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ANTON JULIUS CARLSON

(Reprint from "The Physiologist", Vol. 2, No. 2, 1959)

Dr. Anton Julius Carlson (1875-1956) was a great man, a "scientist's scientist" and the "common-man's scientist." He was a preeminent leader in physiological, educational and civic activities. The influence of a zeal for the truth, a critical judgment, a colorful personality and dynamic teaching has nowhere been better exemplified than in the life of Dr. Carlson. He began at the bottom of the hill; and by his industry, his tenacity of purpose and his talents, he climbed the rugged path which leads to the top of the hill where repose those who have served mankind well.

Dr. Carlson was born in the hill country near Goteborg, Sweden. At seven he was hired by a neighboring farmer for whom he herded sheep and goats in the hills. He observed the shining granite hilltops and wondered who had climbed there to polish them. From a wise and affectionate mother and a teacher of manual training he developed an ambition to know. In 1891, as an orphan of 16 years of age, he followed his brother Gust to the U.S.A. where he worked as a carpenter in Chicago. Within several months his Swedish Lutheran pastor recognised the abilities of the youth and urged him to attend Augustana Academy and College. He entered the Academy in 1892 and as a result of his industry and talents received the B.S. degree in 1898, and the M.S. degree in philosophy in 1899. Not long thereafter his goal of becoming a minister was abandoned, even though it is said that he was a good preacher. He could not rid his mind of his love for Nature and his curiosity regarding living things he had acquired as a boy shepherd. It was only in the field of biological science that his boyhood hunger for learning could be gratified.

He attended the graduate school at Stanford University in 1900, and became an Assistant in Physiology in 1901. He received the Ph.D. degree in 1902. He received a Carnegie fellowship and worked at Woods Hole, Mass., in 1903-04. In 1904 he moved to the University of Chicago to join Jacques Loeb, G. N. Stewart and A. P. Mathews in physiology, pharmacology and biochemistry. In those days it has been said that when Prof. A. P. Mathews proposed a brilliant theory or explanation, Loeb said "Let me have some paramecia," Carlson said, "Bring me a dog," and Stewart said, "Yes, let's do an experiment." Dr. Carlson became Professor and Head of the Department of Physiology in 1914. He retired in 1940, but remained active in lecturing, research and civic affairs until about 1955.

Besides teaching some 5,000 medical students, he took part in graduating 151 students with the degree of M.S., and 112 students with the degree of Ph.D. in Physiology. Between 1910 and 1940 he probably gave post-graduate lectures to some 100,000 physicians.

In 1905 he married his college-days sweetheart, Esther Naioma Sjogren,a splendid woman and an affectionate mother. They had three children. The older son, Robert, is a businessman in California, the younger son, Alvin, is a chest surgeon in California. The daughter,

Alice, married Professor Hough of the University of Illinois.

In World War I Carlson served as a Lt. Col. in the Sanitary Corps of the A.E.F. He was assigned the task of reorganizing the diet of the fighting soldiers at the front and the methods of handling food. On one occasion he said that "if it is true that soldiers fight on their stomachs, then to win the war you had better keep their stomachs adequately filled with good food. Good food and ammunition are on the par." The dietary allotment was increased. After the War he worked with the American Relief Commission in charge of food relief for the war stricken peoples of Europe. This experience along with his observations of the European politicians at Versailles embittered him against war. Prior to World War II he said: "War is futile. One war serves only as a basis for another war." On another occasion he said: "The dictator screams: 'We think with our blood!' and men cheer. New faith, new formulae, new fetishes, new saviours via the sword spring up over night from troubled soils, and with the same old clay in their feet, and with the same old sawdust in their skulls. Science and violence are incompatible."

Dr. Carlson served the American Physiological Society in numerous capacities. He was elected a member of the Society in 1904. He was Secretary from 1910 to 1914, and a member of the Council from 1921 to 1922 and again from 1928 to 1932. He served as President from 1923 to 1925. He was Chairman of the Board of Editors of Physiological Reviews from 1932 to 1950. He was primarily instrumental in persuading the International Committee of Physiologists to hold the International Congress in Boston in 1929.

When he was the President of the Society two very amusing incidents occured. In 1923, Herr Geheimrath Professor Biedl visited the United States and attended the annual meetings of the Society. At this period of the Society's history the adrenals were stirring the emotions of many physiologists and there was no time limit on discussion. Carlson was having great difficulty in controlling the discussion. After a half-hour of discussion Prof. Biedl arose and spoke for twenty more minutes. Then a physiologist of the opposition insisted on speaking. Then Biedl rose again and after speaking for about two minutes, Professor Carlson said: "Biedl you haf said dot vunce; sit down." In 1924, the meetings of the Society were held in a High School in Washington, D.C., where smoking was prohibited. Carlson and Macleod were inveterate pipe smokers. In the midst of the meeting a policeman entered the scientific session and arrested Carlson and Macleod for smoking, and when Dr. Meek, the Secretary of the Society, intervened he was arrested for permitting Carlson and Macleod to smoke. The members of the Society who were present and witnessed this comedy and farce had "pain in the sides" from laughing so much. And, the more they laughed the greater the anger of the policeman and the perplexity of Carlson, Macleod and Meek. The policeman asked Carlson to speak English; he told Macleod that a physiologist should know better than to use tobacco; and then he walked away with these three masters of debate in custody after telling them that "ignorance of the law is not a defense."

Dr. Carlson served as president of several other scientific and

educational organizations, such as the Union of American Biological Societies (1940-43), Society of Experimental Biology and Medicine (1943), National Society for Medical Research (1945-53), American Association for the Advancement of Science (1944).

When he was President of the American Association of University Professors (1937), his activities were referred to as "Carlson in the Den of Deans." At one of the many meetings of Professors he addressed, he said: "I don't look up to Deans; I don't look down on Deans, I yust look at 'em." On another occasion he was invited to take part in a discussion of the place of science in liberal education. The representatives of the humanities predominated in number and had spoken for two hours. When his turn came he arose and said, "To listen to some of the palaver of you sobersides of academic sophistication yust give me the yim yams." At many such meetings he created consternation by rising to inquire: "Vot is de effidence?" When a former President of the University of Chicago, Robert M. Hutchins, very provocatively proposed that all academic tenure be eliminated because "it would keep all the professors on their toes," Dr. Carlson arose and said: "Mr. President, you made a mistake. Vot you mean is dot it vill keep dem on their knees."

He frequently spoke to lay audiences on almost any subject. At a large civic gathering in Kansas City he was debating the subject of mental telepathy with a practitioner of the art. The telepathist said: "Now, I shall give you an example of an actual occurrence of mental telepathy which occurred this morning. My mother lives in New York City and this morning exactly at 9:00 a.m. I felt that she urgently needed me. Later today I received a telegram stating that exactly at 9:00 a.m. this morning my mother fell and broke her leg. Now, Dr. Carlson, what do you think of that?" Carlson replied: "What about the one hour difference in Eastern and Central Standard time?"

A class period rarely passed without Carlson making some pungent but amusing critical remark to a student. On one such occasion a girl held an electric wire in her hand trying to stimulate a frog's muscle lying in a pool of salt solution. Carlson said to her: "Vake up! You might as vell try to stick your electrode in the Atlantic Ocean and stimulate Ireland." A student with a bibliographic memory was asked a question by Dr. Carlson. The student responded. Carlson said: "Vare did you read dot? In de Sunday fiction sheet?" The student started to defend himself with vigor. Carlson said: "Vell you should have been a lawyer." The student responded with still greater vigor. Carlson said: " I made a mistake. You should have been a Captain of Industry." In another case a second-year medical student who had really studied the relation of the vagus nerves to the stomach questioned a statement made by Dr. Carlson, and proceeded to present his supporting evidence. Dr. Carlson listened intently, took the student to a research laboratory, and said that the space was vacant and that the student could start to experiment on the vagus nerves in his spare time. He further informed the student that there was a scholarship waiting for him at the office of the Dean of the Graduate School, if he needed it. The student is now a well-known physiologist.

Dr. Carlson inspired his students more than most teachers to know the truth by the keenness with which he separated fact from fancy and the vigor with which he sought "de effidence." Students soon learned that behind his scornful frown and pointed criticism there was a kind heart and an abundant generosity for those who were intellectually honest and willing to work.

In medical meetings his rugged aggressive method of criticism was convincing and amusing to all. He frequently arose to criticize when others present desired to criticize but did not have the courage to do so. An illustration of such an occasion occurred at the meetings of the International Congress in Stockholm in 1926. Dr. Serge Voronoff, a surgeon and a famous specialist in monkey-gland transplantation, presented a paper on rejuvenation. He was the last on the program, but many out of curiosity remained to see the show. After Dr. Voronoff's presentation ended, you could have heard a pin drop. Everyone present was waiting for his neighbor to arise and offer criticism. Several looked at Carlson who arose and said: "I know of the case of a man in the United States who had a monkey-gland transplant by a surgeon. After the operation this man felt very young until he receifed the surgeon's bill. Dot vas so high he suddenly felt old again." The meeting ended in an uproar. A bearded French physiologist rushed up to Carlson, embraced and kissed him.

Dr. Carlson's technique of criticism, his wit and humor amplified by a Swedish accent left indelible imprints on the minds of those in his audience. The remarkable fact is that less than ten percent of those whom he criticized and at whose expense he created laughter resented his criticism; and few were embittered.

In his criticism, he rarely meant to hurt. He meant to hurt only the bluffer, the sophisticated and the ostentatious. Even after he had criticized Dr. Voronoff, he asked a colleague whether he had been too severe. In the "privacy" of his laboratory or classroom he was often amusingly severe when some manifestation of stupidity occurred. But, when the mistake was an honest one or the student or colleague rationally explained the mistake, Dr. Carlson would apologize by his facial and bodily expressions, rarely with words. On occasion he would severely criticize some laboratory assistant who had made a mistake because of lack of sleep due to working to make his financial ends meet. Then a few hours later he would loan the student a hundred dollars or more.

His granite-like outspoken intellectual honesty, however, had an Achilles heel. On very rare occasions he was known, when human relations only were involved, to tell a "white lie" to protect a colleague, for whom he had great affection, from embarrassment and humiliation. This was so out-of-character and unartistic that the truth soon caught up with the matter. On one such occasion tears appeared.

No field of physiology escaped Dr. Carlson's investigative skill. This was due to his breadth of interest in biology, the fact that he did not deter a student from investigating his own ideas, and the fact that he had to teach the entire subject of physiology to medical students.

The results of his first major research revealed that the velocity of transmission in a nerve is correlated with the rate of contraction of the muscle it innervates. In a study of the nature of the conducting mechanism in the nerve fiber, he used a nerve-muscle preparation with a nerve which in normal life underwent considerable lengthening and shortening. He found that when the nerve trunk was shortened less time was required for a nerve impulse to pass from the point of excitation to the muscle than when the nerve trunk was elongated. His interest in the nerve impulse led him into the polemic on the origin of the heart beat, a problem which received much attention during the first two decades of this century. Using the horse-shoe crab (Limulus) in which animal a collection of nerve cells are located near to but outside the heart and sends axones into the heart, he found that after the removal of these nerve cells the heart would not spontaneously or automatically contract and relax. Though the crustacean heart muscle more closely resembles skeletal muscle physiologically than that of mammalian heart muscle, Dr. Carlson's discovery provided an outstanding example of automatic rhythmicity in nerve tissue, and provided strong support of the neurogenic theory of the origin of the heart beat. His study of lymph formation and flow during salivary secretion represents a classical contribution to the physiology of the secretory process. He early entered the field of endocrinology and became interested in the thyroid because prior to 1925 about 98% of the dogs in Chicago had goiter. He and his students rechecked much of the literature on all the endocrine glands, separating fact from fancy. In a study of extirpation diabetes, he found that the foetal pancreas near term can apparently function in part for the diabetic pregnant dog. In 1912 a student in his laboratory had insulin in a test tube, and in 1919 another student again had it in a test tube. A spirit of a too rigid self-criticism prevented the development of these discoveries. His largest series of investigations culminated in "The Control of Hunger in Health and Disease," which today remains a classic contribution to the subject. Every student of the visceral sensory nervous system is acquainted with his contributions to this basic area in physiology. In later years he made contributions to the subject of aging and alcoholism.

Dr. Carlson was a critic of the character of our more recent educational process in the home and at school. He complained that our young folks have no "granite in their bread." "Science in schools and colleges is a quiz-kid program. Our young children have a wise stage during their development - the stage when they are everlastingly asking why that is so, and how this or that thing happens. And we drown them with facts and more facts. The result is that we educate out of them the fund of mental curiosity with which they are born." He said: "Medical students and physicians become robots or IBM machines which can regurgitate complicated information but cannot think originally or creatively or digest and absorb new ideas unless such ideas are taught to them as a fact by some authoritative source. Thoughtless conformity and to-always-please are the major sins of today."

At the Fiftieth Anniversary of the American Physiological Society, Dr. Carlson said: "Some of my colleagues, particularly those of advancing years, see clouds ahead on the score of the number and the

caliber of men and women we train annually in our laboratories for service in physiology.... Some even propose a control of recruits on the principle... of the guilds of the middle ages. I think this would be as wasteful and unfortunate as it is undemocratic.... In the first place, none of us can neither pick nor train genius.... I am reasoning on the ancient and formerly biologically sound and acceptable theory that we must create our own opportunities, that we must scratch for our living .... As I read history, all great achievements in science have come through the individual endeavors of relatively free men.... A regimented science is science in eclipse.... Is it not true that when men have bartered freedom for security, they have lost freedom without gaining a security worth having?"

Dr. Carlson never became bored or discouraged with life. He loved to work and work. He always was helping to carry several crosses for good causes, causes which would produce a better life for others and future generations.

His students called him Ajax. This appelation did not arise from signature A. J. C. Neither was it used as a witticism, but with respect and sometimes awe. This name was used as though Carlson was "AJAX" the only heroic figure from the past who never called on man or God for aid, but always fought his own way out of trouble. Ajax was a man of great physical stamina and strength of character, who was devoid of and an enemy of the shrewdness and intellectual dishonesty of a Ulysses.

INTERNATIONAL CONGRESS OF THE TRANSPLANTATION SOCIETY

The First International Congress of the Implantation Society will be held in Paris on June 27-30, 1967. It will be preceded by a colloquium on Organ Transplantation on June 26. For detailed information write to Prof. Ag. J. Dausset, Hospital Staint-Louis, 2 Place du Docteur-Fournier, Paris X^{e}, France.

FEDERATION MEETING
CHICAGO
April 16 - 21, 1967

The destruction of McCormick Place (Chicago's Convention Hall) by fire on January 16 produced many problems since the Federation was counting on using facilities at McCormick Place. The Federation Convention Office, with the cooperation of many people in Chicago and in the Societies, has been able to make substitute arrangements.

Location of activities originally scheduled for McCormick Place: -

Federation Offices - Conrad Hilton Hotel
Registration - Conrad Hilton Hotel
Exhibits - Conrad Hilton and Palmer House
Placement Service - Sherman House
Women's Hospitality - Palmer House
Press Room - Conrad Hilton
Motion Pictures - Palmer House

Since the Federation was also counting on using a number of session rooms at McCormick Place especially for Symposia and Intersociety Sessions other facilities had to be obtained. Several of these needed session spots were obtained by all societies consolidating programs wherever possible and scheduling through Friday (21st) afternoon thus leaving session spaces for Symposia and Intersociety Sessions. We hope that all of those giving papers will not be too critical of where and when their papers are scheduled or of unavoidable conflicts. Shuttle buses will be available between hotels.

GASTROINTESTINAL GROUP LECTURE
April 20, 1967 - Palmer House

Dr. Pierre Desnuelle, Professor of Biochemistry at the Faculty of Sciences, Marseille, France will give the Seventeenth Annual lecture before the Gastrointestinal Group of the American Physiological Society on Thursday, April 20, 1967, during the Spring Meetings of the Federation in Chicago. His topic will be, "Adaptation of the Biosynthesis of Pancreatic Enzymes to Nutritional and Hormonal Factors." For further information write Dr. C. S. Tidball, Dept. of Physiology, George Washington Univ., Washington, D. C., 20005.

SPECIAL APS PROGRAMS
AT THE SPRING MEETING
April 16-21, 1967

SYMPOSIA

"Effect of Gravity on Heart and Lungs" - L. Dexter, Chairman

"Hydrogen Ion Exchange Mechanism in Different Organs and Tissues" - R. W. Berliner, Chairman

"Vasoactive Peptides" - M. Schachter, Chairman

"Mechanisms Controlling the Ionic Permeability of Synaptic and Non-Synaptic Membranes" - W. L. Nastuk, Chairman

TEACHING SESSION

"Impact of National Board Examinations on Teaching in Medical Schools" - W. D. Blake, Chairman

THIRTY-MINUTE INTRODUCTORY TALKS

"Alkali Cations and Formation of Hydrochloric Acid in vitro" - C. A. M. Hogben

"The Physiological Disposition of Norepinephrine" - J. Axelrod

"The Three Element Model of Muscle Mechanics: Its Applicability to Cardiac Muscle" - A. J. Brady

"Some Correlations Between Psychophysics and Neurophysiology" - V. B. Mountcastle

"Altitude Acclimatization" - R. H. Kellogg

"Excitation of the Ventricles" - A. M. Scher

APS
MEETING CALENDAR

1967 Spring - Chicago, Ill., April 16-21

1967 Fall - Howard Univ., Washington, D. C., August 23-26

1968 Spring - Atlantic City, N.J., April 15-20

1968 Fall - No Fall Meeting due to the International Congress

1968 International Physiological Congress - Washington, D. C., August 25-30

1969 Spring - Atlantic City, N.J., April 13-18

1969 Fall - Oklahoma State Univ., Stillwater and Univ. of Oklahoma Med. Ctr., Oklahoma City, Okla.

1970 Spring - Atlantic City, N.J., April 12-17

1970 Fall - Indiana Univ., Bloomington, Ind.

1971 Spring - Chicago, Ill., April 11-16

1971 Fall - Univ. of Kansas

APPEAL FOR ARCHIVAL MATERIAL

Now that the Central Office has its own quarters at Beaumont a library is available in which to keep and display interesting historical material about physiology, Physiological Congresses, the American Physiological Society, and its members. The Executive Secretary will welcome the receipt of any such material for permanent retention in the Society Headquarters.

NOMINATION OF APS OFFICERS

At the 1966 Spring Business Meeting of the Society a new method of preparing the nominating slate for officers was proposed by Council and adopted by the members attending the Business Meeting on a trial basis for 1967.

In order to avoid the time-consuming process of establishing a slate of nominees by repeated balloting at the Business Meeting and in order to permit a larger number of members to participate in the nominations for President Elect and for Councilman, nominations are to be made by mail. Members have already received, or will shortly, two different colored cards, a white card for President Elect nomination and a yellow card for Councilman nomination. A list of persons not eligible is printed on each card. In the case of the white card for President Elect the present President, President Elect and Past President names are listed. In the case of the yellow card for Councilman the names of the present Councilmen are listed.

The cards are to be mailed back to the APS Central Office before March 10, 1967. The nominating slate will be made up of those receiving 10 or more nominating votes. After the election of the President Elect the remaining nominations for President Elect will be added to the Councilman nominations.

This is your Society, please participate.

APPEAL FOR APS JOURNALS

The Central Office of the Society is continuing an attempt to secure back issues of its publications. We now have copies of all the APS journals except a few volumes of the American Journal of Physiology. We still need:

American Journal of Physiology
Vols. 51 thru 66
Vols. 96, 97, 98 and 99

If any person, member or non-member, interested in physiology has duplicate or unneeded copies of the volumes cited above they would do us a great service if any of the volumes could be made available to the Central Office of the Society.

XXIV INTERNATIONAL CONGRESS OF PHYSIOLOGICAL SCIENCES

August 25-31, 1968
Washington, D. C.

The 1968 International Congress of Physiological Sciences will be held at the Sheraton-Park and Shoreham Hotels in Washington, D. C., August 25-31, 1968. This represents one of the oldest international congresses in the biomedical field, and has been held every three years since 1888, with a few exceptions during the two world wars. The 1965 Congress was held in Tokyo, Japan. The last Congress held in the United States was in 1929 in Boston, Massachusetts. It has met only one other time in North America in Montreal, Canada in 1953.

This Congress is sponsored by the International Union of Physiological Sciences (IUPS). The adhering member of that Union in the U.S.A. is the National Academy of Sciences, which will sponsor the Congress with the support of the American Physiological Society and the Society of General Physiologists. The management of the Congress has been entrusted to a Secretariat in the offices of the Federation of American Societies for Experimental Biology.

The program will open with a plenary session on Sunday afternoon or evening, August 25, 1968. Scientific sessions will be scheduled on Monday through Friday, August 26-30, with the closing plenary session on Saturday morning, August 31. A daily series of short invited lectures on "Recent Advances in Physiology" will be an innovation on the program. From many suggestions for symposia received from Member Countries, the Program Committee will select, perhaps 20 for half-day programs. There will also be the usual invited lecturers and many sessions of contributed papers on all aspects of physiology and allied sciences. Rooms for informal discussion will be provided in close proximity to session rooms.

Physiologists and other scientists working in allied fields may become active members of the Congress by payment of the registration fee of $35.00. Members of the families of active members, who are not themselves scientists, may register for $15.00 as affiliate members entitled to participate in the social events of the Congress.

Plans are being made for a number of additional symposia, before and after the Congress, in various locations. The Visiting Physiologists Committee will do everything possible to arrange lecture tours or visits to American laboratories and points of interest on the American continent. Correspondence on that subject may be addressed to the chairman of that Committee, Dr. Chandler McC. Brooks, via the Secretariat. The scientific program will be augmented by tours of laboratories in the Washington area. Exhibits of pertinent laboratory equipment, apparatus, books and journals, and pertinent pharmaceuticals will be on display throughout the week of the Congress.

Limited funds for travel and subsistence expenses in Washington may be available to some registrants from abroad. It will be necessary,

however, for most registrants to obtain funds for travel from sources other than the Congress.

The social program of the Congress will open with a mixer on Sunday, August 25. Other social events will include dinners in private homes for registrants from outside the United States, sightseeing tours in Washington, a special opening of the National Gallery of Arts, and a Congress Reception. Additional events are planned for affiliate members.

A definitive announcement of the Congress will be distributed in October, 1967. This will provide the necessary forms and detailed information with regard to submission of abstracts, travel or subsistence allowances, advance registration and fees, hotel reservations, and plans for scientific and social programs.

The officers and committee chairmen for the Congress are as follows:

President	Wallace O. Fenn
Executive Vice-President	Maurice B. Visscher
Vice-Presidents	Philip Bard
	David W. Bishop
	Detlov W. Bronk
Secretary	Hermann Rahn
Committee Chairmen:	
Program	John R. Pappenheimer
Finance	Robert E. Forster
Visiting Physiologist	Chandler McC. Brooks
Local Arrangements	Frederic C. Bartter
Ladies Committee	Dr. Louise H. Marshall, chairman
	Mrs. W. O. Fenn, honorary chairman

For further information, please write to:

Secretariat
XXIV International Congress of Physiological Sciences
9650 Rockville Pike
Bethesda, Maryland 20014 U.S.A.

Telephone: (301) 656-2900

PRESIDENT'S MESSAGE

R. E. FORSTER

Spring Meeting

The burgeoning products of our investigatory enthusiasm continue to plague those of your representatives who are responsible for the organization of the Spring Meetings with the Federation (Physiologist 8:3-5, 1965). The accompanying graph (Fig. 1) shows the number of abstracts accepted for the Spring Meetings from 1948-1967 . The rate of increase averages about 3% per year and shows no sign of decreasing; rather the opposite. The number of papers actually programmed by the Society does not necessarily equal the number accepted, because some will be transferred to sessions of other societies and the APS will accept some papers transferred from other societies. The changes in the number transferred has varied primarily because of changes in the rules governing the submission of abstracts in the other societies. The Spring Meetings in 1967 will be the first in which more papers were transferred into the Physiology Sessions than transferred out. Also shown are the number of regular individual sessions for the same time period. This datum is actually more important than the total number of papers submitted because it is the number of separate sessions that determines the number of meeting rooms required. "Regular" sessions do not include symposia, which have averaged 5 per year over the last 5 years.

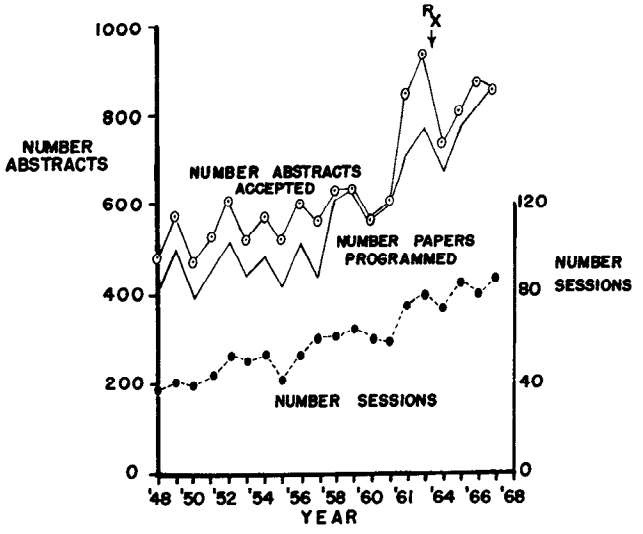

Fig. 1. Graph of total number of abstracts accepted by the APS (o-o) the number of papers actually programmed (———) and the total number of physiology sessions (●---●) for the years 1948 to 1967 inclusive. R_X indicates the institution of the restriction that a member's name can appear only once on the program.

This increase in the number of 10-minute papers submitted each year, in itself an encouraging indication of activity and interest in physiology, has this obvious disadvantage as a corollary, that the speaker-minutes must increase in proportion, unless the length of each presentation is shortened to less than ten minutes, which appears to be self-defeating. The number of speaker-minutes at the Spring Meetings can be extended by:

1. Increasing the duration of the Spring Meetings to more than five days. This expedient appears universally unsatisfactory.

2. Increasing the number of simultaneous individual sessions in physiology from the present level of about 9. Even now there are conflicts of interest with different topics being discussed at the same time and if the number of simultaneous sessions were to be increased, this would be exacerbated. In addition, the total number of rooms seating more than 200 that would be required would become greater than available any place but Atlantic City. Certainly the present number of meeting rooms demanded by the Federation is not available in any but two cities now.

3. Increasing the number of meetings per year. Obviously there could hardly be more than one Federation Meeting per year, but the Society could take more advantage of its present two meetings per year. The Fall Meetings are still relatively uncrowded and the membership should be encouraged to present their work there. In the more distant future, when the Fall Meetings become too congested, it should be possible to hold more than two meetings per year, or to have meetings of sub units of the Society, either geographical or topical.

Another alternative is to prevent the increase or even to decrease the number of physiological papers presented orally. Basically there are two approaches to doing this, an egalitarian and selective. 1) The egalitarian is based on the premise that each member has the unalienable right to present a paper at the Spring Meeting without review by his peers. Therefore, if there is to be any restriction on the number of papers presented, it must be a limit on the number of opportunities each individual member has to present a paper without considering the topic or quality of the paper. The Society, with its long tradition of democracy has always elected this approach, or rather has seized upon it as the least of many evils. 2) The selective approach holds that if the number of presentations must be limited, the better papers should have the privilege, the total number being set by the number of available accomodations. The problem arises in who is to do the selecting.

At the Fall Meeting of 1963, owing to the known limitations on meeting rooms in Chicago for the then forthcoming Spring Meeting of 1964, the Society voted to accept the following temporary restriction on their right to present papers: (Physiologist 6: 318, 1963).

"A person's name can appear only once (on the program). An APS regular, retired or honorary member must be one of the authors." In the Business Meeting in the Spring of 1964, the officers having had some

experience with the operation of this ruling and the membership having suffered under it, the Society voted to retain the restriction permanently (Physiologist 7: 45, 1964). The therapeutic effect of the restriction can be easily seen in Figure 1. The rate of increase has not been altered however, and even such continued self-restraint on the part of the membership will not solve the problem much longer and new measures will be required.

Possible extensions of the egalitarian solution are to limit presentations at the Spring Meetings to members only, and when that fails, to limit a member to the presentation of less than one paper per Spring Meeting on the average, for example to two papers every three years.

A selective solution has been applied by the American Society of Biological Chemists. Any member of that Society wanting to present a paper orally at the Spring Meeting in 1965 submitted twenty five copies of an abstract. These papers were grouped according to topic and sent to 15 to 20 members of that Society, who had previously agreed to act in this capacity, and ranked in order of their preference. Only those papers receiving the higher rankings were presented, although all were printed in the Federation Proceedings. About 40 per cent were not presented orally. This mechanism has the advantage of a large jury, but much may depend on the initial topic classification. There is of course a great deal of additional labor involved on the part of the panels and the executive staff. The procedure appears to have worked well in 1966 and is being applied again in 1967, however I hope you will make your own inquiries amongst your associates and see how satisfactory it appears, particularly to the junior people in the field. It is certainly possible that a member may have great difficulty getting an opportunity to present his work orally.

There is a possibility that if the membership of our Society were aware that quality judgments were going to be made about their abstracts, the papers would improve and some poorer ones might be withheld automatically.

It does not seem reasonable to expect that the number of papers will continue to rise at the same or a slightly increasing rate indefinitely. The population of the United States is not increasing this rapidly, nor is the financial support, and sooner or later the rate must slow down. It would be unfortunate to take solace in this comforting thought, because there are no indications that the end is in sight.

I hope that you will all give this matter your earnest attention. Any suggestions would be welcomed by Council.

Porter Programs

In 1921 Professor William T. Porter established an award supporting talented students training for careers in physiology. This award became known as the Porter Fellowship, was administrated by the APS and supported by funds from the Harvard Apparatus Company, which was also founded by Professor Porter. For many years this was one of a few scholarships available for predoctoral students in physiology, and was

highly sought after. Many distinguished scholars and teachers held it at one time. However, in recent years large scale government support of predoctoral training has made the Porter Fellowship less unusual, interest in it has lagged and the number of candidates has decreased. This led to special efforts on the part of the Porter Fellowship Committee and Council to alter the terms of the award in order to make it more competitive with government fellowships, but the results have not been entirely satisfactory. The need for this type of fellowship has decreased.

Therefore, after correspondence with the Harvard Apparatus Company, Council has established the Porter Physiology Development Program for the purpose of stimulating and assisting in the improvement of underdeveloped American departments of physiology, to take the place of the Porter Fellowship. The Harvard Apparatus Company has enthusiastically endorsed this change and has offered to increase substantially its financial contribution, supplying funds for the purchase of critical equipment as well as for stipends and training of staff. It also seems likely that considerable additional support can be obtained for this type of program from foundations. Unfortunately this means that the Porter Fellowship has come to an end after 46 years. Council has made this decision with the greatest reluctance and only after several successive Councils have become convinced that the fellowship program can no longer be maintained or transformed into a unique scholarship. Of course the present Porter Fellow will continue to receive support as agreed under the fellowship.

The Porter Physiology Development Program will be administered under a subcommittee of the Education Committee.

ELEVENTH BOWDITCH LECTURE

Effects of Distortion of Sensory Input on the Visual System of Kittens*

DAVID H. HUBEL

A prime objective of neurophysiology is to learn how cells in the nervous system function during the everyday and moment-to-moment activities of an organism. This amounts to learning how the brain is constructed and how the parts function when the organism perceives, thinks or acts. An equally important though perhaps less obvious objective is to understand how the structure and function of the nervous system are affected by the previous history of the organism. The ability to undergo long term alteration as a result of experience is an essential property of nervous systems of all animals, and in higher forms the very act of learning presumably involves such changes. To understand the nervous system one must sooner or later address both phases of the problem - the day-to-day functioning and the modification of function by experience.

In designing experiments one soon realizes that the two problems must be undertaken in sequence - that at least a sketchy outline of the everyday workings of the normal nervous system is necessary before there can be much hope of detecting effects of varied experience. One difficulty in understanding the function of neural structures arises largely from the extreme specialization of the nerve cells themselves. Of course it is well known that a structure like the cerebral cortex is divided into a number of areas, some concerned with audition, others with motor function, and so on. However, within any one of these, a given piece of tissue such as the cortical grey matter contains many classes of cells that are more or less intermixed. Different types of cells, and even cells in the same class which may morphologically appear the same, tend to respond to very special and quite distinct stimuli. This characteristic of the nervous system makes it profoundly different from any other tissue in the body, and arises from the intricate and highly organized interconnections between cells. The system is thus virtually inaccessible except at a single-cell level. Because techniques for recording from single cells have only been available in the last few decades, knowledge of how most parts of the brain work is still very scanty. The most rapid progress has been made in the spinal cord where relatively simple reflexes can be isolated, and in sensory systems such as the somatic, auditory, and visual, where one can study the responses of neurones close to the input end of the nervous system. The visual system, which concerns us here, has the advantage of a relatively simple and direct anatomical pathway from the retina through geniculate to striate cortex (Fig. 1): here it is possible to examine and compare cells from one structure to the next with the hope of reaching

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*The material from this lecture represents the condensation of work published in six papers (See references 8, 10, 20, 21, 22, 23).

some conclusions about how information is handled as the pathway is traversed.

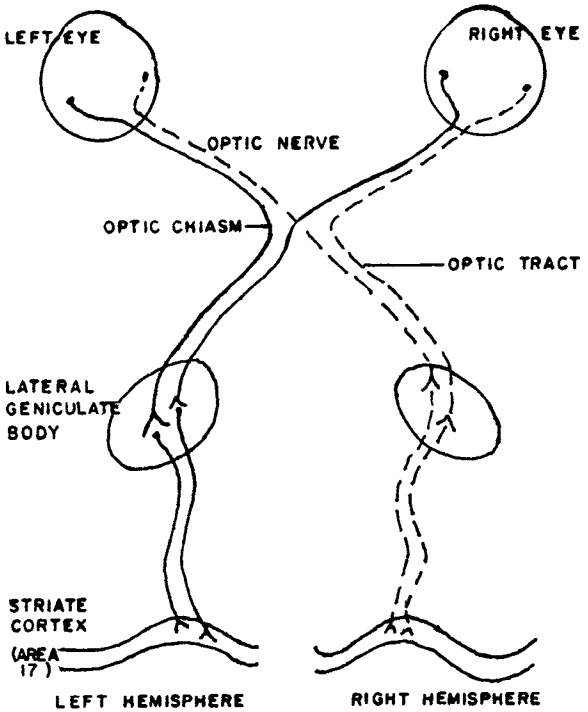

Fig.1. Diagram of visual pathway from retina to cortex in a higher mammal. Note that the left hemisphere receives its input from the two left half-retinas and hence from the right visual field, and that each hemisphere receives input from both eyes.

During the past 10-15 years a number of studies have been made at various levels in the vertebrate visual system (1, 2, 3, 6, 9, 11, 12, 13, 14, 15, 24, 25). Our own work in normal visual physiology has been done mainly in the cat and monkey, and provides a background for a series of experiments in animals deprived of normal visual experience. To make these deprivation experiments understandable it is necessary to start by summarizing some of this work on the normal cat.

NORMAL VISUAL PHYSIOLOGY

In trying to understand the normal visual system we begin by examining how a single cell in the pathway is linked to the environment. How, by its connections to retinal receptors, does a cell "see" the outside world, and what combination of retinal stimuli will best activate the cell? In a typical experiment we record from single cells or fibers at various points in the visual pathway and stimulate the eyes with light.

The cat or monkey is anesthetized, its head is fastened securely in a stereotaxic apparatus, and the eyes are held open and face a large white screen at a distance of 1-1/2 meters. The stimulus consists of lights or shadows varying in size, shape, or wavelength projected on the screen and hence onto the two retinas, which can be stimulated together or separately. An electrode consisting of a fine wire insulated to within 10 - 20μ of the tip is inserted into the retina, optic nerve, or brain, until it comes close enough to a single cell or fiber to sample the small extracellular currents associated with the all-or-none impulses. In any particular recording situation the relative constancy in size and shape from one impulse deflection of the oscilloscope to the next provides the evidence that the electrode is recording from one cell body or axon.

We then observe the effects of stimulating the retina upon single elements in the visual system, and try to determine the optimum stimulus for each cell. Having observed one cell for a few minutes or hours, we advance the electrode and study others, going from cell to cell along a straight line path. Electrolytic lesions can be made at 2 or 3 points along a track, so that later when the brain is sectioned in the plane of the track the positions of all the cells studied in a penetration can be determined. A cell's behavior can thus be correlated with its anatomical position.

Responses of Single Cells in Visual Cortex

In the visual cortex, as in other areas of the central nervous system, cells are extremely specialized. The great majority give practically no response to an abrupt increase or decrease in the total illumination of the retina. This comes at first as a surprise - it seems natural to expect that a stimulus capable of activating all of the retinal receptors should have a powerful influence on any visual cell. The reasoning of course fails because the visual pathway presumably contains inhibitory as well as excitatory synapses, and the effects of simultaneously stimulating different sets of receptors can cancel one another with unexpected precision.

Nevertheless, if the stimuli are properly chosen, all cells in the striate cortex can probably be influenced, and most can be made to fire vigorously. Each cell responds only to stimulation of a limited retinal region called the receptive field of the cell, and ignores stimuli applied outside this region. The receptive field of a cortical cell in the cat may be as small as about $1/2^{o}$, or about 125μ on the retina, or as large as 10^{o}. Presumably the rods and cones outside the receptive field have too few connections, or connections that are too indirect, for them to have any easily detectable effect on the cell.

Uniform illumination of the cell's receptive field then, is without any appreciable effect on the cell's firing, since this amounts to the same thing as diffusely illuminating the retina. More specific stimuli must be used to make the cell respond. It turns out that for most cells the receptive field must be crossed by some kind of straight-line stimulus. The line may be made up of a bright slit on a dark background, a

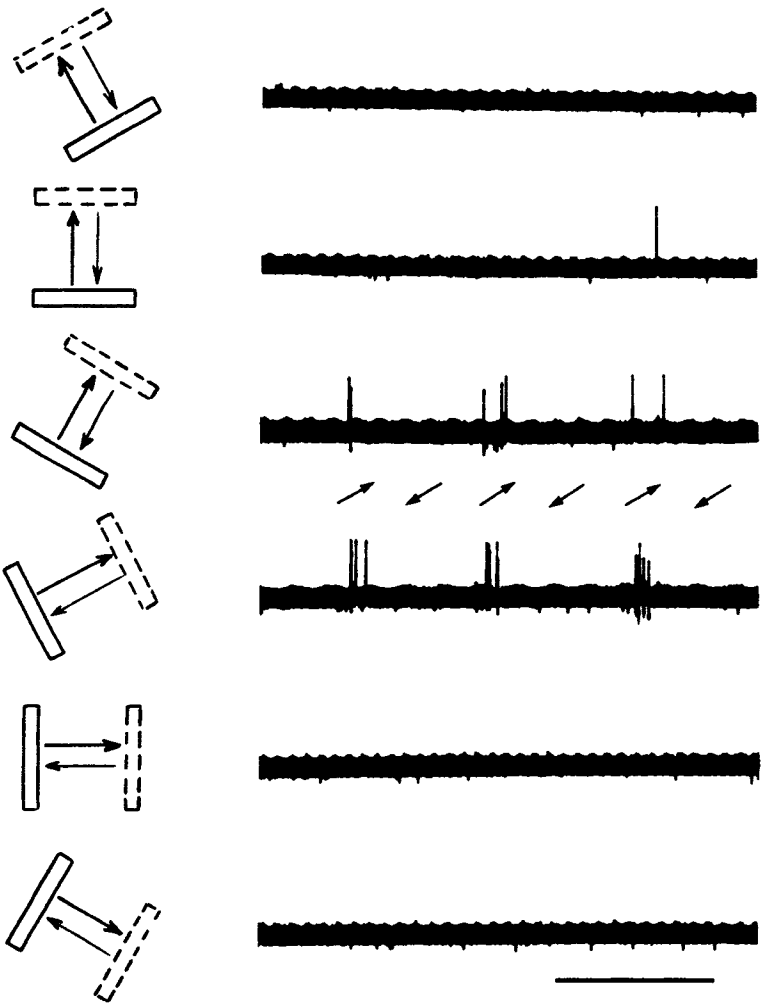

Fig.2. Records from a cell in the right striate cortex of a normal adult cat. A retinal region about 1½ mm x 1½ mm (about 4^{o} x 4^{o} in the projected visual field) is illuminated by a small rectangle of light subtending 0.5^{o} x 8^{o}, which is moved back and forth over the region in different orientations as shown. Microelectrode recordings photographed from an oscilloscope are shown to the right; time, 1 sec. From (5).

dark bar on a bright background, or a boundary between darkness and light; a given cell prefers one of these types of line and responds less well or even ignores the others. If the line crosses the receptive field in just the appropriate orientation the cell will fire vigorously. The orientation that elicits the optimal response varies from cell to cell, some cells preferring vertical, others horizontal, and others oblique, with all possible orientations represented. A typical cell will respond vigorously over a range of orientations of about 10 - 30°, the response declining outside this range, and failing completely for stimuli 90° from the optimum. Sweeping an optimally oriented line across the receptive field is usually a powerful stimulus, as in the cell whose responses are shown in Fig. 2. Here a stationary line had little influence on the cell, but a line moving up and to the right evoked a brisk response consisting of several impulses, whereas movement in the opposite direction was without effect. Almost all cells are sensitive to this sort of movement, but many show less selectivity, responding almost equally to movement in the two diametrically opposite directions.

This kind of highly specific response has been seen in chronically prepared animals in the absence of anesthesia and with the animal fully alert. They have also been seen in the monkey cortex. It seems clear that the connections underlying the specificity of response to line stimuli must be in the cortex, since neither retinal nor geniculate cells show any tendency to prefer one orientation over another. Furthermore, while reacting best to restricted stimuli, many retinal and geniculate cells respond well to diffuse light. Various models have been proposed to explain the behavior of the cells in terms of neural connections (6, 9).

Functional Architecture

From anatomical studies and work with evoked potentials recorded with gross electrodes it has long been clear that the retina is mapped upon the cortex in an orderly fashion (16, 18). Our single-cell work confirms this, but also tells something about the detailed arrangement of cells. All the cells in any small region of cortex have their receptive fields in roughly the same part of the retina, and usually the fields overlap extensively. As one goes from cell to cell in a penetration through the cortex there is a small more or less random variation or staggering in the positions of the fields. Cells situated a centimeter apart will have their fields in separate regions of the retina, the exact position depending on the detailed topographic map. More interesting and unexpected is the finding that almost invariably the receptive field orientations of two neighboring cells are, as far as one can tell, identical. As an electrode advances through the cortex there are usually long sequences of cells all having the same receptive field orientation, with sudden shifts in orientation between the sequences. The cells turn out to be aggregated into more or less cylindrical regions of common receptive field orientation which extend from surface to white matter. These columns probably vary considerably in size, with cross-sectional diameters ranging from about 50 - 100μ in up to around 0.5mm. The number of cells in a column is hard to estimate, but for the largest column it might be a few tens of thousands. A column is apparently a functional unit of cortex, its cells having rich interconnections, with

few interconnections between cells in different columns. Any given small region of retina is thus represented in the cortex by many columns subserving different orientations, vertical, oblique or horizontal. There is no suggestion that cells with any particular receptive-field orientation, such as vertical or horizontal, are more common than cells with any other. To look after the entire retina, with all possible orientations represented, and additional specialization within the individual columns for light lines, dark lines, and edges, obviously requires a vast number of cells, but this is no cause for scepticism or concern, since a vast number of cells is just what the cortex has.

Binocular Interaction

It is obviously important to understand how the inputs from the two eyes combine, if we are to interpret the results of closing one eye. As seen in Fig. 1, the first structure in the retino-cortical path to receive binocular input is the lateral geniculate body. At that stage the influences of the two eyes are for all practical purposes kept strictly separate, the geniculate being divided into discrete layers, with the arriving optic fibers segregated so that all cells in a given layer get input from one eye only. In the 3-layered geniculate of the cat the uppermost and the inferior layers receive input from the contralateral eye, the middle from the ipsilateral.

In the cortex the situation is more complex. In the cat we find that about 80% of cells receive input from both eyes, the remaining 20% having input from a single eye, either the ipsilateral or the contralateral. It is therefore important to learn how, in a cell with binocular input, the influences of the two eyes compare. Putting the question in concrete terms, one can record from a single cell, and map out the receptive field first in one eye and then in the other, comparing the two with respect to position, orientation, optimum stimulus, and so on.

The results are clear and consistent. First, the receptive fields are situated, as far as one can tell with present methods, on exactly corresponding points in the two retinas. This means that if a cell's receptive field as measured in the left eye is 2^{o} above and 3^{o} to the left of the fovea, in the right eye it will also be 2^{o} up and 3^{o} to the left of the fovea (Fig. 3A). Second, for each cell the properties of the optimal stimulus for the left eye are exactly the same as those for the right. If an edge works best in the left eye, it will work best for the right; if the orientation is 2.30 o'clock for the left it will also be 2.30 o'clock for the right; if downward movement is favored in the left eye, it will be favored in the right; whatever rate of movements is optimal for one eye will be optimal for the other. Finally, in one important respect the two eyes do not necessarily have identical effects: when the retinas are stimulated separately with the optimum stimulus the two resulting responses are not necessarily equal in strength. The response evoked by the ipsilateral eye may exceed that from the contralateral eye, (measuring the response by the number of impulses in a unit of time), or it may be less, or the two may be equal. All shades of relative ocular dominance are found, from complete dominance by the contralateral eye, through equality, to complete dominance by the ipsilateral. Cells thus apparently

vary in the relative richness of connections from the two eyes, though in other respects the two sets of connections seem to be exact duplicates.

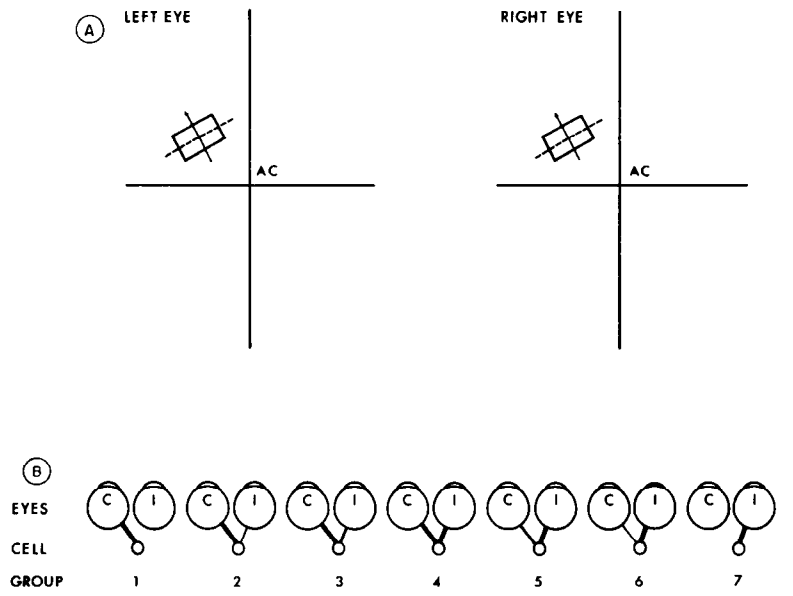

Fig.3. A. Receptive fields of a typical cell in cat striate cortex, as mapped for the left and right eyes. Each diagram represents the visual field as seen by one eye; AC represents the area centralis (equivalent of the fovea of primates), or center of gaze. Receptive fields are in corresponding regions of the visual fields of the two eyes, and the orientation and preferred direction of movement are the same.

B. Diagram illustrating the seven ocular dominance groupings. A cell (small circle) in the right hemisphere may be influenced equally from the 2 eyes (Group 4); it may receive input only from the contralateral (C) eye (Group 1) or only from the ipsilateral (I) eye (Group 7). For the intermediate groups one eye may influence the cell much more than the other (Groups 2 and 6) or the difference may be slight (Groups 3 and 5).

Proceeding from cell to cell in a penetration through the cortex, one can observe the relative influence of the two eyes on each cell. From one cell to the next this generally differs, and it becomes convenient to have a rough way of measuring the relative dominance. We therefore divide cells into seven categories depending on their ocular dominance. As illustrated in Fig. 3B, a group 1 cell receives its input exclusively from the contralateral eye, a group 7 cell exclusively from the ipsilateral. Groups 2 - 6 represent the binocularly driven cells: Group 4 represents cells driven equally from the two, while for groups 2 and 3 the contralateral eye predominates markedly or slightly: and for 6 and 5 the ipsilateral eye predominates markedly or slightly. Thus for a

given cell one has only to decide whether the two eyes have equal influence or not, and if not whether the dominance is slight (groups 3 and 5) marked (groups 2 and 6) or complete (groups 1 and 7). The classification is rough and the decision is occasionally arbitrary, since two observers may disagree on whether, for example, one eye predominates slightly or markedly. Nevertheless it is unlikely that a cell would ever be misassigned by more than one group.

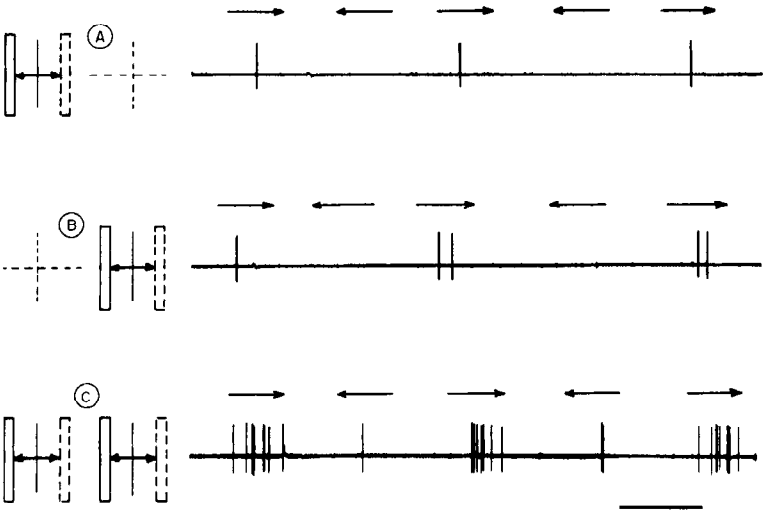

Fig.4. Movement of a ½ x 2° slit back and forth horizontally across the receptive field of a binocularly influenced cell. A, left eye; B, right eye; C, both eyes. The cell clearly preferred left-to-right movement, but when both eyes were stimulated together it responded also to the reverse direction. Field diameter, 2°, situated 5° from the area centralis. Time, 1 sec. From (6).

When a cell with connections to both eyes is stimulated by both eyes in corresponding parts of the two retinas, as happens when an animal fixes on an object, the response evoked is much greater than that from either eye alone. This is illustrated in Fig. 4 for a cell that responded optimally to a vertical slit moved across its field from left to right. With either eye alone this stimulation evoked only one or two spikes, but with both together a burst of 8 - 12 spikes was evoked. Even leftward movement, which produced no response to a single eye, now gave a weak but clear response.

To examine animals brought up under conditions of asymmetric eye input, one needs to know as accurately as possible what to expect from an electrode penetration in a normal cortex. A typical experiment done for this purpose in a normal adult cat is shown in Fig. 5. The center

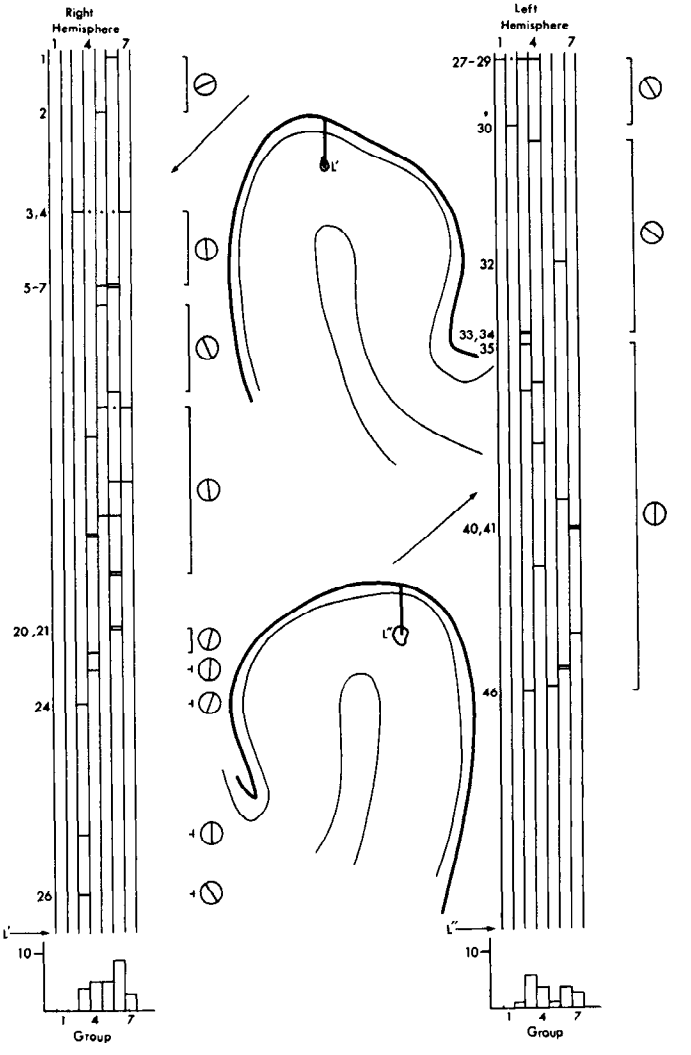

Fig.5. Reconstruction of two penetrations, one in each hemisphere, through striate cortex of a normal adult cat. In the middle of figure are shown tracings of coronal sections through the postlateral gyri. The electrode tracks are shown terminated by electrolytic lesions L' and L''. To either side the tracks are reconstructed, each cell indicated by a short horizontal line placed in its appropriate ocular-dominance group. Two horizontal lines close together, or dots between pairs of lines, indicate two-unit recordings. For each group, the total number of cells are shown in the histogram below. Lines to the right within the circles indicate by their tilt the receptive-field orientation of the cells within the brackets. From (10).

of the slide shows tracings of two coronal sections through striate cortex, the upper from the right hemisphere, the lower from the left. In each hemisphere the electrode track, traced from histological sections, is shown entering the cortex and extending through about one-half of the thickness of grey matter. A small electrolytic lesion made at the end of each track for marking purposes is shown as a small circle. For each cell studied the electrode depth was noted, and the ocular dominance and receptive field orientation were recorded. This information is summarized on the sides of the figure, where the short horizontal bars indicate the relative depths at which cells were recorded, and the vertical columns the ocular-dominance group of each cell. At the bottom the results are summed up by histograms indicating the number of cells recorded in each group.

In these two penetrations it can be seen that most ocular-dominance groups, especially the middle ones (3- 5) are fairly well represented. In addition there is a suggestion of segregation of dominance groups within the cortex. For example, in the penetration in the right hemisphere (shown to the left in the figure), almost all of the cells recorded during the first two-thirds of the penetration either favored the ipsilateral eye or were neutral, whereas in the final one-third most cells favored the contralateral. In the penetration through the left hemisphere there was no such emphasis, but instead a mixture of group 4 cells and cells favoring one or other eye; there were also simultaneous recordings of cells many groups apart. Studies of this type indicate a tendency for the cortex to be subdivided by ocular-dominance grouping, with some regions of cortex predominantly influenced by the contralateral eye and containing few cells in groups 5 - 7, others mainly ipsilateral in emphasis, and still others mixed. It should be stressed that even in a contralaterally dominated region the great majority of the cells receive input also from the ipsilateral eye; the point is that most cells favor the contralateral. The regions can extend from cortical surface to white matter and may be columnar, but they are clearly independent of the orientation columns. Fig. 6 shows a surface map of a small area of cortex in which both orientation columns and regions of ipsilateral eye dominance were mapped by making many very superficial microelectrode penetrations. The boundaries in the two systems, far from being superimposed, seem quite independent.

The importance of a segregation of cells by ocular dominance for our present discussion is a practical one. In assessing the normality of the cortex in a deprived animal by making a small sampling of cells in a few penetrations, the regional variation in ocular dominance may become important. To get an idea of the variation in the adult normal cat we prepared ocular-dominance histograms from 12 successive penetrations (Fig. 7). In most penetrations all but one or two groups were represented, but as expected, some, such as numbers 4, 5, and 6, were predominantly contralateral in emphasis, and others, such as number 9, were predominantly ipsilateral. Clearly a penetration must give results far more asymmetric than numbers 2, 4 or 5 in Fig. 7 before one can consider the cortex abnormal. The problem of sampling becomes less important of course, as more cells are studied in a penetration or when several long penetrations are made in one animal.

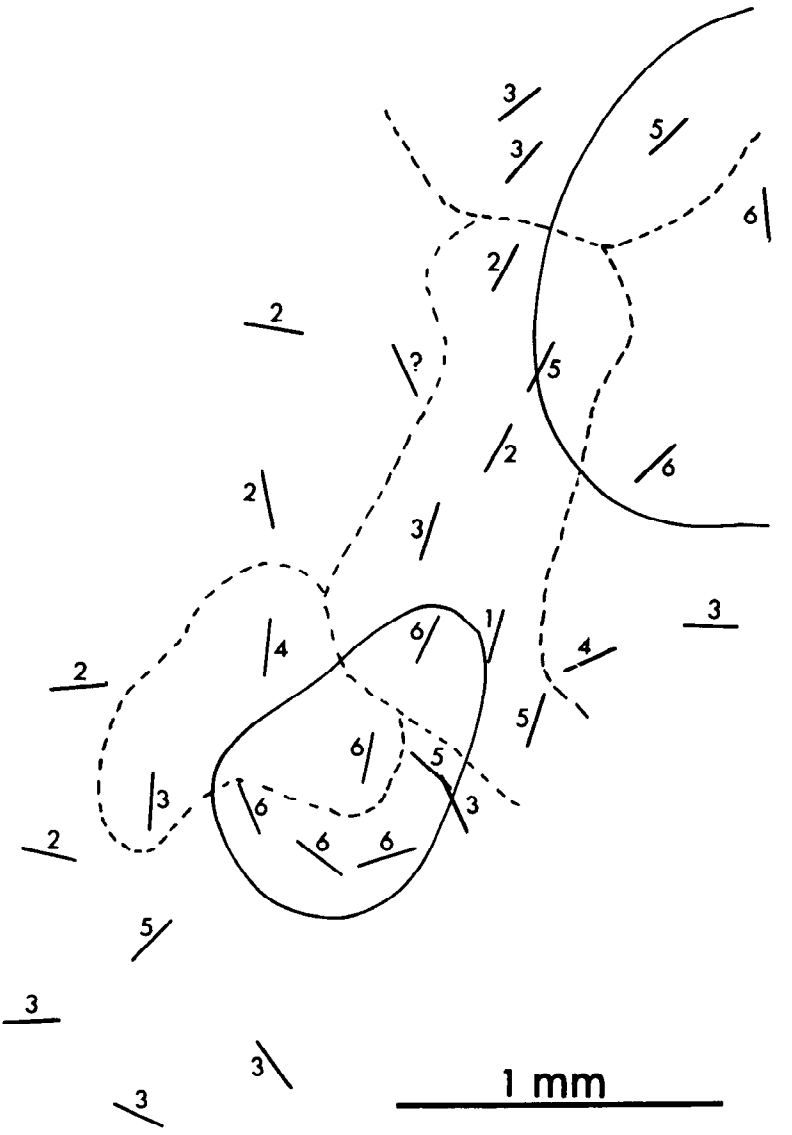

Fig.6. Map in normal adult cat showing receptive-field orientations and ocular-dominance of first cells, encountered near the surface, in 31 penetrations. The region of the right striate cortex covered by the entire map measures about 1½ x 4 mm. Interrupted lines separate regions of relatively constant receptive-field orientation, partly outlining 3 columns. The numbers refer to ocular-dominance groups. Continuous lines separate areas of strong ipsilateral dominance from areas of mixed or contralateral dominance. From (7,10).

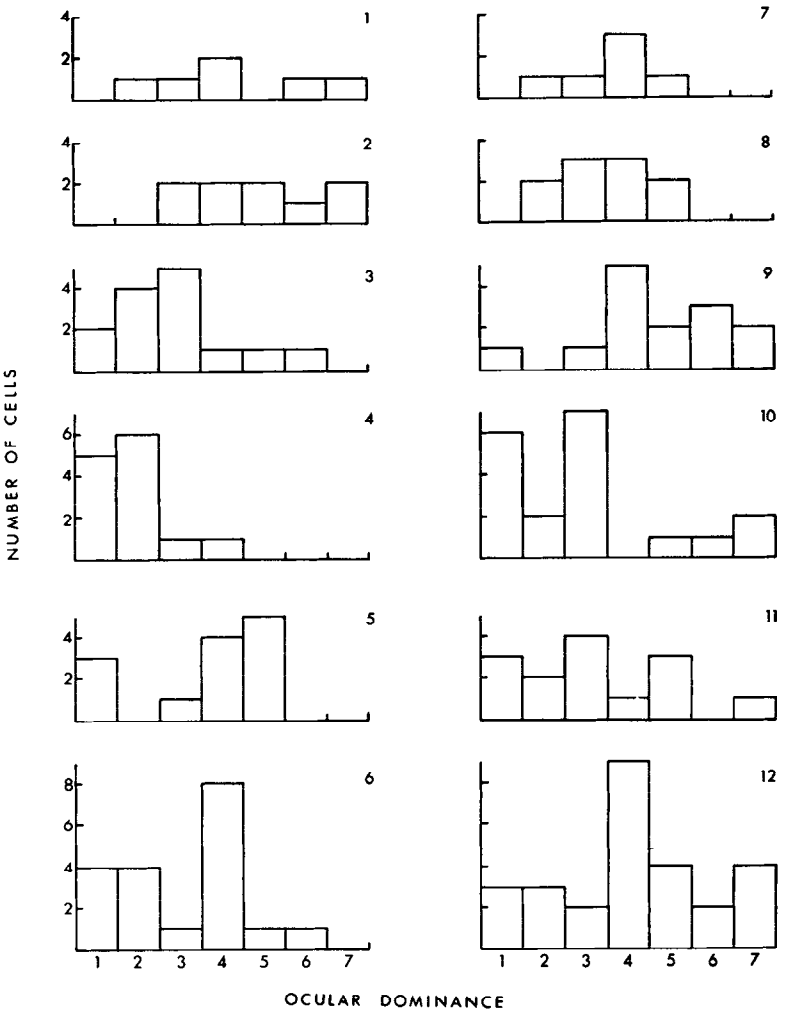

Fig.7. Ocular-dominance histograms from 12 separate consecutive penetrations in striate cortex of normal adult cats. Each histogram is compiled as illustrated in Fig.5. From (21).

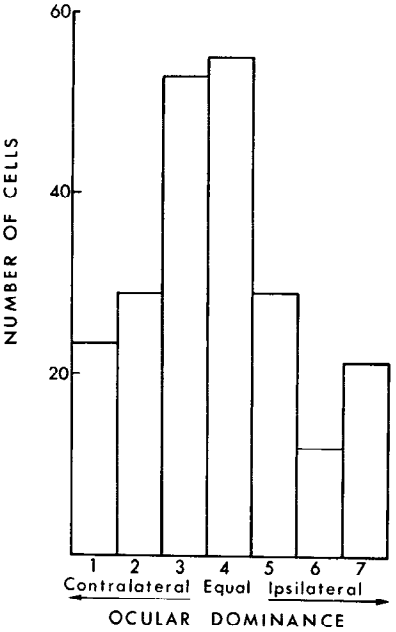

Fig. 8. Ocular-dominance distribution of 223 cells recorded from striate cortex of adult cats, in a series of 45 penetrations. From (6).

An idea of the relative ocular dominance in the cortex as a whole can be obtained from the pooled results of many penetrations. A histogram based on 223 cells from 45 penetrations is shown in Fig. 8. Groups 1-3 contains about twice as many cells as groups 5-7, suggesting a minor overall skew distribution in favor of the contralateral eye. The extreme groups 1 and 7 together make up about 14% of the total.

To sum up: in judging an individual penetration, one can consider Fig. 8 to represent the normal, and regard as probably abnormal only departures much greater than those of penetration 2 and 4 of Fig. 7.

PHYSIOLOGY IN VISUALLY DEPRIVED ANIMALS

Opaque Occlusion

A few years ago it seemed to us that with the knowledge of the normal visual system of cats and monkeys, visual physiology had reached the stage where the effects on the central nervous system of gross changes in past experience might be detectable. We therefore did the preliminary experiment of sewing shut the lids of the right eye of a newborn kitten, and letting the animal live a relatively normal life for three months. A recording was then made from the visual cortex, with the object of looking for any possible abnormalities, particularly any changes in relative dominance of the two eyes. The kitten was anesthetized and the right eye opened. The cornea and media were clear, the fundus seemed normal, and the direct and consensual pupillary reflexes were normal, indicating that at least some of the retina and optic nerve fibers must have survived.

The results of a recording from the left hemisphere, shown in Fig. 9 could hardly have been more extreme. None of the cells examined could be influenced by the eye that had been closed. Most cells responded to the left eye only - the eye that had been open all along. A small number were driven by neither eye, something that one does not see in normal cortex. Encouraged by this unexpected result we quickly repeated the experiment in two other kittens with much the same outcome. Of the first 84 cells recorded, only one was affected by the closed eye, and this was abnormal in its responses.

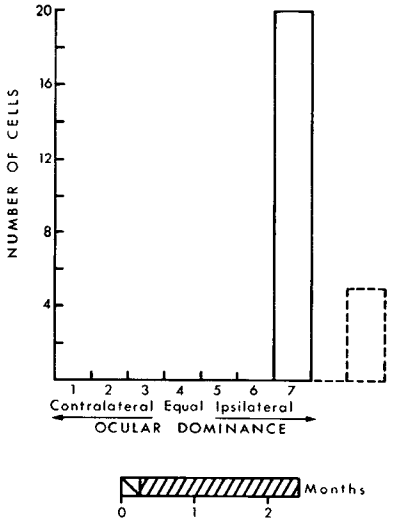

Fig.9. Ocular-dominance distribution of 25 cells recorded in the visual cortex of a 2½-month-old kitten. Experimental procedures are indicated beneath; during the first week the eyes were not yet open; on the eighth day the lids of the right eye were sutured, and they remained closed until the time of the experiment (shaded region). The left eye opened normally on the ninth day. Recordings were made from the left visual cortex, contralateral to the eye that had been closed. Five of the cells, represented by the interrupted column on the right, could not be driven from either eye. The remaining 20 were driven only from the normally exposed (left, or ipsilateral) eye, and were therefore classed as group 7.From (21).

Finding even one cell that responded to the eye that had been closed suggested that there probably were others, and for reasons that will become apparent later it seemed important to find out just how scarce or plentiful these cells were. Given a tendency to spatial aggregation of cells favoring one or other eye, it seemed possible that in the deprived animals there might persist groups or pockets of cells still capable of responding to the occluded eye. We therefore made an intensive search for such cells, doing 5 more penetrations in two right-eye deprived kittens, recording from 115 more cells. The results are shown in Fig. 10. In the first kitten (Fig. 10 left) no cells were influenced from the right eye, compared with 50 normally driven from the left. In the second kitten, however, there were a few cells that could be driven from the right eye, and these indeed showed a tendency to be aggregated. The largest cluster of cells was seen near the end of penetration 4 in the left hemisphere.

Fig. 11 shows a final histogram containing information on all cells recorded from kittens raised from birth with monocular eye closure. Of 199 cells only 13 responded to the deprived eye, and it is interesting that of these, 12 responded to the previously closed eye in an abnormal way, either inconsistently or without the orientation specificity seen in normal cells.

The conclusion from this first set of experiments is that monocular occlusion for three months is capable of producing a profound abnormality in the visual pathway. The results raised a number of obvious questions, which we now set about trying to answer.

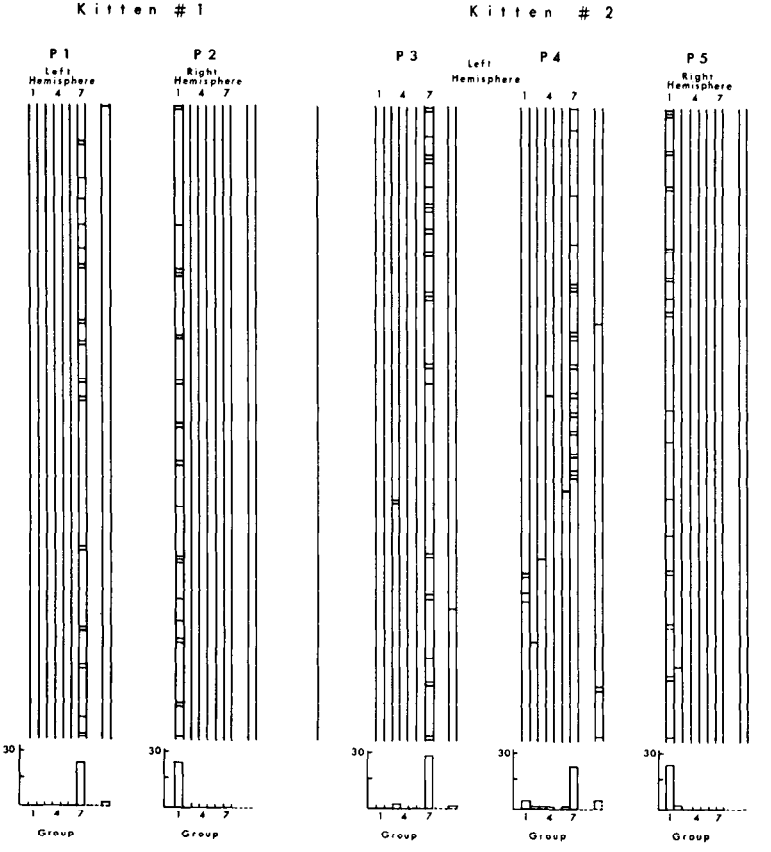

Fig.10. Schematic reconstructions of five microelectrode penetrations in two kittens. Kitten 1, was 8 weeks old and kitten 2, 10 weeks; both had the right eye closed by lid suture at 8 days. Each penetration extended into cortical gray matter for about 1.5 mm. The penetrations are drawn so as to indicate relative positions of individual cells; each cell is represented by a short horizontal line placed in the appropriate vertical row according to ocular-dominance group. The separate row to the right of group 7 is for unresponsive cells. The total number of cells in each group is indicated in the histogram at the bottom. From (22).

Site of Abnormality

One cannot conclude, from the above experiments alone, that anything was wrong with the cortex itself. Cortical cells, it is true, failed to respond to stimulation of one eye, but there was no guarantee that the abnormality was not in the retina or geniculate. This was easily tested in the same experiments by putting electrodes also into the

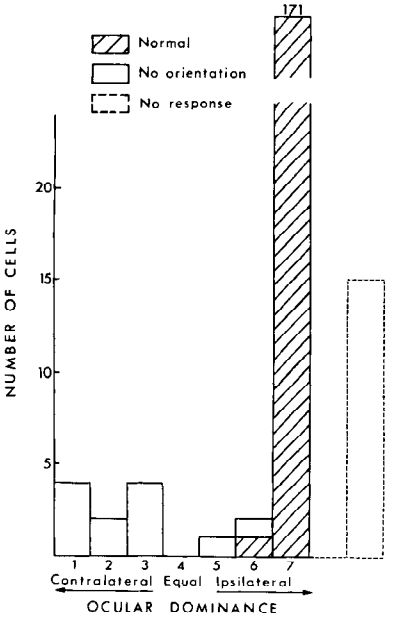

Fig.11. Ocular-dominance distribution of 199 cells recorded in the visual cortex of 5 monocularly deprived kittens. The animals were 8-14 wekks old and all had the right eye closed by lid suture from the time of normal eye opening. Shading indicates cells that had the usual specific response properties to visual stimulation; absence of shading indicates cells that lacked the normal orientation specificity. Interrupted lines indicate cells that did not respond to either eye. From (22).

geniculate. Here there were plenty of cells that responded apparently normally to stimulation of the previously occluded eye. One had the impression that the activity was not quite as rich in the layers receiving afferents from the deprived eye, but there certainly was no abnormality comparable to that seen in the cortex. This made it very likely that the site of abnormality was the cortex, a conclusion strongly reinforced by subsequent findings.

In view of this relative normality of geniculate-cell responses it came as a great surprise to find that histologically the cells were quite abnormal. Cells in the layers that received input from the eye that had been closed were smaller, paler, and more closely packed than those in the other layers. Careful measurements showed these cells to be decreased in cross sectional area by 40%. We have learned subsequently that the small size of the geniculate cells represents chiefly a failure of cells to grow at the normal rate, rather than a genuine atrophy. At birth the cross sectional area of geniculate cells in the dorsal layer is about 1/3 of the normal adult size. With one eye closed the cells in the layers getting input from that eye increase in size, but at a reduced rate, attaining 2/3 of normal size in three months. By contrast, a normal kitten's geniculate cells seem to be fully grown by that time. If instead of occluding an eye it is removed one week after birth, the cells at 3 months seem not to have grown at all.

Thus while physiologically most geniculate cells seemed normal, anatomically there were rather marked changes. Conceivably the size of a cell may be related to its overall activity or use, and not necessarily

to its ability to respond normally. Our present impression is that there are probably abnormalities at all levels of the visual system, from retina on.

Translucent Occluders

It seemed appropriate at this point to ask what it was about the eye closures that led to such profound effects. Suturing the eyes certainly prevents any stimulation of the retina by forms or contours. It can also be shown to reduce the entering light by about 4-5 log units (a factor of 10,000 to 100,000): but the light that does reach the eyes is probably not insignificant, given a dynamic range of some 10 log units, and the great sensitivity of the dark adapted cat eye. Any diffuse light reaching the retina would undoubtedly activate the geniculate cells to some extent, but should have practically no influence on cortical cells.

To learn whether our results were related to deprivation of form or of light, we brought up a few kittens by covering one eye with a translucent contact occluder - a plastic with the consistency of opal glass or a ping-pong ball. This undoubtedly abolished all form vision, but reduced the incident light by only about 1-2 log units. On recording from the cortex after 2-3 months the results were practically identical to those obtained with lid suture, with cells virtually unresponsive to the occluded eye, and a small number that failed to respond to either eye. Our conclusion is that form deprivation rather than light deprivation was the important thing in the eye-suture experiments, so far as the cortical abnormality is concerned. In the geniculate of the kittens deprived with translucent occluders the cells receiving input from the deprived eyes were again shrunken, but this time the decrease in cross sectional area amounted to only about 10%, a change that was difficult to be sure of by simple inspection under a microscope. Form deprivation, then, is not nearly as damaging to geniculate cells as is deprivation by eye suture - a finding that is reasonable in view of the responsiveness of geniculate cells to diffuse light.

Behavioral Testing

The vision of these animals, deprived by lid suture or a translucent occluder, when tested at 2-3 months, was of course normal in the eye that had been open, but seemed very defective if not entirely absent in the deprived eye. With the good eye covered, the animal when placed on the floor bumped into obstacles such as table legs; when put up on a table it groped towards the edge and on jumping failed to land on its feet. Objects moved in front of the kitten were not followed, and visual placing reactions were absent. These behavioral results agree with those obtained by rearing kittens in darkness (17).

Studies on Newborn Kittens

In thinking about the results of dark rearing it has been customary to attribute the resulting blindness to a sort of failure to learn, as though the animal had been born without the necessary connections, and had not gone on to develop them because of the absence of a normal

visual learning experience. However attractive this idea may be, it is not the only possibility. Connections already present and fully developed at birth might be lost through disuse. To test this second possibility we did some recordings on kittens a few days after birth, before the time at which the eyes normally open. (In the cat this occurs at about the 8th to 10th day). To our surprise we found that all of the specific types of response seen in the adult cat's striate cortex are present in the newborn visually naive animal. Fig. 12 for example, shows the responses of a cortical cell in an 8-day-old kitten; here active firing occurred when a 1:00 oriented slit was moved across the receptive field, but there was no response to a 4:00 slit. The newborn animal also possesses a columnar arrangement of cells by receptive field orientation, and the binocular apparatus described above.

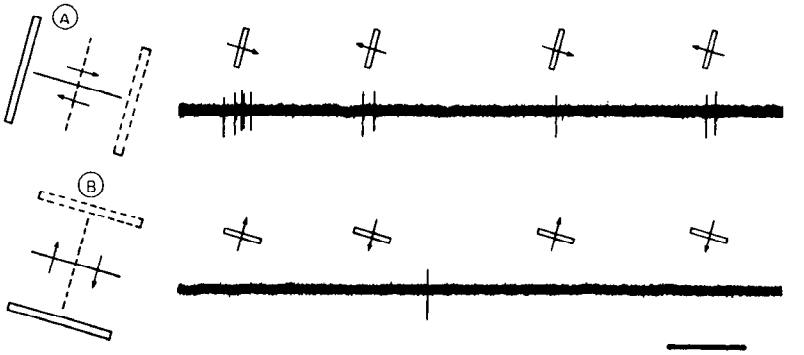

Fig.12. Single-cell responses from cortex of an 8-day-old kitten with no previous visual experience. A rectangle of light 1^{o} x 5^{o} is moved back and forth across the receptive field in the contralateral eye. Unit binocularly activated, ocular-dominance group 3. Receptive-field sizes about 5^{o} x 5^{o}; fields situated in the central part of the contralateral visual field. A; stimulus oriented 12:30 - 6:30 (parallel to receptive-field axis). B; stimulus oriented 9:30 - 3:30 (at right angles to the optimal orientation). Rate of movement, 5^{o}/sec. Time, 1 sec. From (8).

This is not to say that the system is necessarily fully developed at birth. Histologically the cortex of the newborn kitten is in many ways different from that of the adult. Physiologically, the sensitivity to orientation of lines tends to be somewhat less impressive in the newborn animal than in the adult. This seems to have nothing to do with experience but to be a matter simply of development, since if one or both eyes are kept closed by suturing the lids for 3 - 4 weeks after birth (too short a time for deprivation effects to take place) the responses are then just as precise and specific as in the adult. Up to the level of the striate cortex the connections are thus innately determined and do not require visual experience for their development. Needless to say this puts a certain burden on the underlying genetic mechanisms.

Delay of Eye Closure

From the evidence so far given, one would conclude that the connections up to the striate cortex are for all practical purposes formed at birth or develop soon after, even without visual stimulation; if the connections are not used, they tend to become non-functional. Preliminary studies in which deprivation is begun on the 8 - 10th day and continued for varying lengths of time indicate that the critical period is somewhere around the 4th and 6th week; monocular deprivation ending before the 4th week of life produces little or no physiological defect, while lid closure for more than 6 weeks gives the full-blown picture seen at 3 months. In some ways this is not surprising, since for the first 4 weeks a kitten seems to make little use of its vision but stays with its mother and litter mates under the sofa.

If it is true that our eye-closure results are related to deterioration of connections already formed, rather than to a failure of a pathway to develop, is it really necessary to raise the animals with an eye closed from birth, or might one just as well work with older cats? To test this we delayed the time of operation for several weeks and then closed an eye for a few months. Fig. 13 shows histograms from an animal whose right eye was closed from the second to the sixth month. The cortex was unquestionably abnormal in that only a very few cells favored the deprived eye, while a pathologically high proportion failed to

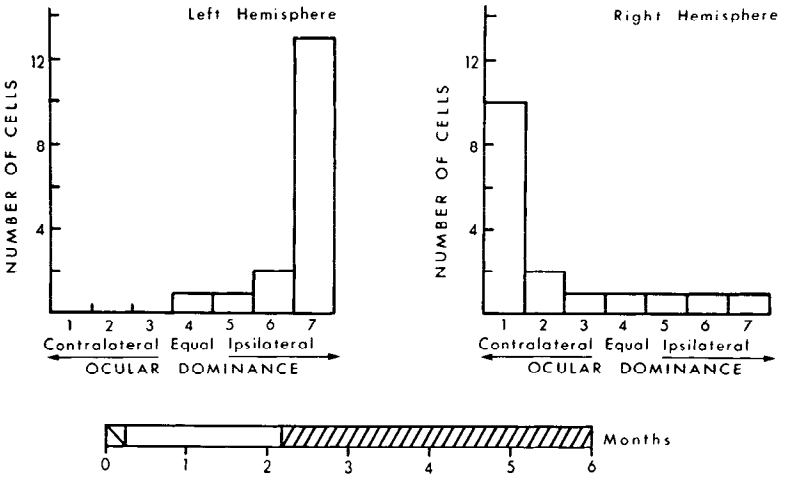

Fig.13. Histograms of ocular-dominance distribution of 32 cells recorded in two penetrations, one in the left visual cortex and one in the right. Kitten whose right eye was closed by lid suture at 9 weeks, for a period of 4 months. Seventeen cells recorded from each hemisphere. All cells were influenced by patterned-light stimulation. From (21).

respond to it at all. On the other hand the abnormality was nothing like as severe as in animals deprived from birth. Apparently each month of normal vision makes the animal less susceptible, and an adult deprived for three months failed to show any abnormality at all. This animal was by definition an adult, being the mother of one of our litters. It seems, then, that at birth this part of the nervous system possesses a certain flexibility, expressed as a sensitivity to the effects of distorted sensory input, and that somewhere between infancy and adulthood this flexibility is lost.

The importance of age on the effects of sensory deprivation will come as no surprise to the clinical ophthalmologist. A man of sixty who has a cataract removed after five years of blindness sees well as soon as the loss of his lens is compensated for by glasses. In contrast, when congenital cataracts are removed in a child or adult the subject cannot see immediately, and vision returns at a painfully slow rate, possibly never reaching normal (19). In the cat recovery likewise seems to be very slow. Fig. 14 shows the result of closing the right eye for the first three months of life and then having it open for the next year and two months. During the time the right eye was open we closed the left eye in an attempt to promote recovery as much as possible, just as a clinician patches the normal eye in treating amblyopia ex anopsia. The result was that all of the cells we observed strongly favored the eye that had been open for the first three months, even though that eye had subsequently been closed for more than a year! There was thus very little recovery from the early eye closure, though there was clearly some. In this and other experiments many of the cells that could be driven from the originally deprived eye were abnormal, responding inconsistently and without the usual sharply defined optimum stimulus orientation. It was as if some connections had become re-established, but more or less at random.

Behaviorally also the recovery of these animals seems limited and incomplete. After months with an eye open an animal will still react inappropriately or be slow to react to visual stimuli. Ultimately it becomes able to follow large objects, and after a year or more it may develop some ability to discriminate form. Whether vision ever becomes entirely normal is not yet clear.

Binocular Closures

Up to this point the results seem to be accounted for in a straightforward way by assuming that at an early age deterioration of cortical connections is the result of disuse. Two further experiments have made us realize that the sutiation is more complicated and far more interesting.

The first experiment was to take four kittens and suture both eyes closed for the first 3 months. We had hoped to avoid this radical procedure, but became convinced that we must do it if our results were to be compared with those obtained in dark reared animals. We assumed that, unless the two pathways from eye to brain interacted in an unexpected way, the result should be predictable from the one-eye closures.

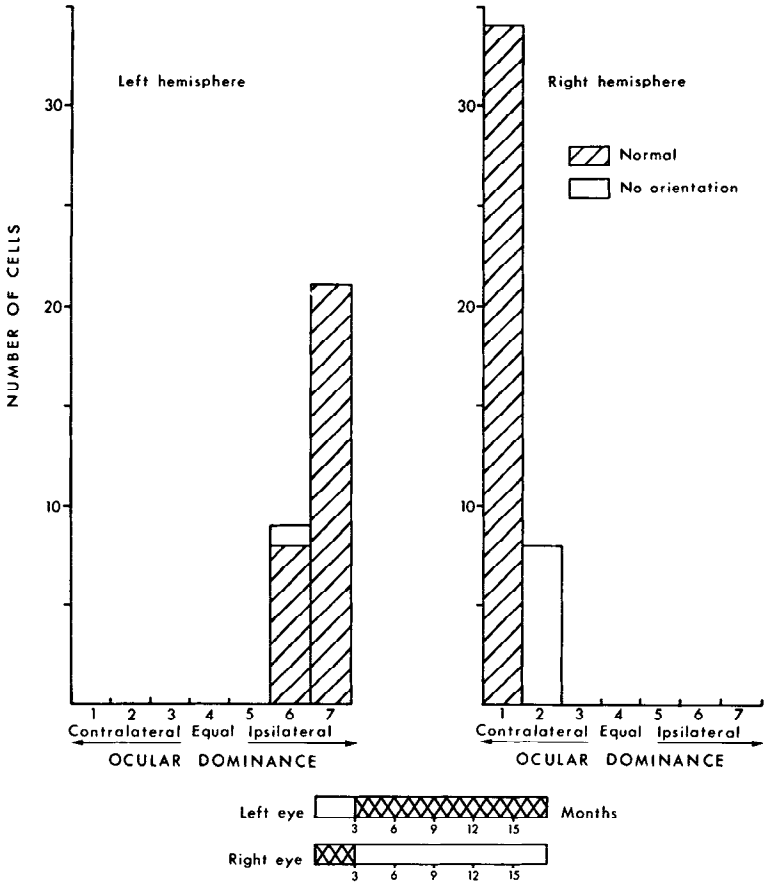

Fig.14. Ocular dominance of 72 cells recorded from a cat in which the right eye was closed for the first 3 months of life, following which the right eye was opened and the left eye closed for the next 14 months. From (23).

Just as closing one eye gave a cortex with large areas devoid of cells responsive to that eye, so on closing both eyes we expected to find large areas of cortex containing no responsive cells, with only occasional islands of cells responding aberrantly to one or other eye. This was not at all the result. Most cells that were recorded (73%) responded to visual stimuli, and of those that responded more than half were, as far as one could tell, quite normal. The number of unresponsive cells may well have been greater than 27%, since such cells are

only detected by their spontaneous activity or their firing when injured by the electrode. Nevertheless there were not large regions of unresponsive cortex. The results from 126 cells recorded in 4 kittens are given in Fig. 15. While the unexpected thing in these animals was the large number of normal cells, it should be emphasized that the cortex was still far from normal, both with respect to the unresponsive cells and to those that fired inconsistently and lacked the normal response specificity.

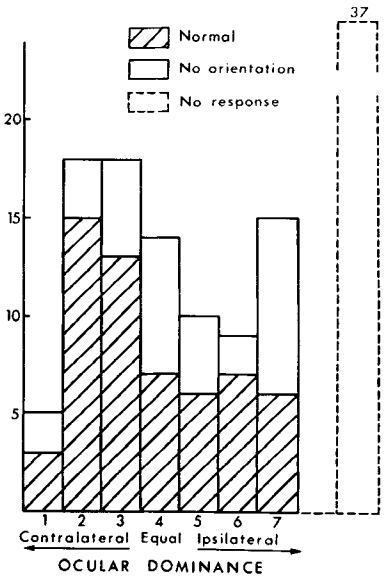

Fig.15. Ocular-dominance distribution of 126 cells recorded from the 4 binocularly deprived kittens in 10 penetrations. From (22).

This result means that the effects of a right-eye closure upon a single cortical cell cannot be predicted unless one is told whether the left eye was also closed: it seems that the chances of the connections surviving are much less if the left eye is kept open. We have no idea of the detailed mechanisms involved, and though it is tempting to imagine the left eye taking over control of a cell when the connections from the right are at a disadvantage, there is no direct evidence that anything like this occurs. But in any case it is not entirely easy to account for the results of monocular closure in terms of simple disuse.

When tested behaviorally these animals seemed to be quite blind. This may seem strange in view of the normally responding cells in the cortex, but it must be remembered that the striate cortex represents only one stage, and surely an early one, in the visual pathway, and nothing is known about the integrity of connections at later stages. In the monocularly closed animals many cells in the striate cortex and beyond receive normal input from the good eye, whereas in binocular closure they are obviously cut off from all visual input.

Strabismus

The second surprising experiment was motivated by clinical considerations. An adult who develops a squint (strabismus, or non-parallel eyes) usually continues to see double indefinitely if vision in both eyes is normal. In an infant or child with squint, vision in one eye is apparently soon suppressed, so that double vision is ordinarily only transient. If the squint persists one of two things happen - the vision in one eye may deteriorate, so that ultimately the eye becomes useless (amblyopia ex anopia), or the eyes may alternate, each fixing

in turn. In alternating squint, vision in both eyes may remain normal.

We decided to produce a squint in newborn kittens to see whether we could obtain an amblyopia and study the mechanisms involved. We therefore cut the medial rectus muscles in each of four kittens, producing florid divergent squints in all of them. The result was disappointing, for three months later the cats all had perfectly normal vision in both eyes. Even before testing the animals we had expected this, since they all appeared to be fixating first with one eye and then with the other.

With little idea of what might be found, we decided to record from the cortex of one of the animals. The result is shown in Fig. 16. At the outset the penetration seemed unremarkable, with many cells responding perfectly normally. As the penetration progressed, however, we were surprised to find a decided lack of binocularly driven cells. Cell after cell would fall into group 7, then there might be a mixture of sevens and ones with occasional cells from other groups interspersed, and finally there would occur another long sequence, either all group 7 again or all group 1. The resulting histogram, shown at the bottom of the track reconstruction, was quite unlike anything we had ever seen in normal animals. The squint had evidently produced a sharp decline in binocularly activated cells.

Very similar results were found in the other three animals. The most extreme result was obtained in an animal brought up with squint for a year; here only four cells out of 64 could be driven from both eyes, these belonging to groups 2 and 6. Out of a total of 384 cells recorded in all 4 animals with squint, 79% were monocularly driven, compared with 20% in the normal cat (Fig. 17).

In these experiments it seems clear that the decline in cells of groups 2 - 6 does not represent a simple dropping out of these cells. Not only were the penetrations (such as that of Fig. 16) especially rich in cells, hardly supporting the idea that 80% of cells were missing, but there were long sequences of group 1 cells or of group 7 cells, instead of an almost random mixture of groups 1 and 7, as would have occurred had the other cells simply become unresponsive. On the other hand, a shift in ocular dominance, with cells of groups 2 and 3 moving into group 1, and 5 and 6 moving to group 7, explains the findings perfectly, given the normal tendency for segregation of cells by eye preference (see Figs. 5 & 6). With squint, then, it seems that for each cell the dominant eye tends to take over, at least relative to the non-dominant eye: whether the influence of the dominant eye increases absolutely is not known. The scarcity of group 4 cells suggests that for a given cell even a slight imbalance in the influence from the two eyes tends to increase, leading finally to a complete loss of the control from one eye.

The squint experiments seem to us particularly interesting in that the overall input from the two eyes is presumably normal. What is not normal is the time relationships between the impulses from the two eyes. This becomes easier to visualize if one considers a particular binocularly driven cell in the cortex, say a group 3. As described above, the two receptive fields of this cell occupy corresponding positions on the two

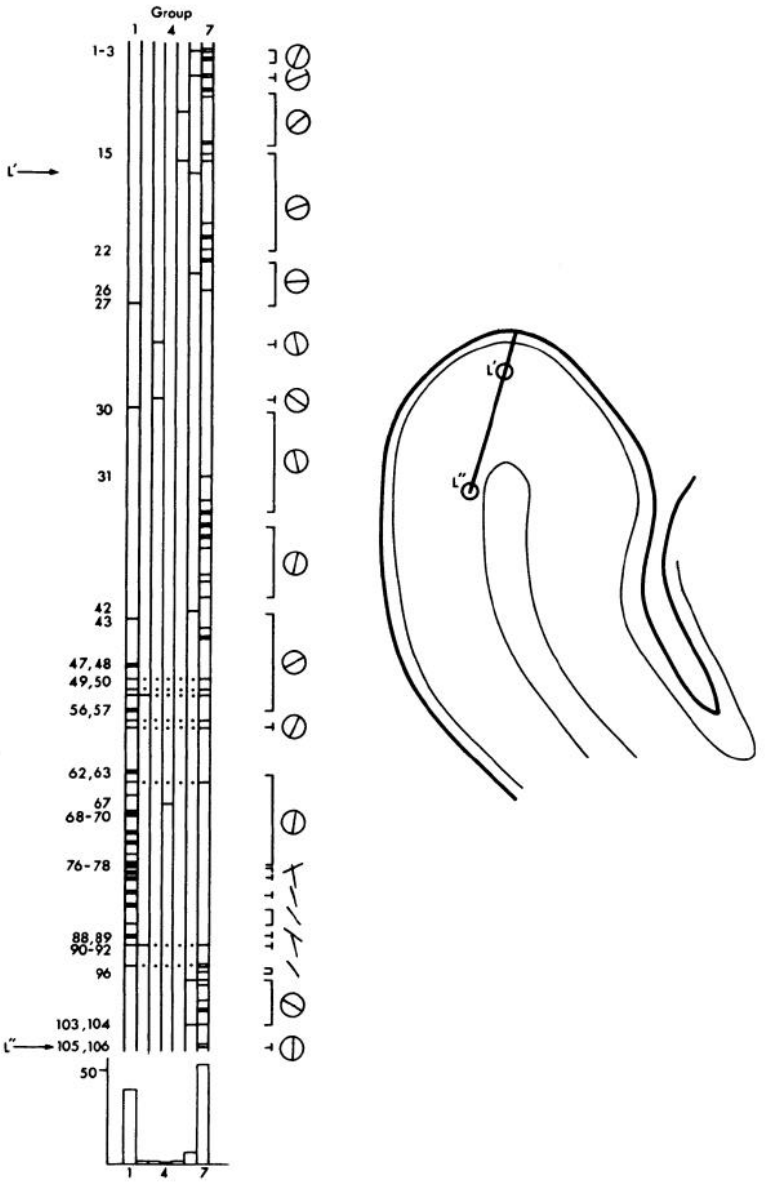

Fig.16. Reconstruction of a penetration in right striate cortex of kitten age 3 months, with divergent strabismus from 8 days. For conventions see Fig. 5. From (10).

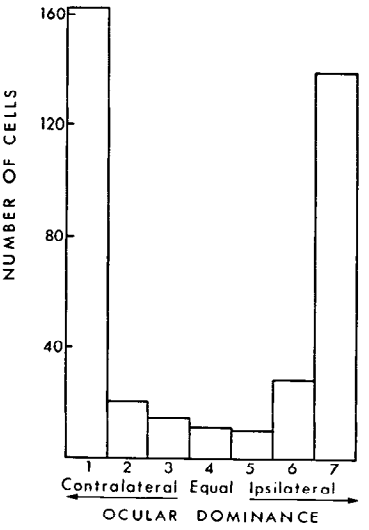

Fig.17. Ocular-dominance histogram for 384 cells recorded from 4 kittens with strabismus. From (10).

retinas, and are similar in organization. Furthermore, when the eyes fix normally on an object the image falls on corresponding parts of the retina. From this (and neglecting parallax) it follows that when the cell receives input tending to activate it from the dominant eye, it will also receive an activating input from the nondominant eye. This is true whether the cell under consideration itself represents the site of convergence of inputs from the 2 eyes, or is further downstream. In an animal with strabismus the relationship is entirely changed: if the cell is excited from one eye, it may be excited or inhibited or it may receive no input from the other, depending on what contours happen to cross the receptive field in that eye. Somehow, if the situation persists in the young animal, the nondominant input apparently declines and ultimately is lost. Just as in the monocular versus the binocular closures, the detailed mechanisms are at present a mystery, but from both lines of evidence one can at least say that the two pathways are interdependent.

A final experiment was done with the idea of testing whether the squint results were produced by the lack of synergism between the 2 eyes, or whether they were related more to some kind of active antagonism or competition. To prevent the eyes from working together we brought up two animals for three months with an opaque occluder placed over one eye on one day and the other eye the next, alternating eyes each day. After three months the animals seemed to have normal vision. The experimental results are seen in Fig. 18. The effect was similar, and if anything was even more extreme than that produced by squint. It seems, then, the squint result comes from the eyes not working together, rather than from some form of active competition. Binocular occlusion (Fig. 15) did not give any radical decline in binocularly activated cells, so that one must stipulate that, for the squint result, one must have stimulation of the eyes, but no cooperation.

FINAL COMMENTS

In summing up this work, one may say that in the cat's visual system the cortical connections may be seriously damaged by distortion of sensory input in the early months of life, in the absence of any direct tampering with any part of the pathway. The effects may depend on disuse, but this can only be part of the story: a full acount must take

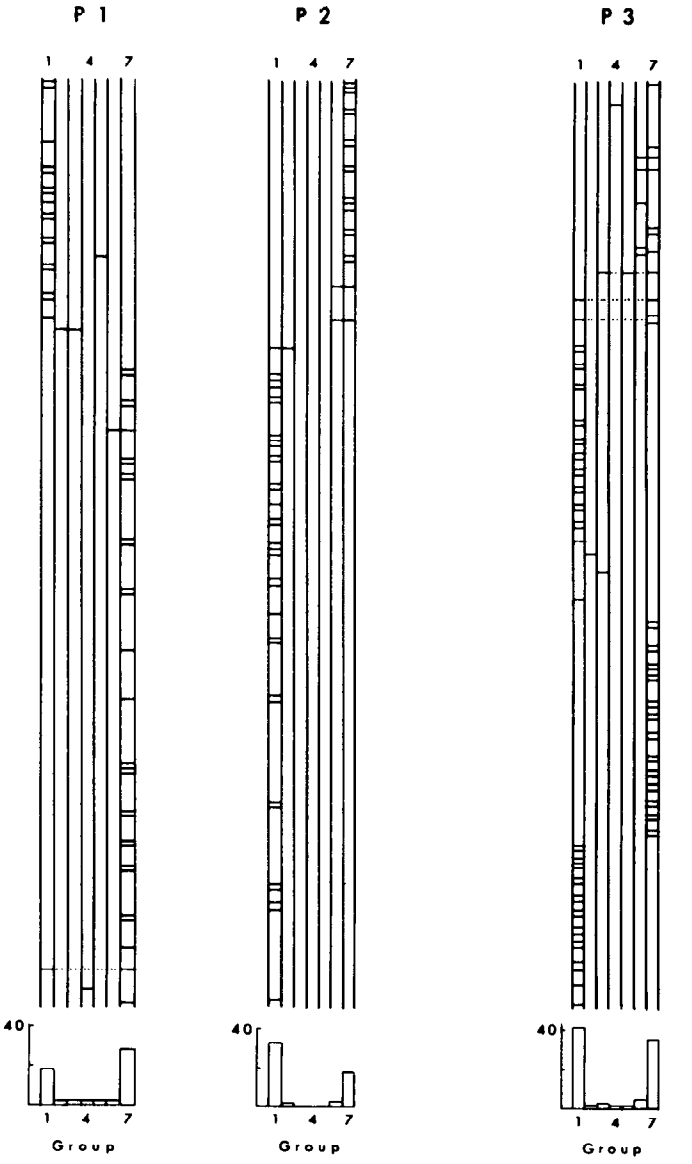

Fig.18. Schematic reconstruction of three penetrations in the striate cortex of two 10-week-old kittens raised from the time of normal eye opening with an opaque contact occluder covering one eye one day, and the other eye the next. Each penetration extended into cortical gray matter for about 1.5 mm. From (10).

into consideration the interrelationships between the different inputs to the systems.

There is a remarkable correspondence between the form of the sensory distortion and the damage produced. Deprivation of form with continued exposure to light tends to spare the geniculate, most of whose cells respond to diffuse light, but it affects the cortex, whose cells are influenced by form but not by light as such. In light deprivation (which includes form deprivation) the geniculate is also affected, at least morphologically. Finally, interference with the ability of the two eyes to work together produces adverse effects strictly confined to the connections that presumably are important for binocular vision. The extent to which this list may be expanded by future work can only be guessed at now, especially since the main obstacle to extending such studies is our ignorance of the brain mechanisms involved in much of perception, to say nothing of emotions or motor activity. Some of the next steps are rather obvious: as one comes to understand more about things like color physiology, binocular stereopsis, or form recognition, appropriate deprivation experiments will become possible. It will be important to compare visual deprivation results in the cat and monkey, once enough is known about the physiology of vision in the normal monkey, especially because the time course of the susceptible period may be quite different in different species, with the monkey intermediate between cat and man, and probably considerably closer to man. Perhaps the most exciting possibility for the future is the extension of this type of work to other systems besides sensory. Experimental psychologists and psychiatrists both emphasize the importance of early experience on subsequent behavior patterns - could it be that deprivation of social contacts or the existence of other abnormal emotional situations early in life may lead to a deterioration or distortion of connections in some yet unexplored parts of the brain? If so, one may hope that someday even the concepts of Freud may be explained in neurophysiological terms.

REFERENCES

1. Barlow, H. B., R. M. Hill, and W. R. Levick. Retinal ganglion cells responding selectively to direction and speed of image motion in the rabbit. J. Physiol. 173: 377-407, 1964.
2. Dejours, Sarah F. Receptive fields of optic tract fibers in lizards. (Sceloporus SPP). (Doctoral dissertation). Harvard Univ., Cambridge, Mass., 1965.
3. DeValois, R. L., and A. E. Jones. Single-cell analysis of the organization of the primate color-vision system. In: The Visual System: Neurophysiology and Psychophysics. edited by R. Jung and H. Kornhuber. Berlin: Springer, 178-191, 1961.
4. Gregory, R. L., and J. G. Wallace. Recovery from early blindness: A case study. Exp. Psychol. Monographs. London: W. Heffer & Sons, 1963.
5. Hubel, D. H., and T. Wiesel. Receptive fields of single neurons in the cat's striate cortex. J. Physiol. 148: 574-591, 1959.
6. Hubel, D. H., and T. N. Wiesel. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J. Physiol. 160: 106-154, 1962.

7. Hubel, D.H., and T.N. Wiesel. Shape and arrangement of columns in cat's striate cortex. J. Physiol. 165: 559-568, 1963.
8. Hubel, D.H., and T.N. Wiesel. Receptive fields of cells in striate cortex of very young, visually inexperienced kittens. J. Neurophysiol. 26: 994-1002, 1963.
9. Hubel, D.H., and T.N. Wiesel. Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat. J. Neurophysiol. 28: 229-289, 1965.
10. Hubel, D.H., and T.N. Wiesel. Binocular interaction in striate cortex of kittens reared with artificial squint. J. Neurophysiol. 28: 1041-1059, 1965.
11. Jung, R., and G. Baumgartner. Hemmungsmechanismen und bremsende Stabilisierung an einzelnen Neuronen des optischen cortex. Pflügers Arch. Bd. Physiol. 261: 434-456, 1955.
12. Kuffler, S.W. Discharge patterns and functional organization of mammalian retina. J. Neurophysiol. 16: 37-68, 1953.
13. Lettvin, J.Y., H.R. Maturana, W.S. McCulloch, and W.H. Pitts. What the frog's eye tells the frog's brain. Proc. Inst. Radio Engrs. 47: 1940-1951, 1959.
14. Maturana, H.R. Functional organization of the pigeon retina. In: Information Processing in the Nervous System. Vol. III Proc. XXII. Intern. Congr. Physiol. Sci., Leiden, 1962, edited by R.W. Gerard and J.W. Duyff. Exerpta Medica Fndn., Amsterdam. pp. 170-178.
15. Michael, C.R. Receptive fields of directionally selective units in the optic nerve of the ground squirrel. Science 152: 1092-1094, 1966.
16. Minkowski, M. Experimentelle Untersuchungen über die Beziehungen der Grosshirnrinde und der Netzhaut zu den Primären. Arb. hirnanat. Inst. Zürich. 7: 259-362, 1913.
17. Riesen, A.H. Stimulation as requirement for growth and function in behavioral development. In: Functions of Varied Experience, edited by D.W. Fiske and S.R. Maddi. Homewood, Ill.: Dorsey Press, pp. 57-105, 1961.
18. Talbot, S.A., and W.H. Marshall. Physiological studies on neural mechanisms of visual localization and discrimination. Am. J. Ophthal. 24: 1255-1263, 1941.
19. vonSenden, M. Raum- und Gestaltauffassung bei operierten Blindgeborenen vor und nach der Operation, edited by J. Barth, Leipzig, 1932. Engl. translation under title: Space and Sight. Glencoe, Ill.: Free Press, 1960.
20. Wiesel, T.N., and D.H. Hubel. Effects of visual deprivation on morphology and physiology of cells in the cat's lateral geniculate body. J. Neurophysiol. 26: 978-993, 1963.
21. Wiesel, T.N., and D.H. Hubel. Single cell responses in striate cortex of kittens deprived of vision in one eye. J. Neurophysiol. 26: 1003-1017, 1963.
22. Wiesel, T.N., and D.H. Hubel. Comparison of the effects of unilateral and bilateral eye closures on cortical unit responses in kittens. J. Neurophysiol. 28: 1029-1040, 1965.
23. Wiesel, T.N., and D.H. Hubel. Extent of recovery from the effects of visual deprivation in kittens. J. Neurophysiol. 28: 1060-1072, 1965.
24. Wiesel, T.N., and D.H. Hubel. Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. J. Neurophysiol. 29: 1115-1156, 1966.

25. Wolbarsht, M. L., H. G. Wagner, and E. F. MacNichol, Jr. Receptive fields of retinal ganglion cells: extent and spectral sensitivity. In: The Visual System: Neurophysiology and Biophysics, edited by R. Jung and H. Kornhuber. Berlin: Springer, pp. 170-175, 1961.

BIOMEDICAL SCIENCES INSTRUMENTATION SYMPOSIUM

The Instrument Society of America will hold its Fifth Biomedical Sciences Instrumentation Symposium on May 15-17, 1967 in Albuquerque, New Mexico. The theme of the Symposium will be "Advances in Dynamic Bioinstrumentation for Medicine and Research." For further details write to Dr. R. D. Allison, Scott and White Clinic, Temple, Texas 76501.

THE ROLE OF PHYSIOLOGY IN MEDICAL EDUCATION

WALTER C. RANDALL

Approximately a half century ago, basic science departments of American medical schools were organized as integral branches of medicine, and developed progressively as separate disciplines in human biology, largely in support of teaching programs of clinical departments. In this framework the teaching of basic science was designated "pre-clinical" and relegated to a secondary or supporting role. Comparable attitudes prevailed in considering salaries, influence in affairs of the institution, and stature of the basic science faculty (1). However, the modern major revolution in the biological sciences has been accompanied by radical changes in interdepartmental relationships in medical schools, with resultant "unrest and uncertainty in the manner in which medical students are being prepared in physiology" as emphasized by Dr. Brookhart in his recent Past-President's Address (2). Exasperated cries of "Don't they teach you anything in physiology?" examplify the clinician's dissatisfaction with status quo in many institutions. In fact, the primary instruction in human physiology in some medical schools now falls within the province of the clinical departments. In other schools, most members of physiology departments have neither research nor teaching interests in medical aspects of the discipline. As recently characterized, instruction is sometimes "neatly but begrudgingly relegated to parts of the day and year... Lectures turn out to be a compendium of yesterday's textbooks, and laboratory exercises are frequently contrived and deadly" (1).

We are all aware of the tremendous emphasis which has been placed upon research in physiology departments, sometimes to the disadvantage and even the downgrading of teaching responsibilities. Clauses are inserted in research fellowship appointments stating that only a limited time may be spent in teaching, and even though realistic appraisal of such limitations place little or no restriction on an individual's teaching in a modern department, the onus remains. Most departments have felt the impact of large financial awards for research but relatively little for teaching. There can be little wonder, really, that many young physiologists graduate with the Ph. D. together with the impression that teaching is a chore rather than a challenge and a personally rewarding experience.

The professional physiologist often feels his major commitment is to his graduate students and to the fundamental scholarly pursuits of his research laboratory. He may have reason to believe that his livelihood depends more upon his research productivity than upon his teaching. His lectures may reflect this preoccupation and be poorly related to the particular needs of the medical students. With the burgeoning body of empirical and theoretical knowledge, even the most devoted teacher finds it increasingly difficult to draw the line between what admixture of "old" and "new" should be administered.

On the other hand, concerted effort to improve levels of medical student teaching have received a primary impetus from physiologists. Literally millions of dollars have been spent in updating teaching equip-

ment and facilities. The old U-shaped Hg manometer and smoked kymograph have been replaced by highly sophisticated pressure transducers and electronic recorders in most progressive departments. Medical students have been able to share the sense of "discovery" even in performing old and classical experiments because their records are more precise than those reproduced in current textbooks. Physiology is still as much "alive and exciting" to these fortunate students as ever in the past. Experiments in teaching have been based largely in an intellectual dissatisfaction with status quo in the minds of basic science as well as clinical faculties. In short, the current ferment reflects unrest among conscientious teachers from the total community of medical school faculties.

In recognition of this cascade of evolving problems, most medical schools are experimenting with curriculum. Some are "integrating" teaching efforts and attempting to abolish "departmental lines." Others are eliminating the physiology (and other basic science) department from the organizational framework of the institution. Some would even eliminate the professional physiologist from the medical faculty entirely. There are a few notable instances in which the department name is retained for administrative reasons, but its faculty includes no professionally trained human physiologists (at least in a classical sense). Deans and ad hoc search committees have elected to appoint chairmen to so-called physiology departments even though such appointees have little or no interest in teaching medical physiology. There are those who feel the AAMC should extend the leadership it assumes in the training of medical students to include the training of graduate students in the basic medical sciences (3).

The Council of APS has struggled with the implications and perplexities of these evolving new relationships, and at its Spring Meeting, 1966, asked the Education Committee to consider "The Role of Physiology in Medical Education." A Subcommittee consisting of Drs. Braunwald, Carlson, Cooper, Hardy, Hoff, Mountcastle, Pappenheimer, and Randall accepted the charge to examine the questions, to determine whether a serious problem does in fact exist, and to recommend appropriate action to Council. This Subcommittee reported at the Fall Meeting in Houston that the problem is real, that it is evidently more critical in some institutions than in others, and that it needs careful and systematic study. Among the fundamental questions to which this group has addressed itself are:

1) How are departmental teaching responsibilities being defined and redefined at present?

2) What portends are there for the future of physiology and professional physiologists in medical schools?

3) What are probable relations between teaching manpower needs and supplies for the next decade?

4) Can there be consensus concerning balance between theoretical or molecular (subcellular) biology and organ and system physiology

in the medical curriculum?

5) Is there an ideal course in physiology for medical students?

The Subcommittee has also been requested to consider the emphasis upon research and teaching in modern physiology departments. Can the clinician teach the principles of physiology pertinent to a future role in patient care as well or better than the professional physiologist? What of value may be achieved by the deletion of physiology departments from medical school organization? What losses would be sustained?

With the conviction that "good medical physiology is an essential requirement in the education of a good doctor," the Education Committee has undertaken a course of study which includes an immediate as well as a long-term course of action. The immediate course may be identified in the subject of the 1967 Teaching Session at the Chicago Meeting of the Federation. Dr. William Blake is organizing a program in which a panel will analyze the critical role played by nationally administered examinations in physiology on the determination of content and emphasis in medical physiology courses. The proper and improper uses of National Board Examinations will be considered.

A second course of action includes thoughtful evaluation of modern needs of physiologic training, concepts, and attitudes in the preparation of the medical student for his primary objectives in patient care. Should these approaches be different from those inculcated in training programs designed to produce professional physiologists or physicians desiring a career in scientific aspects of medicine? It is proposed that an attempt be made to study and perhaps evaluate current educational "experiments" in the incorporation of physiology into "core" courses, absorption of physiology and physiologists into clinical departments, education of physicians as "biomedical engineers," etc. Unitary solutions to questions are not anticipated, of course, and the shopworn truism that no single program of training can be meaningful in all institutions is fully recognized. But it is hoped and expected that public forums may be organized around smaller pivotal issues in the complex of problems and that these may be brought to the membership of the Society in a manner which will challenge and excite profitable exchange of ideas and values. These forums, perhaps in the nature of symposia, may be presented at subsequent meetings of the APS. Your reactions will be welcomed by any member of the working Subcommittee.

REFERENCES

1. Wagner, R. R. The basic medical sciences, the revolution in biology and the future of medical education. Yale J. Biol. Med. 35: 1,1962-63.
2. Brookhart, J.M. The APS and medical education. The Physiologist. 9: 353, 1966.
3. Magoun, H.W. Some introductory observations on faculty organization. J. Med. Ed. 39: 57, 1964.