate nucleus?,’’ *Experimental Brain Research*, vol. 39, pp. 41-48, 1980.

Sherman, S. M., Hoffmann, K. P., and Stone, J., ‘‘Loss of a specific cell type from dorsal lateral geniculate nucleus in visually deprived cats,’’ *Journal of Neurophysiology*, vol. 35, pp. 532-541, 1972.

Sherman, S. M. and Stone, J., ‘‘Physiological normality of the retina in visually deprived cats,’’ *Brain Research*, vol. 60, pp. 224-230, 1973.

Singer, W., Tretter, F., and Cynader, M., ‘‘Organization of cat striate cortex: A correlation of receptive field properties with afferent and efferent connections,’’ *Journal of Neurophysiology*, vol. 38, pp. 1080-1098, 1975.

Singer, W., ‘‘Neuronal activity as a shaping factor in postnatal development of visual cortex,’’ in *Developmental Neuropsychobiology*, ed. W. T. Greenough and J. M. Juraska, Academic Press, New York, NY, 1986.

Sirevaag, A. M. and Greenough, W. T., ‘‘---,’’ *Developmental Brain Research*, vol. 19, pp. 215-226, 1985.

Skelton, R. W., Scarth, A. S., Wilkie, D. M., Miller, J. J., and Phillips, A. G., ‘‘---,’’ *Journal of Neuroscience*, vol. 7, pp. 3081-, 1987.

Sur, M., Garraghty, P. E., and Roe, A. W., ‘‘Experimentally induced visual projections into auditory thalamus and cortex ,’’ *Science*, vol. 242, pp. 1437-1441 , 1988.

Tanzi, E., ‘‘Facts and inductions in current histology of the nervous system,’’ *Rivista sperimentale di freniatria e medicina legale delle mentali alienazioni*, vol. 19, pp. 419-472, 1893.

Tsumoto, T. and Suda, K., ‘‘Laminar differences in development of afferent innervation to striate cortex neurones in kittens,’’ *Experimental Brain Research*, vol. 45, pp. 433-446, 1982.

Turner, A. M. and Greenough, W. T., ‘‘Differential rearing effects on rat visual cortex synapses I. Synaptic and neuronal density and synapses per neuron,’’ *Brain Research*, vol. 329, pp. 195-203, 1985.

Uhr, L., ‘‘Toward a computational information processing model of object perception,’’ *Computer Sciences Technical Report #651*, University of Wisconsin-Madison, Madison, WI , July 1986.

Uylings, H. B. M., Kuypers, K., Diamond, M. C., and Veltman, W. A. M., ‘‘Environmental influences on neocortex in later life,’’ *Progress in Brain Research*, vol. 48, pp. 261-274, 1978.

Valverde, F., ‘‘Rate and extent of recovery from dark-rearing in the mouse,’’ *Brain Research*, vol. 33, pp. 1-11, 1971.

Van Essen, D. C., ‘‘Functional organization of the primate visual cortex,’’ in *Cerebral Cortex*, ed. A. Peters and E. G. Jones, vol. 3, Plenum, New York, NY, 1985.

Van Sluyters, R. C. and Lewitt, F. B., ‘‘Experimental strabismus in the kitten,’’ *Journal of Neurophysiology*, vol. 43, pp. 686-699, 1980.

Vrensen, G. and Cardozo, J. N., ‘‘---,’’ *Brain Research*, vol. 218, pp. 79-98, 1981.

Wiesel, T. N. and Hubel, D. H., ‘‘Comparison of the effects of unilateral and bilateral eye closure on cortical unit responses in kittens,’’ *Journal of Neurophysiology*, vol. 28, pp. 1029-1040, 1965.

Wiesel, T. N. and Hubel, D. H., ‘‘Ordered arrangement of orientation columns in monkeys lacking visual experience,’’ *Journal of Comparative Neurology*, vol. 158, pp. 307-318, 1974.

Winfield, D. A., Hiorns, R. W., and Powell, T. P. S., ‘‘A quantitative electron-microscopical study of the postnatal development of the lateral geniculate nucleus in normal kittens and kittens with eyelid suture,’’ *Proceedings of the Royal Society of London*, vol. B 210, pp. 211-234, 1980.

Winfield, D. A., ‘‘The postnatal development of synapses in the visual cortex of the cat and the effects of eyelid closure,’’ *Brain Research*, vol. 206, pp. 166-171, 1981.

Zeki, S. and Shipp, S., ‘‘The functional logic of cortical connections,’’ *Nature*, vol. 335, pp. 311-317, 1988.

Zuckerman, C. B. and Rock, I., ‘‘An appraisal of the roles of past experience and innate organizing processes in visual perception,’’ *Psychological Bulletin*, vol. 54, pp. 269-296, 1957.