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VISUAL DEVELOPMENT*

DAVIDA Y. TELLER

Departments of Psychology and Physiology/Biophysics, Child Development and Mental Retardation Center, and Regional Primate Research Center, University of Washington, Seattle, WA 98195, U.S.A.

and

J. ANTHONY MOVSHON†

University Laboratory of Physiology, and All Souls College, Oxford University, Oxford, England

In Waynesboro, on the surface . . . one summer was very like another: to the casual eye the children playing their games in the big yards behind the iron fences were eternally the same as the girls and boys of the year before and the year before that. But the games of one season were played by another generation than those who had played them three or four years earlier, so quickly does childhood pass into adolescence, adolescence into adulthood.

Helen Hooven Santmyer
And Ladies of the Club

INTRODUCTION

We should say at the outset that probably neither one of us is officially qualified to write this article. The editor specified that the authors for this issue must have been scientifically conscious when the first issue of *Vision Research* was published in 1961. At that time, D.T.'s only contact with visual science had been a remarkable undergraduate seminar in perception from Hans Wallach at Swarthmore. She had just started graduate school in Berkeley, and had been assigned by chance to the young Tom Cornsweet as an advisee. He was having an uphill battle getting her out of the library, where she imagined science was to be found. T.M., on the other hand, was still in the fifth grade; his only interest in visual science was to establish why it was that he had just started wearing glasses, and how he could most finally lose them. Nonetheless, we shall reconstruct and reminisce.

Joint authorship of partly personal material has posed some minor difficulties of identification. Our solution is to recount general facts and concepts in the traditional format, while presenting passages that are unique to each person in the first person, headed by the initials of the reminiscing author (T.M. being Tony Movshon).

D.T.: During my first year of graduate school in 1960–1961, I encountered the field of developmental psychology for the first time. The lectures were given by a disillusioned developmental psychologist, John McKee. He argued that developmental psychology was a very uninteresting subject, because most of its major findings could be summarized under three very uninteresting laws. McKee's first law was: *As children get older, they get better at things*. The second law was: *Whatever it is, girls do it before boys*. The third law was: *Everything develops along with everything else*.

T.M.: Many years later, I sat through a multidisciplinary development conference in Brown County, Indiana, and (in complete ignorance of McKee's laws) felt at the end that the proceedings could be summarized by one general law: *Things start out badly, then they get better; then, after a long time, they get worse again*.

The challenge, as McKee argued, is to build a developmental science with deeper content. In the 1960–1985 era, perhaps the most universal goal of visual science has been reductionistic: to

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†On leave from: Department of Psychology, New York University, New York, NY 10003, U.S.A.

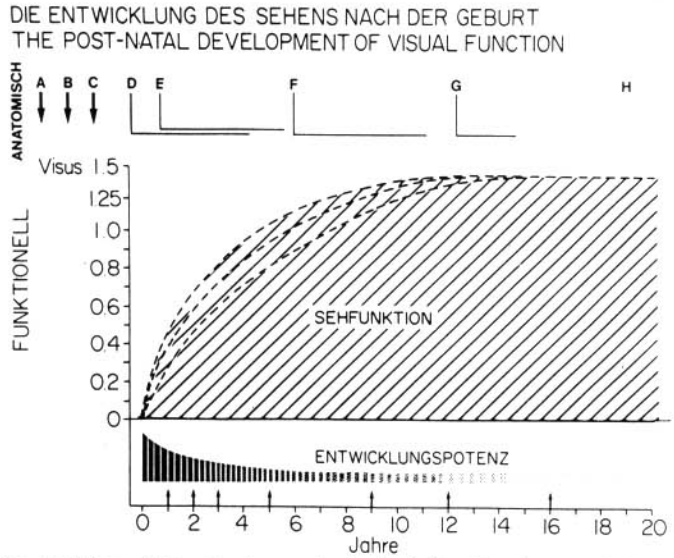

Fig. 1. Fanciful depiction of the development of visual function, its correlation with anatomical landmarks, and the remaining "developmental potential" at each age. Redrawn from Bangarter, 1959.

try to explain the forms and limitations of behaviorally defined visual functions on the basis of the characteristics of its neural substrate. If this goal is accepted, the goal of developmental questions transplanted into visual science is also clear: explain the emergence of visual function, in both its normal and its many abnormal guises, on the basis of elements of the normally or nonnormally developing substrate.

But description is easier than meaningful explanation. It has been most interesting for two authors, one of whom (D.T.) has engaged primarily in behavioral studies, and the other of whom (T.M.) has worked primarily on the physiological substrate, to examine the wavering progress of the field in relation to this post-descriptive goal.

ANCIENT HISTORY (THE 1960's)

At least for the two of us, the modern field of visual development did not begin until the early 1970s. Times before then must be reconstructed, rather than recalled. Let us consider first the state of things when *Vision Research* began in 1961.

Human infancy studies

Since ancient times, authorities on the vision of children and infants have had few facts to go on, but nonetheless have usually argued that the vision of infants must be exceedingly limited, for one reason or another. William James (1890) argued that the infant's world must be, "... a blooming, buzzing confusion". Some textbooks of ophthalmology and pediatrics authoritatively stated that infants saw little or nothing during the early postnatal months. Gunter von Noorden recalls a paper presented at the International Ophthalmological Congress in 1958, in which a graph appeared showing the infant's acuity beginning at zero at birth, and smoothly ascending to adult values at 5–6 years. This graph (Fig. 1) appears in several ophthalmic texts, but he was never able to trace its origins. Many parents, of course, knew perfectly well that such a graph was incorrect, having noticed that, from the time they are born, infants stare at things. Figure 2 shows a more modern version of this graph.

Methodology. The precursors of modern techniques for infant vision testing had been established by 1961. Such early authors as Chase (1937) had used direct judgements of infants' visual tracking as a means of evaluating their visual capacities. Robert Fantz (1958) had published his first paper using the technique of preferential looking for the study of pattern vision. Optokinetic nystagmus (OKN) was known to occur in young infants, and had been used by Gorman *et al.* (1957) to estimate acuity in newborns. Gibson and Walk's (1960) first study of depth perception using the visual cliff had appeared in *Scientific American*, and their monograph on the visual cliff, including many studies of normal and abnormal rearing conditions in several species, appeared soon after.

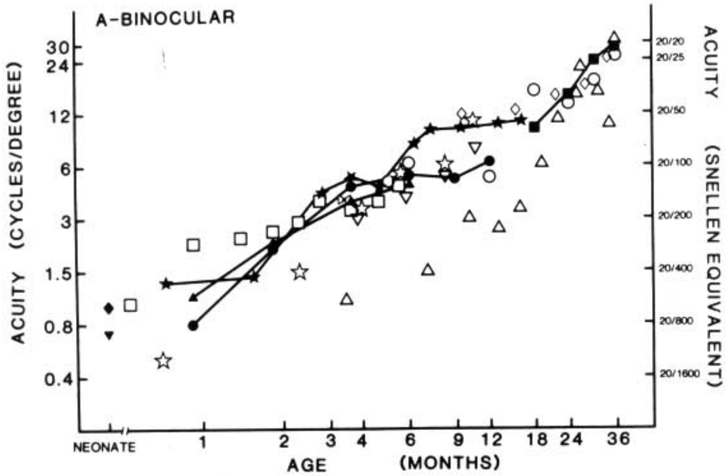

Fig. 2. Compilation of behavioral data showing the development of grating acuity in humans over the first five postnatal years. Reprinted with permission from Teller *et al.*, 1986.

Operant techniques for testing the visual behavior of animals were also well known, but had not yet been much applied in the developmental context.

1962 saw the publication of Fantz *et al.*'s study of the development of visual acuity in human infants over the early postnatal months obtained by means of both preferential looking and OKN; the acuity values they reported remain typical to the present day. However, most infant perception studies in the 1960s concerned pattern perception and the influence of cognitive variables, rather than the more sensory aspects of vision. It is startling to realize that—with the exception of visual evoked potential technology, which was in a very rudimentary stage—the basic elements of the techniques now used for infant visual testing lay ready but neglected for almost ten years. The field waited on motivation and conceptualization rather than on technological advances. (Parallel advances in the electrophysiological study of vision in young children are described by Regan and Spekreijse in the preceding article.)

Amblyopia. In the clinical literature it had long been appreciated that visual losses occur in conjunction with ocular misalignment, optical anomalies and lack of adequate visual stimulation early in life. The effects of early severe visual deprivation on human vision had been comprehensively treated by von Senden (1960). He concluded that profound visual deficits usually followed an extended period of early visual deprivation, although this conclusion was somewhat softened by Gregory and Wallace (1963).

Gunter von Noorden writes, "[At that time] . . . it had become universally accepted to treat amblyopia by patching the good eye, and recognized that such treatment is only successful if started at a very young age . . . Thus, the concept of plasticity of visual functions and of a "sensitive period" is not entirely new . . . The interest in amblyopia received an enormous boost during the fifties when treatment by active visual stimulation of the amblyopic fovea (pleoptics) was introduced in Europe . . . While conventional treatment methods eventually proved equally effective and pleoptic training is only infrequently applied now, numerous contributions to the pathophysiology of amblyopia were made during those years . . . It appears desirable that basic scientists presently working in amblyopia research attempt to gain access to this data pool, as many concepts employed in current discussions, for instance plasticity, sensitive periods, abnormal binocular interaction, and amblyopia of arrest, have actually been with us since the turn of the century."

Another hint at the plasticity of vision arrived from the experimental side. Don Mitchell writes "The spark that kindled my first experimental venture in visual development was ignited during the course of a study on orientation differences in contrast sensitivity for gratings generated by interference within the eye . . . Both Ralph [Freeman] and I found that vertical and horizontal gratings were not perceived equally well. In my case, vertical gratings were much easier to resolve than horizontal gratings, while Ralph showed a similar difference in the opposite direction. Both of us were corrected astigmats and in discussions of these results with Gerald [Westheimer] I can recall mention being made of a possible link between the meridional acuity loss and the nature of our visual experience prior to correction of the refractive error. Gerald mentioned that suggestion of a causal link between the two would be heresy and that we should set such thoughts aside for the moment . . ."*

Animal studies

In 1960, the neurobiology of visual development was dominated by the work of Roger Sperry, who had been studying the formation and regeneration of retinotectal connections in lower vertebrates for nearly two decades. Sperry's work had shown that the characteristics and organization of this projection survived all sorts of experimental manipulations, and led him to evolve the hypothesis of *neuronal specificity*. This hypothesis, as Sperry put it in 1963, suggested that "the patterning of synaptic connections in nerve centers, including those heretofore ascribed to functional molding in various forms, must be handled instead by the growth mechanism directly, *independently of function*, and with very strict selectivity governing synaptic formation from the beginning" (our italics). Sperry's relentless emphasis on the independence of neural *development* from neural *function* in the developing animal was to have a short life after 1961. In fact, most subsequent work on visual development, especially in higher vertebrates, has concentrated precisely on establishing the way function guides development.

The influence of complete visual deprivation on visual behavior and anatomy in animals had been studied, most notably by Austin Riesen and his colleagues. It was clear by 1961 that depriving animals of vision in early life could profoundly disrupt their visual behavior. With occasional exceptions, however, there was little positive evidence concerning the neural substrate of this effect. Richard Held and his colleagues had begun their studies of the role of visual feedback in sensorimotor integration during development, including the famous "kitten carousel" experiment, but their most important developmental contributions were yet to come.

Methodology. Many of the basic techniques for studying the development of visual anatomy and physiology in animals simply did not exist in 1961. Single unit recording, perhaps the most important method used in this field over the last quarter-century, was well established in the peripheral nervous system, but was practiced with confidence in the central nervous system of mammals by relatively few laboratories, notably those of Vernon Mountcastle, David Hubel, and Torsten Wiesel. Its application in fragile infant animals was even more difficult. The techniques then available for tracing neural connections in adults were perilous and not easily adapted to young animals: the dramatic developments in neuroanatomical technique that have led to so much recent progress were a decade and more away. Of course, classical descriptive studies of the developing nervous system were available in abundance, but these revealed little concerning the development of neural *function*. Unlike the situation in human development, then, in 1961 the basic methods that have proved most important in studying development in animals were in a very immature form, and concurrent technological advances have importantly shaped the history of the field.

Wiesel and Hubel's work of the 1960s. Torsten Wiesel and David Hubel initiated the physiological study of visual development in mammals in the early 1960s. As Torsten Wiesel recalled in 1982 (p. 583): "(We) decided to investigate how the highly specific response properties of cortical cells emerged during early postnatal development. We were also interested in examining the role of visual experience in normal development, a question raised and discussed by philosophers since the time of Descartes. The design of these experiments was undoubtedly influenced by the observation that children with congenital cataracts still have substantial and often permanent visual deficits after the removal of the cataract and proper refraction. Also, behavioral studies had shown that animals raised in the dark or in an environment devoid of contours have a similar impairment of visual function". The work they did in this period provided methodological as well as conceptual breakthroughs, and defined the territory within which many of us were to work for years to come.

One of Wiesel and Hubel's (1963) most strik-

*Gerald Westheimer replies, ". . . I have read with considerable interest Don Mitchell's reference to our conversation. This goes back just about 20 years but I recall discussing the implications of associating meridional acuity differences with uncorrected astigmatism. Eye shape, receptor packing and even ganglion cell receptive fields. . . might exhibit anisotropies that are genetically tied to astigmatism, nor can it be guaranteed that accommodation will always place the same end of Sturm's interval on the retina. Proving convincingly that uncorrected astigmatism causes meridional acuity differences did not appear such a simple task. . ."

ing observations concerned the effects of early unilateral eye closure, which produced a telling parallel between visual behavior (the animals were effectively blind in the deprived eye) and visual physiology (few cortical cells could be influenced through the deprived eye). Donald Mitchell speaks for many of us when he writes, "The 1963 paper by Wiesel and Hubel . . . made a tremendous impact on my thinking. Even then I realized that this paper held promise for an eventual understanding of the origins of amblyopia."

This points up an important aspect of Wiesel and Hubel's early work that came to be neglected later. Observations like those on the behavioral and neural effects of unilateral eye closure seemed to present very powerful examples that revealed the neural basis of visual function. While others later were to pursue these correlations in developmental studies, a great deal of effort was devoted to work that had little bearing on this basic question.

Wiesel and Hubel's early work made a number of clear points. First, the visual cortex of the neonatal kitten possesses at least the skeleton of the organization present in the adult. Second, disruption of binocular visual input, either by unilateral eye closure, alternating eye occlusion, or artificial strabismus, completely disrupts cortical binocular interaction. Third, complete binocular deprivation has an effect less than the sum of two monocular deprivation effects: while producing a cortex whose function is far from normal, this treatment does not abolish visual responsiveness with the finality that monocular deprivation does. Fourth, the physiological effects of abnormal early visual experience are for the most part confined to the visual cortex, and are not expressed to any pronounced degree in the lateral geniculate body. Fifth, the effects of abnormal visual experience are only obtained during a *critical period* early in the animal's life. Each of these findings has come under close scrutiny in the last two decades. While some of them have been modified in detail, and some points of emphasis have changed, they have all stood the test of time and continue to represent basic principles of central visual development.

THE EXPLOSION OF THE EARLY 1970s

In the early 1970s T.M.'s scientific consciousness and D.T.'s interests in visual development arrived more or less simultaneously, so we can actually write memoirs. At the time, the field coalesced into three general topics: behavioral studies of normal development in infants, studies of development and deprivation in animals, and studies of clinical patients (adult and infant) who were thought to represent cases of naturally occurring visual deprivation in humans.

Behavioral studies of infants

Behavioral studies of the development of vision in infants were started soon after 1970 by at least four different laboratories: those of Richard Held at MIT, Davida Teller at the University of Washington, Martin Banks (as a student in the late Philip Salapatek's lab) at the University of Minnesota, and Janette Atkinson and Oliver Braddick at the University of Cambridge. As noted in the preceding paper by Regan and Spekreijse, visual evoked potential studies were also started in Russ Harter's laboratory, to which we add mention of Sam Sokol's. It is interesting that these various groups were drawn to the study of infants almost simultaneously, but for a variety of fundamentally different reasons.

One major motivation was a desire to solve the ancient riddle of nature vs nurture. Dick Held writes, "I became exposed to psychology through the instruction of people like Hans Wallach, and the ideology of Gestalt psychology as interpreted by Köhler. Köhler's approach was essentially nativistic . . . However, I was at the same time exposed to the behavioristic tradition with its learning bias. The question for me was: How could the orderly world of perception . . . be acquired originally? If not originally there, how could learning produce it? These ideas led to the 'kitten carousel' experiment . . . When [Colin] Blakemore was visiting MIT (in 1972) we had a seminar on vision in which he, Whitman Richards, Peter Schiller and I participated. I was impressed with the Blakemore stripe-rearing experiment and asked myself whether there was a human analogue. About the same time the Annis and Frost Cree Indian study appeared, as did the Mitchell-Freeman work on meridional amblyopia. Together they made a story which suggested an experiential origin of both the oblique effect and the meridional amblyopia. How to test the theory? Obvious. Test babies and find out their developmental histories . . ."

D.T.: My own reason was, in retrospect, more comparative than developmental. I had always taken the goal of visual science to be the finding of explanatory relationships between psychophysical and physiological data. It was exciting, for example, to plot Westheimer's sensitization effect and the threshold-vs-background-diameter curves of single cells on approximately the same coordinates, and get curves of approximately the same shape. And yet the more I engaged in such exercises, the less satisfied I became. It seemed that such analogies were more a beginning than an end, and that one still needed an orthogonal dimension against which to challenge such correlations. It began to strike me with increasing force that development might be such a dimension. My motivating logic (such as it was) was as follows: suppose that one had a theory that a certain set of cells or synapses were a necessary condition for the occurrence of a certain visual function. If one could show that that visual function and that element of the substrate emerged in parallel in the life history of the organism, one had weak support for the hypothesis. More forcefully, if the function emerged before the suspected substrate, another theory of the dependence of function on substrate would bite the dust.

Clinical motivations were also important. Sam Sokol writes, "My interest in normal infant visual development was prompted by my introduction to the pediatric patients who were sent to our eye clinic for evaluation. While the clinician could easily evaluate the infant's visual system anatomically, he or she had no reliable technique to assess the patient's visual function. It seemed to me that the development of clinical techniques for the measurement of infant acuity depended on a study of normal visual development."

Finally, both Velma Dobson and Marty Banks, whose original interests came from developmental psychology, report that what attracted them to the field of infant vision was its odd but pleasing potential for combining "hard" science with infant and child studies. For me (D.T.), this juxtaposition of the intensely human and the incontrovertably scientific is best symbolized by infancy researchers' amiable and fully effective jury-rigging of infant diaper-changing tables from oscilloscope carts.

Thus, there were many motives, and each of them led one with mounting excitement to try to study the emergence of visual function in infants. The question was, how?

D.T.: My own attempts began with a skirmish with the developmental literature, and thereby an introduction to Fantz's preferential looking technique. My technician, Ralph (Morse) Tigre, built a wheel on which we mounted some square-wave gratings, so that a grating could be shown at random on the left or right side of a display. We had intended to score first fixations, fixation duration, and so on, as had Fantz. However, on the first look through the peephole, my psychophysical heritage manifested itself. I realized that, rather than scoring anything about the infant's behavior, I could make a forced-choice decision as to whether the grating was on the right or the left, and that if I could do better than chance, the infant must be said to resolve the grating. This was the inception of the forced-choice preferential looking technique, or FPL (Teller *et al.*, 1974; Teller 1979), which has been used in many of the psychophysical studies of infant vision during the ensuing years.

T.M.: My first (and only) exposure to FPL was in 1973, when I was a graduate student in Cambridge. Colin Blakemore had given me free rein with his psychophysical setup, and with a fellow student, Michael Donaghy, we were engaged in some stunningly dull experiments for which I had set up a large CRT display with split-screen capability. Jan Atkinson and Oliver Braddick had learned of the FPL technique, and were anxious to try it out on a newly acquired subject, their month-old daughter Fleur. Mike and I rarely appeared before lunchtime, so we arranged things so they could use the lab in the mornings. The result was a minor war in which they left Fleur's diapers lying around for our edification, and we retaliated by leaving our cigarette butts for them. The outcome of the war was inconclusive, but their experimental results (Atkinson *et al.*, 1974) were more enduring than ours, which remain (deservedly) unpublished.

D.T.: For a summer, Ralph and I tried our new technique on several infants of various ages, including one infant named Peter, who heroically returned with his mother almost daily all summer. Nothing systematic seemed to be happening until one day when I idly piled up Peter's alternate weekly data, which had been plotted on transparent graph paper. There lay a perfect developmental sequence, and I was hooked.

It also occurred to me that summer that my motivation for studying development—the explanation of visual development on the basis of visual physiology—required an animal model, and I resolved to find ways to study the development of visual function in monkey as well as human infants. By the greatest good fortune, Jim Sackett was just then establishing a unique infant primate facility at the University of Washington. My students Ron Boothe and Dave Regal wheeled the preferential looking apparatus across the campus and tried testing the acuity of infant monkeys. It worked, and, along with operant infant techniques largely developed by Ron, has allowed the characterization of normal visual development in infant monkeys. Although we were also drawn into a few deprivation studies early on, the deprivation fever of that time (see below) seemed to me a distraction, since I thought it would be better to understand the normal system before one tried to muck it up.

But moving from an older and more established branch of science to a newer and less secure one had its difficulties. Most of my colleagues had some trouble believing that anything worthy of the name psychophysics could possibly be done on anything as irresponsible as a human infant (their image is portrayed in Fig. 4). Despite the regularity and internal consistency of our data, it has often been an uphill battle to get them taken seriously. Then, once an "adult" psychophysicist does take infancy research seriously, he or she can immediately generate the obvious set of "next questions" and wonder why we haven't answered them. For example, our first paper in 1974 concerned the limited grating acuity of infants. We thought it a tremendous feat to have successfully studied infant acuity at all, but visitors to the laboratory (to say nothing of journal and grant reviewers) unanimously wanted to know, then and there, whether the acuity limit was optical or neural (it is largely neural).

In 1974, I had a bitter disappointment when two grant proposals to study visual development in human and monkey infants were both turned down at NIH. The reviewers concluded that, although I meant well, my aspirations were too unorthodox to be legitimate. They judged that I wanted to study the wrong problem with the wrong techniques at the wrong time for the wrong reasons and from the wrong perspective. Reading this review still brings great pain, as the reviews I have written since have doubtless brought pain to others. Desperate applications to several other funding sources were also refused in short order. I would have given up, except for the encouragement of Carl Kupfer and Jay Enoch, and for a godsend of a telephone call from Fred Stollnitz at NSF, inviting me to apply there for funding.

Meanwhile, Dave Peeples had been awarded a postdoctoral fellowship to work with me on infant color vision. We survived on his supply allowance for almost a year, started our study of infant color vision—chromatic discrimination of red stripes from a white surround—and waited for our ship to come in. When funding finally came, Dave went to Shiga's import shop and found a ship with red-and-white striped sails. We hung it over the oscilloscope cart and drank champagne.

ARVO. ARVO abstracts over the years document an interesting early history of work with infants. In 1973, D.T. submitted her first abstract on infant acuity. It was rejected for being too short. But the following year both she and Melanie Mayer were included in Bob Boynton's symposium on visual psychophysics,* reporting on the absence of oblique effects in infants and their onset in late childhood. In 1975, D.T. and Dave Peeples presented their first paper on chromatic discriminations in infants, and Susan Leehey spoke for Dick Held's group on their new and extensive studies of oblique effects. Infant VEP work was also represented, with Velma Dobson reporting a study of spectral sensitivity, and she and Sam Sokol reporting their work on acuity with pattern reversing

**Comment by the Editor*: When I first read this, I was puzzled, because I could not for the life of me recall chairing a symposium on Visual Psychophysics at ARVO in 1974, although I did distinctly remember doing one on Light and Dark Adaptation in 1972. Checking my 1974 ARVO program provided the answer. That year, I was Chair of the program committee for the Visual Psychophysics and Physiological Optics section, and it was my idea to limit one session of contributed papers to nine, instead of the usual twelve presentations. Rather than to select these papers because they dealt with a common subject matter, we picked them because each seemed to have something unusually new and exciting to contribute. Thus it wasn't an official symposium, although it had some of that character because the papers were a little longer and there was more time for discussion than in the rest of the contributed-paper sessions. Although I still think it was a good idea, it was not universally popular and has not been attempted since. Given the fixed program time allotted to sections, a consequence of our special session was that three papers were rejected that otherwise would have been included somewhere on the program. One of those whose abstract was rejected that year, who wrote one of the papers for this Jubilee Issue, was (to put it mildly) less than enthusiastic about what we had done.

checkerboards. By 1976, more than half of a session was devoted to papers on human and monkey visual development.

Velma Dobson writes, "In 1977 at ARVO, we held a demonstration of two of the new techniques for visual assessment for infants in my motel room, with my 5-week-old son as a subject. Jane Allen set up her portable FPL apparatus on the kitchen table and demonstrated acuity testing, and Indra Mohindra used the darkest place available—the bathtub—to demonstrate dark retinoscopy." The "infancy party" at ARVO also started about then, and has continued as an annual event that gives infancy researchers and clinicians of every persuasion a chance to meet and exchange ideas.

Development and deprivation in animals

The early 1970s brought a new explosion of interest in the role the environment plays in the development of visual function, and along with it a new willingness to risk and master the art of single unit recording in the visual cortex of the young kitten. What had been the private preserve of Wiesel and Hubel became a wide-open playground for an ever-growing number of active research groups.

Peter Spear writes "All of this activity brought forth a wave of young visual neuroscientists; 'visionaries' as we often called ourselves with a certain sense of self-mockery. Many of [us] were scientifically 'born' during that time."

The important motivations for those entering this field paralleled those that led others to study infant development. On the one hand was the Cartesian issue of nature vs nurture, which was the dominant motivation for many. Wiesel and Hubel had laid to rest Sperry's nativist view of neural development, at least in mammals, and a wave of work that followed their lead sought to push the developmental plasticity of the visual system to its absolute limits, almost for no other sake than to test those limits. Another motivator was D.T.'s "orthogonal dimension": what could the abnormalities of vision in animals with deliberately (and measurably) disrupted visual systems tell us about the normal process of seeing?

Two important kinds of observations at the beginning of the 1970s triggered this new wave. One was a re-examination (by Horace Barlow and Jack Pettigrew, then in Berkeley) of the functional characteristics of visual neurons in very young kittens. The second was the analysis of the effect of rearing kittens in environments containing a restricted range of orientations, undertaken by Colin Blakemore and Grahame Cooper in Cambridge, and by Helmut Hirsch and Nico Spinelli in Stanford.

Hubel and Wiesel had reported that the visual cortex of very young kittens without visual experience was qualitatively normal in function. While they noted that visual cortical neurons were in some respects abnormal, they argued that the basic organization of the cortex existed before the animal had received any visual experience. Thus the effect of subsequent abnormal visual experience was seen as disrupting a basic plan that was innately laid down. This view placed them firmly in the nativist wing of the newly burgeoning field.

During the late 1960s, Pettigrew and Barlow began to reexamine the functional characteristics of cortical neurons in newborn kittens, with the goal of studying the development of the selectivity for binocular disparity that they had discovered and described a few years before. To their surprise, they found that the visual cortex of their kittens contained no neurons that they could convince themselves were adult-like; in particular, they felt that the characteristic adult property of orientation selectivity was absent in the kitten's cortex. This finding (Barlow and Pettigrew, 1971) struck at one of the important foundations of the principles of development that Hubel and Wiesel had presented. If the visual cortex was not well-formed before the onset of visual experience, perhaps the visual environment played a much more active role in guiding the development of function that had been supposed.

The stripe-rearing experiments of Hirsch and Spinelli (1970) and Blakemore and Cooper (1970) seemed to be natural extensions of Wiesel and Hubel's early observations on the disruptive effects of monoclular deprivation, and Barlow and Pettigrew's on the striking immaturity of the orientation preferences of cortical cells. These experiments sought to establish whether highly selective changes could be wrought in the orientation preferences of cortical neurons by raising animals under conditions that restricted the range of contour orientation that they experienced (Fig. 5). And the early results showed very dramatic changes in the distributions of orientation preference of cortical neurons, with few neurons remaining that responded best to orientations different from those seen in early life.

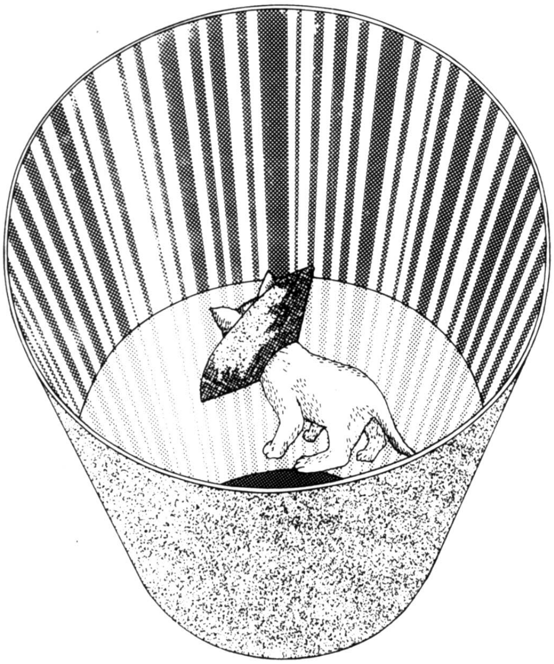

Fig. 5. Kitten being (hopefully) reared in an environment of vertical stripes. The ruff around the neck was intended to keep the kitten from seeing its own body. Reprinted with permission from Blakemore and Cooper, 1970.

As in the case of behavioral work, the original motivations for these studies varied from one research group to another. Colin Blakemore recalls that a major goal of his first experiments with Grahame Cooper was to provide an anatomical marker for the orientation columns that had been described in the visual cortex by Hubel and Wiesel. These regularly-arranged groups of neurons, he thought, might shrink or otherwise change their morphology if they were deprived of the orientations they preferred, and thus be anatomically delineated after a period of orientation-specific deprivation. Indeed, he reports that the idea of recording from the visual cortex of these animals was an afterthought; the original plan had been to confine the experiments to behavioral and anatomical ones. In a letter to Michael Gazzaniga in 1969, he wrote, "I have a wild project starting up. I am going to rear kittens entirely in the dark except for about an hour each day during which some animals will see only vertical stripes and others horizontal... My hope is that after 2 or 3 months all the cortical cells except one set of orientation detectors will have degenerated. At the end of the period I can test them behaviorally to show that they are selectively blind for some orientations [and] look at the brains to try to demonstrate columnar degeneration...".

Gazzaniga's reply was encouraging, but it drew Blakemore's attention to related work in progress at Stanford, where Helmut Hirsch and Nico Spinelli had been working on a similar experiment, for rather different reasons. Helmut Hirsch writes, "... I was fascinated by the possibility that the discovery of orientation sensitive cells might eventually lead to an understanding of the neuronal basis of form perception ... I realized that I could take advantage of the fact that form deprivation alters the course of visual system development to devise a means for testing directly the role of 'line detectors' in form vision ... I hoped to determine whether there [were] visual deficits which [were] specific to the missing classes of cortical line detector cells." D.T. recalls the excitement evoked by Hirsch's use of the term "environmental surgery", and the images it conjured up for the testing of structure-function relationships.

Subsequently, both Hirsch (1972) and others (e.g. Muir and Mitchell, 1973) showed that there were indeed specific behavioral deficits that followed stripe rearing, but these were surprisingly subtle and seemed incommensurate with the magnitude of the physiological effects. Logic suggested that a whole set of implicit but widely held theories about the necessity of cortical "line detectors" for the perception of lines would have to be discarded. It has indeed turned out over the succeeding years to be very difficult, at least in cats, to demonstrate clear behavioral deficits that relate to the effects of any but the most potent forms of abnormal early visual experience. This may not be too surprising, given the startlingly good vision of cats whose striate cortex has been completely removed (e.g. Berkley and Sprague, 1979). But one may still share Helmut Hirsch's sentiments when he writes "I think it is unfortunate that we have made so little progress since then [the early 1970s] in discovering the role that orientation sensitive cells play in form vision. For my money, that is still one of the most important and interesting questions."

In any case, the stripe-rearing results electrified the field. Suddenly, a whole new territory had opened up for exploration (Fig. 6). If rearing an animal in stripes could change the properties of cortical neurons, what other environmental manipulations might be effective? In very short order, people came to examine the influence of a variety of forms of unusual visual input: spots, dots, stroboscopic illumination, astigmatic lenses, moving stripes, moving blobs,

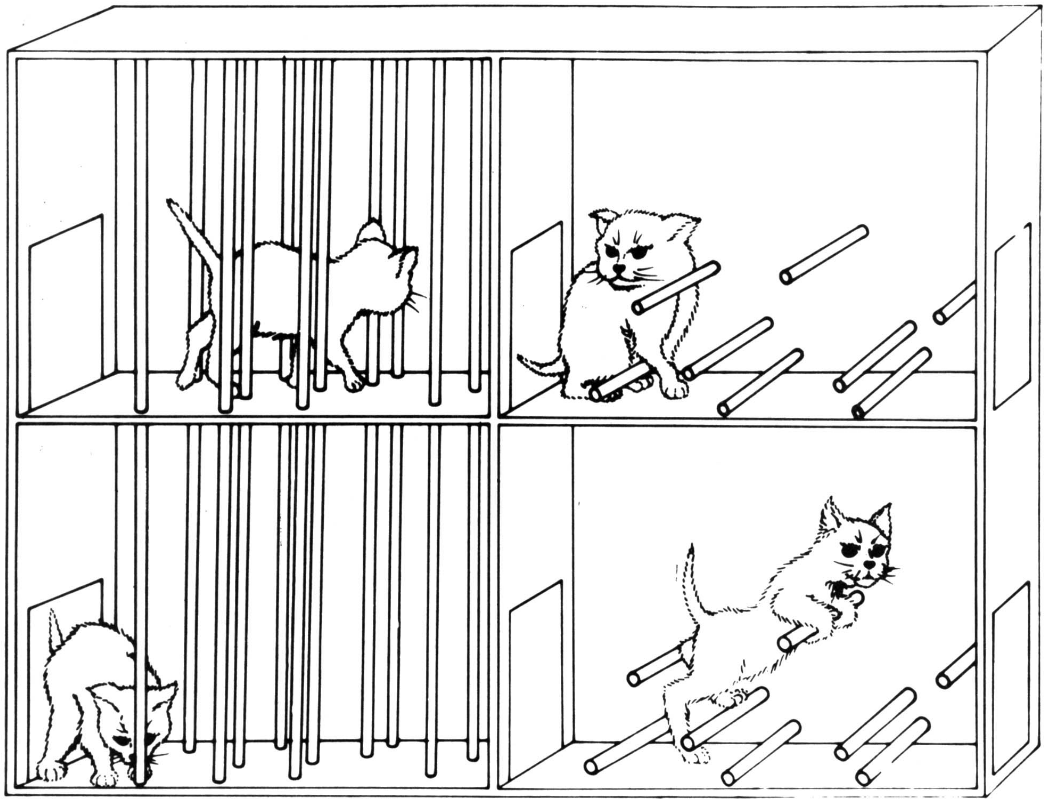

Fig. 6. A fanciful rendition of the results of a never-performed behavioral experiment, showing the purported orientation-specific blindness of stripe-reared kittens. Reprinted with permission from Gazzaniga, 1973.

or whatever the ingenuity of the experimenter could contrive to alter the early stimulation of a kitten's visual system became fair game for experimentation.

Probably the most extreme variant of this view was one that might best be termed the "photographic" theory of receptive field development. The idea here was that the structure of cortical receptive fields could adapt itself very specifically to the kinds of stimuli prevailing in the early visual environment, resulting in the appearance of distinctive receptive field properties not normally found in the adult visual cortex. Some anecdotal evidence of this kind emerged from some of the stripe-rearing experiments, and from experiments in which kittens were deprived of the experience of extended visual contour.

In retrospect, many of these experiments seem to have been very hastily conceived and performed. Published results were often based on small samples of neurons recorded from small numbers of experimental animals. This was due partly to the real difficulties involved in controlling the visual environments of these specially-stimulated subjects with anything like adequate precision, and partly to a lack of appreciation of the difficulties of sampling neurons from the cortex in a way that would minimize various important sources of experimental error. Many of the findings that seemed so exciting then have slipped quietly into oblivion in the succeeding years, and few researchers are now concerned with the effects of the more bizarre environments that came into vogue in that period.

In 1975, an abrupt check was delivered to the selective deprivation field by the work of Michael Stryker and Helen Sherk, who were then graduate students in Peter Schiller's laboratory at MIT. They had been trying to follow up the observations of Blakemore and Cooper in stripe-reared kittens, and had been unable to replicate those findings. The report of this failure, presented at ARVO in 1975 and published in *Science* the same year, had a chilling effect. Stryker and Sherk had used a variety of superior methods in their experiments, including blind recording procedures and techniques designed to overcome sampling bias, and they had studied a larger sample of both cells and kittens than was then customary. How were we all to reconcile their results with those of the many groups which had apparently replicated the basic stripe-rearing effect?

T.M.: I was in my final year as a graduate student in Colin Blakemore's lab when we got news of the MIT results. The stark contrast between the MIT and Cambridge results shook everyone's confidence. In Cambridge, they generated a flurry of activity as we tried to work out how and why Stryker and Sherk's results were so different from ours. Colin Blakemore began to rear some kittens in his apparatus with the idea of taking them to MIT for recording (a project later abandoned), and we scanned the by-then considerable number of stripe-rearing papers in the literature for clues to the difference.

In the end, it transpired that the conflict probably arose more over details of the rearing than anything else. In collaboration with Helmut Hirsch and Audie Leventhal, Stryker and Sherk (Stryker *et al.*, 1978) later replicated the Hirsch/Spinelli variant of the stripe-rearing experiment, and the controversy over the data began to die down, although interpretations continued to differ. But the effects of that first paper remained very sobering, and many people realized that the methods they had been using were probably not good enough to answer the questions they wished to study. Clearly, life was going to be a good deal more laborious in the future than it had been until then, and the era of "record-from-two-kittens-and-send-it-to-*Nature*" papers was over.

It is possible to take a rather jaundiced view of the burst of energy that went into developmental studies in this period. Hubel and Wiesel appeared at the time to have performed the definitive studies of the organization and function of the normal visual system. With the exception of the laborious quantitative approaches being pioneered by Peter Bishop and his colleagues in Canberra (see the paper by Bishop and Pettigrew in the final section of this issue), there were few avenues open to add to what had been said about the adult. But in development, fascinating and important experiments were just sitting there, waiting to be done. And they seemingly could be done with simple qualitative recording methods and relatively small numbers of animals. It is no surprise that a group of ambitious young neuroscientists were drawn to this area of research, like moths to a candle. And it is no surprise that some of them got slightly singed along the way.

Peter Spear writes (perhaps a little more fondly), "A dominant aspect of that period is that it was a time of excitement about the many important findings that were being reported at a rapid pace. I think that the importance of the work that was being done then is reflected in Hubel and Wiesel's Nobel Prize. In some sense, I think we all took some pride in their achievement because we were all working on the same problems . . . That period was also one of rampant controversies. There were controversies about the effects of stripe-rearing, whether or not visual deprivation produces a Y-cell loss . . . Of course, the controversies added to the excitement. But at the same time they were a source of some frustration because it was not always possible to pinpoint the causes of discrepant results in the literature . . ."

Amblyopia and the monkey model

Meanwhile, on the clinical front, the delayed influence of Hubel and Wiesel's work, and the bombshell of the stripe-rearing results, provided new and stronger support for the idea that various human amblyopias might be caused by optical or alignment irregularities during an early critical period in the patient's life. Don Mitchell writes: ". . . I heard about the experiments by Hirsch and Spinelli and Blakemore and Cooper. The relevance of these papers to our earlier observations on human astigmats was very obvious, and I resolved to embark on a systematic study of the meridional variations of acuity in optically corrected astigmats . . ." The results of this study (e.g. Mitchell *et al.*, 1973) added the term *meridional amblyopia* to the vision literature, and provided what seemed to be a particularly clear link between the processes of human visual development and those that had been studied in kittens.

Gunter von Noorden writes that he found Wiesel and Hubel's work extremely exciting, but incomplete in that it concerned only deprivation amblyopia and not the clinically more common strabismic and anisometropic amblyopias. Moreover, he wondered whether the conclusions drawn from cat experiments could be unequivocally applied to similar conditions in humans. His laboratory succeeded in producing strabismic and deprivation amblyopias in monkeys, in expressing the visual deficit in terms of recognition acuity with Landolt "C's", and in confirming that the histological changes described in the lateral geniculate nucleus of amblyopic monkeys also occurred in the brain of a human amblyope. Von Noorden's successes (e.g. von Noorden, 1973) doubtless encouraged some researchers in the infancy field to begin studies of visual development in infants with optical and alignment abnormalities, and others to continue to explore the infant monkey as an animal model for both normal and abnormal human development.

VISUAL DEVELOPMENT: 1975–1985

Human studies

During the decade from 1975 to 1985, VEP techniques have come of age, and operant techniques have been added to preferential looking, so that infants and toddlers of all ages can now be studied. The study of human visual development has, on the whole, been marked by a gradual and rather orderly accumulation of knowledge concerning the most basic, classical aspects of visual function. The majority of studies concern four topics: spatial and temporal resolution, photoreceptors and color vision, stereoscopic vision, and clinical studies. Comprehensive reviews may be found in Boothe *et al.*, 1985, and Banks and Salapatek, 1983.

Studies of spatial resolution have been by far the most numerous. When behavioral techniques are used, many different laboratories have shown, and continue to show, a long, slow development of grating acuity. The grating acuity of newborns is between 0.5 and 1 c/deg, and grating acuity reaches adult levels at about 3–5 years, depending on the definition of adult acuity adopted. Sensitivities to lower spatial frequencies reach adult levels before sensitivities to higher ones, and the cutoff frequencies of infant contrast sensitivity functions are consistent with the development of grating acuity. On the other hand, several laboratory groups also agree in showing that, when tested with VEPs, infant spatial resolution develops much more rapidly, with grating acuity reaching adult levels at 6–8 *months* postnatal. Although some of this difference can be attributed to differences in scoring criteria, much of it cannot, and the difference is not well understood. For further discussion of these discrepancies, see the section on *Visual Development* in the preceding paper.

In addition to the many basic studies on the normative development of grating acuity, several parameters have been explored. Martin Banks and his students (e.g. Banks and Stephens, 1982) have looked at infant spatial vision from the viewpoint of multiple channels theory. Meridional variations have been much studied by Jane Gwiazda and her colleagues (e.g. Gwiazda *et al.*, 1985), particularly in connection with infant astigmatism. Velma Dobson and Angela Brown have shown that acuity varies with luminance in infants much as it does in adults, and this finding rules out any form of "dark glasses" theory as an explanation of the limited acuity of infants (Brown and Dobson, in preparation). Russ Hamer and Marilyn Schneck (1984) have shown that the spatial summation areas of infants are also large, in keeping with their limited acuity. In contrast, Dave Regal (1981) has shown that infants' *temporal* resolution is remarkably good. The pattern of poor spatial and good temporal resolution is reminiscent of models such as Wilson and Bergen's (1979), with the suggestion that the channels tuned to lower spatial and higher temporal frequencies are the earliest to mature.

The second most widely studied area is that of receptors and color vision (reviewed by Teller and Bornstein, 1986). Both behavioral and VEP data show that the rod system is functional in early infancy, and several laboratories have shown that field adaptation is at least qualitatively similar in infants and adults. In color vision, several paradigms for solving the problem of brightness artifacts have been worked out. It has been shown that by 2–3 months postnatal infants can make many chromatic discriminations, including both Rayleigh and tritan types, and so (barring rod intrusion and other artifacts) they must have all three cone types functioning. On the other hand, infants younger than 1 month generally fail to make chromatic discriminations, and these failures are under continuing investigation. I (D.T.) am betting that these failures will turn out not to be caused by the failures of individual cone types, but rather by failures of the postreceptoral system to analyse or preserve chromatic information. My lab group is currently building a video display system that will allow us to modulate stimuli through the white point (cf. Derrington *et al.*, 1984) in order to begin investigating infants' postreceptoral chromatic and luminance channels.

The third major area of interest has been that of stereopsis (which is also the subject of the last section of this Special Issue). In 1980 and 1981, several different laboratory groups demonstrated that below three months of age, infants show no evidence of a response to binocular decorrelation or binocular disparity. Responsiveness to these stimulus dimensions increases rapidly between the third and seventh month, by both behavioral and VEP measures. This latter point is particularly interesting, because it contrasts with the differences in developmental curves between VEP and behavioral techniques in the case of spatial resolution. If VEP measurements routinely showed earlier onsets of visual functions than did behavioral ones, one could conclude that the VEP is a more sensitive measurement technique, or reflects the neural signal at an earlier stage of processing. But the agreement in the stereopsis realm makes the discrepancy in the realm of spatial resolution all the more tantalizing.

The fourth area is that of developmental studies of infants who are at risk for abnormal visual development. From the beginning of studies of infant vision there has been the hope and the expectation that infant vision testing could be useful in the clinical context, for establishing the degree of functional loss and monitoring the effects of treatment. Groups headed by Dick Held, Janette Atkinson and Anne Fulton have been among the leaders in this area, and many case histories of the development of vision in infants with such anomalies as cataracts, strabismus, and various ophthalmic disorders have been published. More tightly controlled and systematic studies are now underway, such as Eileen Birch's and Velma Dobson's on strabismus, and Daphne Maurer's on the effects of congenital and traumatic cataracts on visual development.

The study just now being brought to fruition by Daphne Maurer and her associates (e.g. Maurer *et al.*, 1983; 1986) is a particularly striking example of the influence that basic research can have in the clinic. This group has confirmed in a larger and more carefully studied sample the sporadic reports of good visual outcomes in some congenital cataract cases. They report that with early surgery, diligent use of appropriate optical correction, and (in monocular cases) diligent patching of the phakic eye, the development of acuity in infant aphakes can sometimes be held on course through the first year or more of development. Acuity then tends to fall behind the age norm, and maximum acuities near 20/60 are being found. These results stand in stark contrast to the gloomy prognoses of only a few years ago. Without the animal work in deprivation, the knowledge of human testing techniques, and the resulting age norms, it seems unlikely that this work would (or could) have been undertaken.

My (D.T.'s) group has recently (and ironically) made what we hope is a contribution to clinical testing. Our formal FPL technique has always been too slow and ponderous to be of much use in clinical work, but we have recently abandoned all formality. We made up a set of "acuity cards" containing gratings of different spatial frequencies, and simply allowed the "clinician" to use her head, and judge directly the highest spatial frequency that an infant or child can see. So far, the technique is working rapidly and reliably in both basic and clinical settings (Teller *et al.*, 1986). So, things have come full circle, and I sometimes wonder whether to be embarrassed for having formalized preferential looking 15 years ago, or for liberating it now.

In the meantime, as the field matures, the daily excitement continues. I (D.T.) have been privileged in the past year to serve on the thesis committee of Shinsuke Shimojo, a student in Dick Held's laboratory. Shin posed what I consider to be the first unique question within the field of visual development: if the infant really does not have stereopsis, then what is the infant's pre-stereoptic binocular vision like? Not only did he pose the question, he carried out an ingenious series of experiments to characterize it. Following up Dick Held's analysis of the correlation between the formation of ocular dominance columns and the onset of stereopsis, Shin suggests that the eye-of-origin information needed for stereopsis could be lost by a collapsing of inputs from the two eyes onto common infant cortical cells. He argues (Shimojo *et al.*, 1987) that the infant's view could therefore consist simply of superimposed images from the two eyes. If so, this is an instance in which the infant's vision could be qualitatively different from ours. We shall be hearing more, I am sure, about the possible combination rules for this (still hypothetical) collapsing of binocular information.

A recent colloquium by Ed Rubel brought me another similar shock of excitement, in that it brings together my interests in infant vision and linking propositions (Teller, 1984). Ed and his students have shown that in the chick auditory system, the location on the basilar membrane most perturbed by a particular tone shifts during development. But if that is so, then presumably different tones excite the same hair cells, and thereby the same central auditory neurons, at different ages; or, auditory stimuli may map to brain states in a qualitatively different way in chicks than in chickens. Now, what are we to believe about the mapping from brain states to perceptual states? If we believe it is constant throughout development, then the infant perceptual world could differ *qualitatively* from our own, rather than just being a pale and blurry imitation of it. As I (D.T.) sat contemplating the postnatal migration of receptors into the infant fovea, the changing characteristics of receptive fields, and the incomplete central pathways of infants, and wondering what a weird and wonderful world one might see through such a transformed information processing system, I could hear Peter Detwiler in the back of the room, intoning "peep, peep, peep" in a deep bass voice.

ANIMAL STUDIES: 1975–1985

Deprivation work

After 1975, studies of the normal and abnormal development of the visual cortex of the kitten, and later the monkey, continued to appear in growing numbers (reviewed by Sherman and Spear, 1982). But some of the thrust had gone out of the field. It was as if the momentum established in the previous 5 years was carrying everyone forward, in some cases without a clear goal or direction. As the dust settles, we are probably as well guided by the principles established by Wiesel and Hubel's early work (above) as by most of the varied literature since that time.

T.M.: A turning point for me came in 1979 when the *Annual Review of Psychology* asked me to do a piece for them on visual development and deprivation, which Rick Van Sluyters and I duly produced (Movshon and Van Sluyters, 1981). As we began to work, we realized that the field was in such disarray that the conventional techniques of writing a review were simply going to be inadequate: the article would have consisted of endless unsatisfactory constructions of the form, "so and so (1975) reported thus and so, on the other hand so and so (1976) found this and that, and so and so (1977) found the other..." We were thus *forced* to take an idiosyncratic and personal view of what had been going on in the field, simply in order to make something more-or-less orderly out of the material. The resulting article, as we warned our readers, trod on some toes, although we concealed some of our stronger views by prefacing sections of the article with quotes from Dante's *Divine Comedy*.

Surprisingly, we had rather little negative feedback about the article, although one author complained that we had used "mischievous phraseology" when discussing his work. Despite (or perhaps because of) our odd turns of phrase, the experience of writing this paper convinced me that the basic qualitative electrophysiological methods of the past decade were fundamentally bankrupt. They had produced a field where confusion was the rule rather than the exception—other, better, and more quantitative methods were essential for the continuing study of development. It is not accidental that the section of our article called *Methodology in Developmental Studies* is headed by Dante's grim inscription from the gates of Hell, "All hope abandon, who enter here."

Other new sub-fields of much greater promise have sprung up, however, particularly in neuroanatomy and in behavioral and neural studies of normal development. These are providing most of the interest and energy in the field now, and will probably form the focus of many efforts in the coming decade.

Mechanisms of plasticity

One of the most striking new ideas to emerge has concerned the regulation of cortical plasticity. Wiesel and Hubel had established the existence of a critical period in which abnormal experience could modify cortical function, and Takuji Kasamatsu and Jack Pettigrew at Cal Tech decided to try to establish the mechanisms that regulated the critical period. They settled on the idea that the wide-ranging projections from the catecholaminergic systems of the brainstem to the cortex were crucial in this regulation, and performed a series of provocative experiments in which they showed that disrupting this input to the cortex could apparently abolish the system's sensitivity to environmental influences (e.g. Kasamatsu and Pettigrew, 1979). These very difficult experiments have remained controversial and have not always proved to be replicable, but they represented an important new approach to basic developmental questions in vision.

Another controversial area concerned the mechanisms of the effects of monocular deprivation that Wiesel and Hubel had found. On both physiological and anatomical grounds, Wiesel and Hubel had suggested that these effects were simply a consequence of the deprivation having rendered ineffective the normal excitatory input from the deprived eye to the cortex. In the mid-1970s, several observations suggested that a more active suppression mechanism might also be important. Peter Spear and his colleagues (e.g. Kratz *et al.*, 1976) showed that removing the non-deprived eye could restore some responsiveness to the deprived eye, while Frank Duffy's group (Duffy *et al.*, 1976) reported that bicuculline (which blocks the inhibitory neurotransmitter GABA) could also restore responsiveness in the cortex. It had become almost traditional for important new results to become embroiled in controversy, and both of these findings rapidly did. In retrospect it seems that there is indeed a suppressive component to the cortical effects of monocular deprivation, but that it is only secondary in importance to the "deafferentation" that accompanies the deprivation effects.

Studies of development

A less dramatic but productive research area that started up during the middle 1970s concerned studies of the *behavioral* development of visual function (reviewed by Mitchell and Timney, 1984). Richard Held and his colleagues at MIT had studied the influence of early experience on the development of visuomotor function, and developed some basic techniques for analyzing visual behavior in young kittens. The operant methods available for studying visual function in adult cats had been developed to a highly sophisticated level by people such as Mark Berkley at Florida State and Randolph Blake at Northwestern. But it was Don Mitchell's decision to use an adaptation of the Lashley jumping stand that made it possible to study visual function in very young kittens, and opened up the possibility of doing *parallel* behavioral and neural studies of development. Figure 7 shows the apparatus (Mitchell *et al.*, 1976). By simply manipulating the patterns on the two cards at the bottom, and the height of the stand, effective control of the stimulus could be obtained.

T.M.: I visited Dalhousie (where Mitchell had moved) several times in 1976 to do some collaborative experiments with Don and Max Cynader, and during the first of those visits Don introduced me to the thoroughly charming business of running kittens on the jumping stand. The *Methods* sections of jumping-stand papers are always written to sound suitably stern; people talk about opening the trap-doors (see Fig. 7) to let the kittens fall through if they make errors, and so forth. In reality, Don was far too soft-hearted to actually *use* the trap door, and I don't think I ever saw him do it. If a kitten was not performing reliably, Don would charm and cajole the animal into a suitable state, and things would move smoothly along. Some people have complained that few other groups have been able to make the jumping stand work as reliably as Mitchell's can, and I've always thought that this is because it is much easier to describe rules governing the administration of reward and punishment than

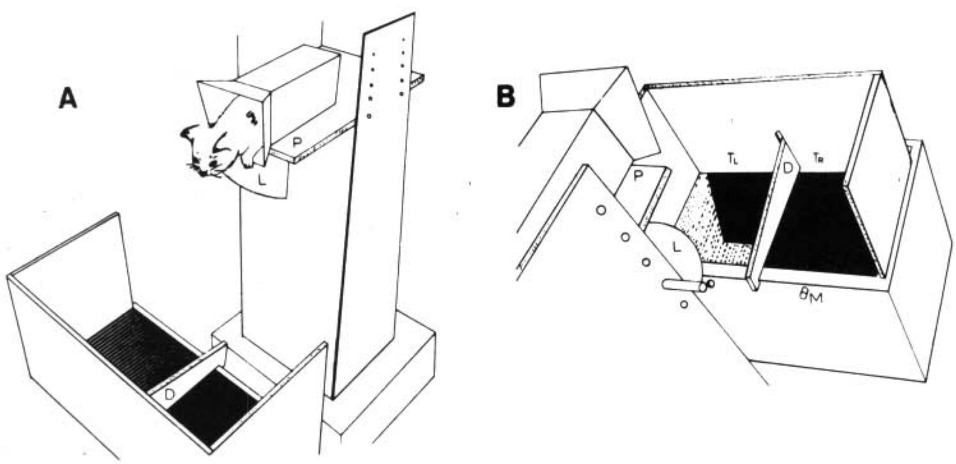

Fig. 7. The Lashley/Mitchell jumping stand, with the (unused) trapdoor. Reprinted with permission from Mitchell *et al.*, 1976.

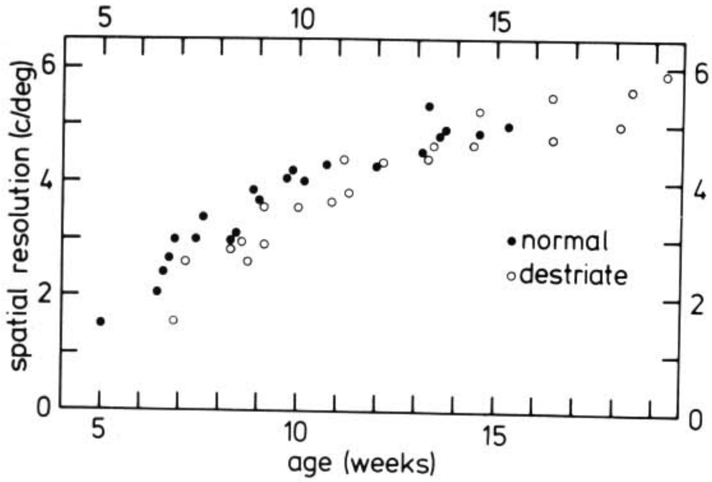

Fig. 8. The development of grating acuity in normal and destriate kittens. Obviously the visual cortex is not a necessary condition for the normal development of visual acuity. Data supplied by Donald Mitchell (personal communication).

it is to objectify the process by which a kitten* can be cajoled and charmed into doing its best.

The availability of the jumping-stand stimulated a new interest in the relationship between the development of neural function and the development of behavior, with occasionally startling results. For example, Don Mitchell and his co-workers (Kaye *et al.*, 1981) studied the development of visual acuity in kittens whose striate cortex had been completely removed shortly after birth. The results of this study (for example, Fig. 8) threw a very substantial spanner into the developmental works, for they showed that acuity development proceeded quite normally in these animals. Those who would believe that the striate cortex was the seat of visual performance on acuity tasks, and that studies of striate cortical development were, *de facto*, studies of the neural basis of visual performance, could take little comfort from these data.

Another interesting comparison could be made between Mitchell's data and the physiology. As far as was known, the development of the receptive field properties of kitten cortical neurons was essentially complete by the age of six weeks or so. By that time, almost all visual cortical neurons have receptive fields that cannot easily be distinguished from those in adult animals. But studies of acuity development typically showed that acuity at six weeks was distinctly poor, and that its development proceeded for another three months or so before adult levels were reached. Studies of the development of the kitten's optics conducted around this time in Ralph Freeman's lab in Berkeley (e.g. Bonds and Freeman, 1978) revealed no ready optical explanation of this effect. Several groups then proceeded to make accurate measurements of the development of spatial resolution and contrast sensitivity in kitten neurons. These revealed that quantitatively assessed receptive field properties (as opposed to the qualitative descriptions available before that time) revealed a developmental time course that matched the behavioral data. Subsequently, a number of interesting studies of retinal development initiated in Mark Dubin's laboratory in Colorado have revealed two phases in this process. During the first few weeks of life, the receptive fields of kitten ganglion cells appear to refine themselves on the retina, presumably by reducing the effective extent of their dendritic arbors. Later in development, the effective spatial resolution of the fields *on the retina* does not change greatly; instead, the effective resolution of the cells is a consequence of the growth of the eye, which makes the resolution of the fields *in the image* improve greatly. More recently, Mastronarde *et al.* (1984) have shown that the retina grows unevenly after birth, in a way that serves to improve spatial resolution in the central retina much more than in the periphery. This is reminiscent of some of the processes of retinal development in primates, where the fovea is known to be a relatively late-developing feature of retinal organization.

*Or an infant (D.T.).

These and other studies of the *normal* development of the visual system should probably have preceded, rather than followed, studies of the effects of partial or complete deprivation. Indeed, if one were to take Wiesel and Hubel to task for anything, it is for introducing to the field the notion that the visual system's developmental plasticity could be studied before its normal development was more fully understood.

Neuroanatomical studies

Hubel and Wiesel's interest in both the normally and the abnormally developing visual system had shifted during the early 1970s from cats to monkeys, and from neuronal properties to functional architecture. Their work in this period (e.g. Hubel *et al.*, 1977) revealed that monocular deprivation had striking effects on the neuroanatomical distribution of inputs to the cortex from the two eyes. While in a normal monkey inputs from the two eyes to layer IV are arranged in alternating bands of roughly equal size, after monocular occlusion the bands associated with inputs from the deprived eye are markedly contracted, while those from the non-deprived eye expand in complementary fashion. They also observed that in young animals, the ocular dominance columns seemed to be more poorly defined than in older ones. In a striking tour-de-force, Pasko Rakic (1977) showed that inputs from the two eyes to the cortex were completely overlapped in fetal monkeys, and began to segregate a few weeks before birth, but were not properly formed into adult-like eye dominance columns until some weeks after birth. Simon LeVay *et al.* (1978) analyzed this segregation in the cat's visual cortex and showed that a similar sequence took place there. These anatomical results revealed clearly and directly some of the cellular events that underlay the formation and maintenance of cortical eye dominance, and opened up a new set of tools for studying development generally. Powerful new anatomical techniques are being developed at an altogether alarming rate, and their application to developmental questions is one of the most promising trends of the recent past.

Experimental amblyopia

Another area that has blossomed in recent years is the study of animal models of human amblyopia. The well-documented effects of monocular occlusion form a very satisfactory model of the amblyopia that follows deprivation in humans, and in the mid-1970s, we seemed to be well on our way to understanding the mechanisms that produce this clinical condition. However, as our clinical colleagues continue to point out, while occlusion studies are interesting, the most common and difficult forms of amblyopia in humans are those that follow early strabismus or anisometropia—what could we tell them about *those* conditions? Following von Noorden's lead, Ronald Harwerth and his colleagues at the University of Houston, and Ronald Boothe and his colleagues at the University of Washington (and now at Emory University) have developed and studied what appear to be valid monkey models of both of these forms of amblyopia (Harwerth *et al.*, 1983a, b; Boothe *et al.*, 1982). There are important differences between these conditions and simple deprivation in a number of respects, and it is becoming evident that the combined application of behavioral, anatomical and physiological techniques can reveal important aspects of the mechanisms of amblyopia.

Recently, for example, one of us (T.M.) in collaboration with Anita Hendrickson and Ron Boothe, has been conducting cross-disciplinary studies of a monkey model of anisometropic amblyopia (e.g. Kiorpes *et al.*, 1986). These studies show that the neural changes underlying this form of amblyopia can be *qualitatively* rather than merely *quantitatively* different from those associated with deprivation. For example, it has been commonly supposed that the neural basis of amblyopia would be related to the eye dominance shift in the cortex that Wiesel and Hubel first described. But some of the anisometropic monkeys show no detectable shift in cortical eye dominance; the feature that they share is a degradation in the spatial properties of cortical neurons driven by the amblyopic eye.

In addition, it is no longer necessary to rely entirely on artificial means to create amblyopic animals: Lynne Kiorpes and Ron Boothe (1981), with the cooperation of the Washington Regional Primate Center, isolated and studied a substantial group of *naturally* strabismic monkeys, and showed that they, like strabismic humans, are often amblyopic. These animals are still involved in a breeding program, so none have yet come into the hands of the anatomists and physiologists, but we may be sure that studies of their visual physiology and anatomy will emerge, and shed new light on the mechanisms of amblyopia.

Neither of us is really fit to judge impartially the present state or future prospects of the monkey models of development and amblyopia: D.T. was instrumental in sponsoring development of many of the techniques and paradigms for infant monkey work in the first place, and T.M. is committed to an extended study of monkey models. But infant monkey work seems to be the best avenue available with which to study the development of visual *function*, and the way in which visual behavior and visual neurobiology are related. We cannot but feel that its importance for understanding the development and functional organization of both the normal and the abnormal visual system will be very great.

TOWARD THE FUTURE

It is edifying to compare T.M.'s views of the physiology of visual development with D.T.'s views of human developmental work. T.M.'s picture of the physiology—wild with exuberance, unreplicable results, weird and wonderful expriments—makes it seem like a bumptious child next to D.T.'s picture of the methodical, slow and relatively steady progress of infant vision research. This contrast has many origins.

Of most fundamental importance are the well-established history of visual psychophysics and the regularity of the process of development itself. In the study of normal development, at least initially, the canonical questions have been set by the history and the commonly accepted knowledge base of visual psychophysics, in combination with the implicit acceptance of McKee's first law. During normal development nature is playing out the assembly of a superbly coordinated design, and it is as though the scientist's first job is merely to stand back and measure the emergence of its canonical functions. So we could not help but ask, by what time course does grating acuity improve? What is the earliest age at which each receptor type can be shown to be functional? When does stereopsis come in?

In deprivation, on the other hand, there are no obvious canonical questions, especially if the normal course of development is unknown or ignored. There are instead a large number of possible ways to interfere with the normal course of development, and a large number of ways that epigenesis can fall apart when forced off its natural landscape. In fact, now that some of the broad outlines of the normal emergence of specific visual functions are known, it may be possible to use this knowledge to design more intelligent deprivation experiments, and thereby to gain some guidance in the search for sensitive periods in which deprivations of highly specific visual inputs could lead to highly specific visual disorders.

A second factor is the enormously increasing diversity and novelty of methods and tools that the neurobiologist has been able to bring to bear on his questions during this era. Although single-unit recording has always been central to the field, a physiologist can always rely on the pace of modern technical advances to provide a new handle on a problem. The modern laboratory computer now allows us to obtain reliable data in situations that would be impossible otherwise. Our neuroanatomical and neurochemical colleagues are forever coming up with another antibody, or tracer, or metabolic marker, or transmitter blocker that we can use to try to dissect the function of the systems we study. Indeed, the diversity of methods can be two-edged. The problem is often to avoid being seduced by the plethora of techniques available, and to choose the ones that can provide meaningful answers to the questions we ask. And there is always the danger that, since our understanding is by definition incomplete, a new method will give us an odd answer and send its users baying down a blind alley.

Behavioral research on infants, in contrast, has been largely confined to a small range of generally conservative techniques, usually one or another variant of forced-choice preferential looking. Although this technique is almost insufferably slow at times, the staring behavior that forms its basis is an extremely reliable phenomenon, and the logic of forced-choice data collection involves few wayward assumptions. Both VEP and OKN techniques have also generally been used with taste, and are currently coming into their own in highly sophisticated forms. On the other hand, the differences sometimes seen when even *two* substantially different techniques—preferential looking and visually evoked potentials—are brought to bear, make us shudder at the inevitable consequences of the development of a broader variety of techniques in the future. Things will get worse before they get better.

A third important and related factor is that in physiology, for better or for worse, data have been relatively cheap to collect. It is not—or at least used not to be—terribly effortful to run a few kittens through this or that experiment just to see how things would work out. Even now, a pilot experiment in a new area can be undertaken relatively easily. But in infancy work, where the dominant techniques have been slow and the overhead of each experiment is enormously high, data come very expensively indeed, and a very cautious selection process is forced on each new project. This kind of caution and forethought may become a more prominent feature of the physiology as it matures; perhaps the difference is that the infancy research was forced to be mature almost as soon as it was born.

Fourth, individual personalities are obviously at work. In the physiology/deprivation field, there have been many research groups, and it has somehow always seemed important for each group to establish its own identity—its own special "line". The level of paranoia has always been high, probably because there has been a real risk of being "scooped" in physiology. In the bad old days of 1974, I (T.M.) approached a well-known developmental physiologist about the possibility of doing postdoctoral work in his laboratory. I arranged to visit, and after a suitable exchange of pleasantries I asked, "So what experiments are you working on at the moment?" The response came back instantly, "Does Macy's tell Gimbel's?"

In contrast, for whatever reason, there has in general been a high level of cooperation and communication among infancy researchers in different laboratories. There have been some quarrels—most notably between Dick Held's group and my own (D.T.)—but in general these have had more to do with logic and methodological details than with empirical substance; D.T. has made a major nuisance of herself, for example, by insisting that an acuity estimate has a standard error of measurement, and that the standard error for all discrete trial techniques (including all staircase rules) is governed by the slope of the psychometric function and the square root of the number of trials (e.g. McKee *et al.*, 1985).

And finally, we voice the suspicion that to some degree disorder is in the eye of the beholder, and that had T.M. been in infancy work and D.T. in physiology, the fields might have been described in more nearly similar, or even opposite, terms. But there's a chicken-and-egg problem here, too. The things that drew D.T. into the study of development would have seemed terribly stolid to the T.M. of the time; the issues that excited T.M. and motivated his work in deprivation would have struck D.T. as fanciful at best, irresponsible at worst. So did the people make the fields, or did the fields attract the people?

T.M.: As I trace my own history, and the way it colors my portions of this piece, I see an initial enthusiasm for developmental research acquired in the heady days of 1972, which carried me through and beyond my doctoral work. A period of disillusionment followed in the later 1970s, when the potential of the available methods appeared to be exhausted and the field was mired in seemingly inexplicable conflicts; it seemed much more worthwhile then to pursue studies of the adult visual system. But in the last few years, my enthusiasm for developmental work has been rekindled. New quantitative approaches to developmental physiology are now in wide use and provide much richer, more robust and more reliable data than we could have hoped to obtain a decade ago. Striking advances in neuroanatomical techniques are being applied with precision and skill, and are becoming more and more interpretable and more and more closely linked with the physiology. Other advanced techniques from molecular biology are making their way forcefully into developmental neurobiology, and have begun to have an impact on visual developmental work. Sophisticated behavioral techniques now make it possible to obtain startling amounts of accurate data from both normal and specially-reared animals.

Equally importantly, my reasons for engaging in developmental work have shifted. When I first became interested in development, the great issues that motivated me were the classical ones of nature and nurture, genes and environment, in the same way as they motivated Dick Held, Torsten Wiesel, and a host of others. Now I find myself much more aligned with D.T.'s posture. I believe that the central problem in the study of vision is to understand the relationship between the activity of elements of the nervous system and the act of seeing. The study of development adds an important new dimension to this quest. It's not that I am no longer interested in the grander questions, but I no longer believe that the pieces of the field of developmental neurobiology to which I can contribute are going to provide the definitive answers to them.

D.T.: In the study of infant vision, I think we now have enough data accumulated that it is time to review it seriously with respect to my original purposes. This year at the Optical Society meetings I will be organizing a symposium on infant vision. The papers will be given not by infancy researchers but by "adult" visual theorists, who have been asked to address two questions: *In what way do the infancy data, as they presently stand, constrain models of vision?*, and conversely, *In what ways can "adult" vision models be used to understand the infancy data?*

The convergence of purpose that has come to light during the writing of this paper also brings a smile. In response to an early draft, my old rival Dick Held writes "... I feel strongly that we are at the stage where we can transcend the question of whether or not we can obtain data and demonstrate basic function. I think we are, and will continue to do more in the direction of making original contributions to basic visual science ... I confess that I didn't think this way only a few years ago. What has convinced me are studies like those of Banks and Dannemiller on contrast sensitive channels which demonstrate a presumptively genuine difference in the structure of the very young infant's visual system relative to the older infant. Here is a developmental process which is not just a quantitative change ... Shin's thesis is another case in point ... we are generating models which actually seem to predict new and unexpected results ... we are now raising questions which are taken seriously by animal workers and even neural scientists ... these developments are only a beginning and I am very optimistic about the future in this regard. I believe that you could be more assertive about the developmental studies of infants providing 'an orthogonal dimension'..."

Finally, what of McKee's Laws? Have we exceeded the descriptive and the obvious? Yes, and no. The First Law, that as children get older, they get better at things, no longer seems devastating. Different visual functions get better at different rates and in different epochs. A high critical flicker fusion frequency is evident in very young infants. So, probably, are all four receptor types, yet so far chromatic discriminations do not seem to be reliable until two or three months. Stereopsis and good vernier acuity apparently have their onsets between 3 and 6 months. Grating acuity development follows a long slow time course, apparently not reaching adult levels until 3–5 years postnatal, at least by behavioral measures. Also, deprivation studies tell us that if the visual environment is too weird, vision simply does *not* get better; and we must ask, under what range of conditions does the First Law hold? Furthermore, the idea that infant vision might be qualitatively different from adult vision, rather than just a reduced version of it, flies fully in the face of the First Law. So the First Law loses its sting; the data base is rich and complex enough to be interesting.

The Second Law has been generally ignored. Where sex differences have been sought in the development of acuity and color vision, they have generally not been found, and I (D.T.) am fond of saying that there is only one interesting sex difference.* However Held and his co-workers have recently begun to report differences, in the expected direction, in the onset of stereopsis, and we shall doubtless hear more on this topic.

In the Third Law still lies the rub. The problem is this: if everything develops in correlation with everything else, what form of experimental design can sort out the fundamental from the trivial correlations and lead us to discover *mechanisms?* The problem is made more difficult by the fact that communication between behavioral and physiological scientists has not always been tight. Researchers who have studied the development of visual function have chosen particular functions to study for particular reasons. Researchers who have studied development physiologically have chosen other functions for different reasons. The selection of experiments in each domain has been largely haphazard with respect to the other, and there has been little in the way of convincing theory to link the two. What, then, does it mean if a behavioral and a physiological function are seen *post hoc* to develop in correlation? It seems as though little can be concluded, unless the research is driven by systematic theory and/or predictive networks which include behavioral, physiological, and anatomical experimentation in the same domain.

EPILOGUES

D.T.: I would close by saying that it is a great privilege to have a career that brings such continuing excitement and joy. My only regret is that the sands have run more than half way through the glass. So many experiments ... so little time.

T.M.: "D.T.—Sorry this is late again ... I, too, have found a quote, which I'd like to see

*I concur (T.M.).

worked in if you can think of a good place for it."

> "...a scientist must also be absolutely like a child. If he sees a thing, he must say that he sees it, whether it was what he thought he was going to see or not. See first, think later, then test. But always see first. Otherwise you will only see what you were expecting."
>
> Douglas Adams
> *So Long and Thanks for All the Fish*

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