

T-70

CHAPTER 12

Psychosurgery

Karl H. Pribram

Experimental psychosurgery is one of the oldest tools for analysing the mind-brain-behaviour relationship. It is also one of the most misunderstood and misunderstood of the techniques available to the neuroscientist. Because of the disparity between the amount of psychosurgery performed and the disrepute the technique currently enjoys (see for example Deutsch, 1960; Weiskrantz, 1968), I decided to accept this opportunity to discuss my views with the hope of clarifying at least my own stance on this matter.

The issue, as I see it, is as follows: scientists, medical practitioners and laymen alike have the expectation that there are brain 'centres' for psychological 'faculties' (or to use that more modern word, 'factors') and these 'centres' can be discovered simply by removing one or another brain locus and observing the resulting 'deficit' in behaviour. In an earlier paper (*Toward a Science of Neuropsychology*, 1954), I tackled this issue by referring to the clinical neurologists' propensities for improper brain-map making:

'With the increasing popularity of the "interdisciplinary approach" there would be no apologia necessary for a science of neuropsychology were it not for the bad repute into which this area of investigation has fallen. Such well-deserved infamy stems, in part, from the dualism which has plagued all of the behavioral sciences during the past 50 years and, in part, from the excessive "psychologizing" of physiologists and "physiologizing" of psychologists which fills our journals and monographs. The first figure serves to illustrate the results of such schizoid endeavors.'

'The deficiencies of the conceptualizations diagrammed here become obvious once they have been pointed out. What psychophysicist would assign the same numeral to different classes or assign different numerals to the same class? Yet, flagrant disregard of this simple rule of the most elementary of scaling techniques pervades practically every cytoarchitectonic study and is shown at its worst in Figure 12.1. What biologist would, in his own field, classify together such diverse categories as ocular adversive movements, optic awareness, vision intensity, color recognition, place memory, constructive thinking, and constructive action, without some referent of internal consistency and some attempt at ordinal ranking? Finally, where is there available a discussion of the reliability and the validity of the techniques used to construct this monstrosity? The vast

differences between various textbook diagrams and the differences between these and our clinical experience suggest the answer to this question.'

In the two decades since this was written, this psychosurgical disorderliness has spread to experimentalists with grave practical consequences. Only recently I listened to a learned talk on the effects of removal of two parts of the amygdaloid complex. Two tests were used to assay the results: so-called 'active' and 'passive' avoidance conditioning. And, according to what has become custom in psychosurgical circles, 'double dissociation' was obtained: removal of one structure resulted in impaired active, but not passive, avoidance; removal of the other structure had the converse effect. These interesting and important findings were coupled to others that indicated a lowered adrenocorticosteroid response after both lesions. The conclusion drawn was that the amygdala is the 'centre' for the organization of fear which becomes manifest through two separate structures; one subserving active flight, the other a more passive freezing type of reaction. As far as these results and interpretations go, there seems at first little to fault them. But look what happens next: the data become grist in the psychosurgical mill, the Attorney General of the State of California is, according to the newspapers, calling publicly for amygdalectomies on all violent criminals now housed in the state's prisons! In his words, 'amygdalectomy will remove the brain centers responsible for fear and anger' and society will be made safer forever after. The torch is next seized by the president of the American Psychological Association who, in his presidential address, advocates the application of psychosurgery to those in the corridors of power to prevent them from foisting their violent animal natures on the rest of humanity: . . . 'to control the animalistic, barbaric and primitive propensities in man, and subordinate these negatives to the uniquely human, moral, and ethical characteristics of love, kindness, and empathy.' (Specifically the psychotechnologies are to be) . . . 'imposed on all power-controlling leaders and those who aspire to such leadership. The type of psychotechnological medication would be a type of internally imposed disarmament. It would assure that there would be no absurd or barbaric use of power. It would provide the masses of human beings with the security that their leaders would not or could not sacrifice them on the altars of their personal ego pathos vulnerability and instability . . . in medicine, physical diseases are controlled through surgery and medication. But the techniques are not used only to treat the diseases of individuals but are also used preventively . . .' No wonder the scientific community becomes suspicious of a technique which promises to produce so much damage on such scanty evidence.

Experimental psychosurgery could and should be proceeding in a very different direction. To pursue the example of amygdalectomy, the questions might well be asked: Can the procedure be used to analyse the mechanisms that produce the experience we call fear? Are tests of 'active' and 'passive' avoidance truly indicators of fear or are we being misled because, in fact, the

'active' avoidance situation entails memory and the 'passive' avoidance condition entails conflict? Are performances on other tasks disrupted by amygdectomy, tasks which cannot be interpreted to be indicators of 'fear'?

Answers to some of these questions have been obtained: why are they not taken account of? Fear is ordinarily evoked by pain; sensitivity to pain has been found essentially unaltered by amygdectomy (Bagshaw and Pribram, 1968); performances on alteration tasks similar to the avoidance paradigms, but which are indicators of memory functions rather than of fear (e.g. go/no-go delayed alternation), have been shown to be disrupted by amygdectomy (Pribram, Lim, Poppen and Bagshaw, 1966); a memory-based cybernetic mechanism of emotions including the feeling of fear has been detailed (Pribram, 1971). Finally, it has been shown unequivocally that amygdectomy *per se* will *not* reduce violent behaviour unless certain conditions are present in the social environment (Mirsky, Rosvold and Pribram, 1957).

Many of these results have been available for *years*, even decades. Why are they ignored in deliberations on the application of psychosurgery? The argument may be made that the pressing need of the community for a palliative to violence demands action now and that the Gordian knot of the mind-brain-behaviour relationship cannot await unravelling and must be cut through by some more simple approach.

But this cannot be the whole answer. In a less immediately practical area of investigation, the course of psychosurgical history has been similar. In the sixties, a report of the analysis of the functions of other parts of the temporal lobe was published (Stepien, Cordeau and Rasmussen, 1960) and widely acclaimed as providing the answer to the functions of this lobe of the brain. The report claimed to have shown, in monkeys, that the temporal neocortex served the functions of short-term memory and this was contrasted to reports based on the effects of hippocampal psychosurgery in man (Milner, 1958), which suggested the involvement of that structure in long-term memory. The monkey study was performed on four subjects and in a re-analysis a year later was shown to have been erroneously reported (Cordeau and Mahut, 1964). The investigators involved in the original study were certainly sufficiently careful and reported their re-evaluation, yet this has had no effect on subsequent quotations. Further, the reports on man often fail to emphasize the fact that the amygdala as well as the hippocampus were removed in *all* subjects who showed the memory deficit, and recent studies (Warrington and Weiskrantz, 1971) have thrown doubt on the conclusion that the hippocampus is primarily involved in the long-term memory function *per se*.

Again, one may ask, why does the scientific community seize oversimplified and erroneous psychosurgical reports and distort others in the direction of oversimplification and error while ignoring a carefully constructed body of evidence built laboriously with meticulously controlled procedures? Carefully controlled sophisticated psychosurgical studies on temporal neocortex that have held up over decades of replication are legion (see over 100 references listed in the Appendix) and those on amygdala and hippocampus are certainly

not lacking (see Eleftheriou, 1972 and Isaacson and Pribram, 1975). Here, no practical urgency dictates acceptance. Where else in science is sloppiness, insufficient care and control, muddy thinking and downright misrepresentation of results so consistently rewarded, while exquisitely, carefully conducted research is either totally ignored or laughed off as philosophically unsound?

There must be reasons why these attitudes prevail. Many of the reasons are historical in origin, deriving in fact from a philosophical issue which needs exposition. To begin historically, the problem centres on the polemic between those whose brain investigations purported to show that the brain is made up of many suborgans, each of which presumably has some identifiable function, and those whose research pointed toward the integrative functions of the brain as a whole. As I pointed out in *Towards a Science of Neuropsychology* (1954) and as Luria (1973) has so clearly communicated, the issue concerns in part the meaning of the term 'function'. When we ask questions about functions of other organs and organ systems we come up against the same problem. Ask what is the function of the lungs and a clear answer can be given. The lungs are a respiratory organ. But ask about the systems involved in respiration and the lungs are only a part of the answer: red blood cells, tissue fluids, membranes, respiratory regulatory mechanisms of the brain stem, etc., etc. must be taken into account. The same problem besets experimental psychosurgery. Ask what is the function of the eyes (or even of the lateral geniculate nucleus or the occipital cortex) and the ready answer is vision. Ask, on the other hand, what neural systems are involved in vision and the geniculostriate system shares the spotlight with the superior colliculus, tectum, temporal cortex and frontal eye fields, to name only a few of the brain loci that must be included. Of course, the lungs and red cells perform different functions in respiration and so also do the occipital striate and the temporal cortex perform different functions, and it is the job of experimental psychosurgery to specify the difference.

But this is not all. There are also technical problems. Lung tissue and red blood cells are easy to tell apart: not so when different parts of the brain cortex are thought to constitute separate suborgans. Unless care is taken to identify a part of the brain on anatomical, electrophysiological or neurochemical grounds as forming some sort of unit, one may easily be misled into performing psychosurgical experiments which are invalid because only parts of several subsystems are surgically invaded and the resulting disturbance in behaviour therefore lacks uniformity. The procedure of double dissociation of behavioural effects already mentioned, or its extension, the intercept of sums technique (Pribram, 1954), a multiple reciprocal dissociation procedure, provides controls internal to the psychosurgical experiment which, when taken seriously, prevent the type of error and distortion referred to earlier. The procedures of double and multiple dissociation prescribe that we ascribe a function to a part of the brain only when the behavioural change produced by the resection or brain stimulation can be uniquely related to the part under investigation. Thus, we do *not* view the amygdala as the neural locus of the fear mechanism because other parts of the limbic forebrain and of the brain stem core have been shown

to be involved in avoidance behaviour and because, as already mentioned, behaviour on tasks such as delayed alternation is also disrupted.

These psychosurgical procedures of double and multiple dissociation of the effects of brain resection and stimulation have been superbly effective in delineating neural systems related to one or another behavioural task. For example, resections of the frontal and limbic cortex and of the head of the caudate nucleus selectively disrupt alternation behaviour (see reviews in Konorski, Teuber and Zernicki, 1972 and in Pribram and Luria, 1973); resections of the temporal neocortex and of the putamen and tail of the caudate nucleus, as well as some brain stem structures in the region of the tectum selectively disrupt visual discriminations (see Appendix).

I ask again, therefore, why have these clear-cut results been accepted with such hesitation and suspicion by other neuroscientists and the scientific community at large? Results from microelectrode analyses which run into all sorts of sampling problems as well as those of adequate stimulus control are accepted as neurophysiological dogma with hardly any question as to procedure: someone reports that *one* cell in the cortex of the inferior temporal gyrus of monkey is sensitive to a cut-out of a monkey hand (Gross, 1967, 1972) or that a few cells in the suprasylvian gyrus of cat respond to a series of a specified number of flashes (Thompson, Mayers, Robertson and Patterson, 1970) and the data are hailed as indicating the existence of loci containing pontifical (or at least cardinal) neurones, wise to the ways of monkey hands and counting. No one asks over what range of stimuli and permutations of the input was the output of these neurones invariant; no one asks what measure was used to determine output (was it really only that an increase in firing rate was heard by someone over a loudspeaker?); no one asks how many other cells elsewhere in the brain were investigated to ascertain whether there too such sensitivities reside. Answers to such questions are invariably demanded of investigators using psychosurgical techniques and take their toll in time and effort: why is the scientific community so selective in addressing such demands?

I believe a large part of the problem lies in specifying the meaning of the behavioural tasks used to determine the effects of psychosurgery. The concept of a neurone responsive to a hand or that of a neurone which can count is grasped easily. But what is delayed alternation? Or what does a visual discrimination deficit mean? True, the concept vision is easy enough to deal with, but what does it mean to 'discriminate'? Are the changes in alternation and discrimination behaviour to be referred to the domain of memory, or attention, or states of awareness, decision processes or perhaps all of them or none?

Herein lies the difficulty and I believe that this difficulty is akin to that posed by the discovery of relativity in physics. If I ask a physicist to describe your motions, he will, in all good faith, respond: I cannot do so simply, it all depends. It depends on the frame of reference within which you ask for an answer. The ordinary everyday frame of reference provides the answer 'yes, you are still.' Asked from the view of an astronaut ensconced in a space station, however, the

answer would be that you are describing a path of rotation around the earth's axis. Taken from a yet more remote point in the universe, your trajectory would be described by a series of intertwined ellipses.

The problem in psychosurgery is similar but much more in evidence and immediate since the frames of reference composing our internal, psychological, universe have not as yet been specified as clearly and concisely as those composing the external, physical universe.

The problem is compounded, of course, by the fact that the psychosurgical experiments are undertaken to make such specification possible. We know vision from audition because we can readily discern eyes from ears. Thus we should, once the evidence is in, be able to distinguish clearly between fear and anger, between awareness and choice, etc. once we can clearly specify the neural systems and mechanisms involved in each. It is the bootstrap nature of the investigations that makes the results so difficult to communicate.

If this source of difficulty were understood both by the investigators using psychosurgical procedures and by the scientific and lay community, the errors, distortions, and misstatements that are now so common would, I believe, become fewer. First, investigators ought to specify clearly the frame of reference within which their investigation is taking place. This specification must adduce some evidence as to why that particular frame was chosen. Second, the relationship among frames of reference must be clarified. This is the task of psychology as a science, a task which has been sorely neglected. Just what is the relationship between attention and decision; between conditioned avoidance and fear and memory? Which conceptual frames are the more encompassing: memory? awareness? choice? Which are most restricted: vision? fear? operant behaviour? Are there systems within universes or do the universes intersect? Factor analysts have addressed these problems but as yet no generally accepted description of the relationship between psychological frames of reference has emerged. Must psychosurgical procedure come to the rescue of psychology in this sphere of inquiry? And if so will the resultant 'truths' be received with as much reservation as the demonstrated facts on the difference between movement and action (Pribram, 1971, chapters 12 and 13); the difference between visual, auditory and somatosensory amnesias (Pribram, 1969)?

In conclusion, psychosurgery properly employed has to date proved to be one of the most powerful tools for scientifically investigating the mind-brain-behaviour relationship. To the credit of experimentalists using the technique, psychosurgery has never been practised in isolation. It has always utilized to the utmost the available neuroanatomical, electrophysiological, neurochemical and clinical neurological procedures to specify locus and to aid in the interpretation of results. By contrast, neuroanatomists and neurophysiologists routinely attribute memory functions to a structure or suggest that a neural circuit serves as the substrate of emotions when psychosurgical evidence has conclusively demonstrated that this is not so. The argument is always made that such negative results are not definitive; but I have reviewed here the double

and multiple dissociation procedures, which, when properly employed, *do* make the negative findings meaningful in the context of related positive findings.

The results of experimental psychosurgery have had a peculiar fate. Either they have been prematurely (i.e. on the basis of weak evidence) heralded as saviours of troubled mankind and uncritically applied to practical purposes or they have been almost totally ignored by fellow neuroscientists. Thus, the Nobel Prize was awarded for the application of frontal psychosurgery to mentally disturbed patients (see Fulton, Aring and Wortis, 1948 and review by Pribram, 1950). This application was based on the experimental observation of two chimpanzees, one of whom had suffered a brain abscess from improper psychosurgical technique and the other who had not shown the reported effect (Crawford, Fulton, Jacobsen and Wolfe, 1948). Again today, as reviewed here, amygdectomy is proposed as a treatment of choice for violent behaviour when experimental evidence has demonstrated unequivocally that the effects of amygdectomy depend on the social situation in which the amygdectomized subject is placed. *Increased* violence has been reported (Bard and Mountcastle, 1948; Fuller, Rosvold and Pribram, 1957; Rosvold, Mirsky and Pribram, 1954) to follow amygdectomy—not just taming. These results are completely ignored not only by officials who recommend that the procedure be applied to prisoners, but by the scientific community advising the officials.

The failure to accept the results of experimental psychosurgery appears in part due to a failure of the scientists using psychosurgical procedure to specify clearly the frame of reference in which their results are reported. This failure in turn rests on the failure of psychology as a science in putting its house in order: psychologists have not addressed the problem of the relationship between frames of reference in the internal psychological universe, a problem which physicists have long ago clarified with respect to the external physical universe.

Thoughtful and careful psychosurgical experiment can address this question of the variety of frames of reference in psychology and the relationship among them. While continuing to add to the accretion of brain facts, this issue of clarifying the frames of reference in which mind-brain-behaviour data are to be placed is probably the most pressing that faces the scientific use of psychosurgery today. Resolving this issue would make a major contribution not only to behavioural and neuroscience, but to the entire intellectual community concerned with the relationship of humanistic and scientific enterprise.

12.1 REFERENCES

- Bagshaw, M. H. and Pribram, J. D. (1968) Effect of amygdectomy on stimulus threshold of the monkey. *Exp. Neurol.*, **20**, 197–202
- Bard, P. and Mountcastle, V. B. (1948) Some forebrain mechanisms involved in expression of rage with special reference to suppression of angry behavior. *Res. Publ. Ass. nerv. ment. Dis.*, **27**, 362–404

- Cordeau, J. P. and Mahut, H. (1964) Some long-term effects of temporal lobe resections on auditory and visual discrimination in monkeys. *Brain*, **87**, (1), 177-188
- Crawford, M. P., Fulton, J. F., Jacobsen, C. F. and Wolfe, J. B. (1948) Frontal Lobe Ablation in Chimpanzee: A Resume of 'Becky' and 'Lucy'. In Fulton, J. F., Aring, C. D. and Wortis, S. B. (Eds.) *The Frontal Lobes* (ARNMD series, volume XXVII), The Williams and Williams Company, Baltimore
- Deutsch, J. A. (1960) *The Structural Basis of Behavior*, The University of Chicago Press, Chicago
- Eleftheriou, B. E. (Ed.) (1972) *The Neurobiology of the Amygdala*, Plenum Press, New York
- Fuller, J. L., Rosvold, H. E. and Pribram, K. H. (1957) The effect on affective and cognitive behavior in the dog of lesions of the pyriform-amygdala-hippocampal complex. *J. comp. physiol. Psychol.*, **50**, 89-96
- Fulton, J. F., Aring, C. D. and Wortis, S. B. (Eds.) (1948) *The Frontal Lobes* (ARNMD series, volume XXVII), The Williams and Williams Company, Baltimore
- Gross, C. G., Schiller, P. H., Wells, C. and Gerstein, G. L. (1967) Single unit activity in temporal association cortex of the monkey. *J. Neurophysiol.*, **30**, 833-843
- Gross, C. G., Rocha-Miranda, C. E. and Bender, D. B. (1972) Visual properties of neurons in inferotemporal cortex of the macaque. *J. Neurophysiol.*, **35**, 96-111
- Isaacson, R. L. and Pribram, K. H. (1975) *The Hippocampus; A Comprehensive Treatise*, Plenum Press, New York
- Konorski, J., Teuber, H. L. and Zernicki, B. (Eds.) (1972) The Frontal Granular Cortex and Behavior. *Acta Neuro-Biologicae Experimentalis*. International Congress of Physiological Sciences, 1971, Jablona, Poland, 32(2)
- Luria, A. R. (1973) *The Working Brain: An Introduction to Neuropsychology*, The Penguin Press, London
- Milner, B. (1958) Psychological defects produced by temporal lobe excision. *Res. Publ. Ass. nerv. ment. Dis.*, **36**, 244-257
- Mirsky, A. J., Rosvold, H. E. and Pribram, K. H. (1957) Effects of cingulectomy on social behavior in monkeys. *J. Neurophysiol.*, **20**, 588-601
- Pribram, K. H. (1950) Psychosurgery in midcentury. *Surg. Gynec. Obstet.*, **91**, 364-367
- Pribram, K. H. (1954) Toward a Science of Neuropsychology: (Method and Data). In Patton, R. A. (Ed.) *Current Trends in Psychology and the Behavioral Sciences*. University of Pittsburgh Press, Pittsburgh
- Pribram, K. H. (1969) The Amnesic Syndromes: Disturbances in Coding? In Talland, G. A. and Waugh, N. C. (Eds.) *Pathology of Memory*, Academic Press, New York
- Pribram, K. H. (1971) *Languages of the Brain*, Prentice-Hall, Englewood Cliffs, New Jersey
- Pribram, K. H., Lim, H., Poppen, R. and Bagshaw, M. H. (1966) Limbic lesions and the temporal structure of redundancy. *J. comp. physiol. Psychol.*, **61**, 368-373
- Pribram, K. H. and Luria, A. R. (Eds.) (1973) *The Psychophysiology of the Frontal Lobes*, Academic Press, New York
- Rosvold, H. E., Mirsky, A. F. and Pribram, K. H. (1954) Influence of amygdalectomy on social interaction in a monkey group. *J. comp. physiol. Psychol.*, **47**, 173-178
- Stepien, L. S., Cordeau, J. P. and Rasmussen, T. (1960) The effect of temporal lobe and hippocampal lesions on auditory and visual recent memory in monkeys. *Brain*, **83**, 470
- Thompson, R. F., Mayers, K. S., Robertson, R. T. and Patterson, C. J. (1970) Number coding in association cortex of the cat. *Science*, **168**, 271-273
- Warrington, E. K. and Weiskrantz, L. (1971) Organizational aspects of memory in amnesic patients. *Neuropsychologia*, **9**, 67-73
- Weiskrantz, L. (Ed.) (1968) *Analysis of Behavioral Change*, Harper and Row, New York

12.2 APPENDIX

- Ades, H. W. (1946) Effects of extirpation of prestriate cortex on learned visual discrimination in monkeys. *J. Neuropath. Exp. Neurol.*, **5**, 60-65
- Ades, H. W. and Raab, D. H. (1949) Effect of preoccipital and temporal decortication on learned visual discrimination in monkey. *J. Neurophysiol.*, **12**, 101-108
- Bagshaw, M. H., Mackworth, N. H. and Pribram, K. H. (1972) The effect of resections of the inferotemporal cortex or the amygdala on visual orienting and habituation. *Neuropsychologia*, **10**, 153-162
- Blum, J. S., Chow, K. L. and Pribram, K. H. (1950) A behavioral analysis of the organization of the parieto-temporo-preoccipital cortex. *J. comp. Neurol.*, **93**, 53-100
- Brown, T. S. (1963) Olfactory and visual discrimination in the monkey after selective lesions of the temporal lobe. *J. comp. physiol. Psychol.*, **56**, 764-768
- Brown, T. S., Rosvold, H. E. and Mishkin, M. (1963) Olfactory discrimination after temporal lobe lesions in monkeys. *J. comp. physiol. Psychol.*, **56**, 190-195
- Butler, C. R. (1969) Is there a memory impairment in monkeys after inferior temporal lesions. *Brain Res.*, **13**, 383-393
- Butter, C. M. (1968) The effect of discrimination training on pattern equivalence in monkeys with inferotemporal and lateral striate lesions. *Neuropsychologia*, **6**, 27-40
- Butter, C. M. (1969) Impairments in selective attention to visual stimuli in monkeys with inferotemporal lateral striate lesions. *Brain Res.*, **12**, 374-383
- Butter, C. M. and Doehman, S. R. (1968) Size discrimination and transposition in monkeys with striate and temporal lesions. *Cortex*, **4**, 35-46
- Butter, C. M. and Gekoski, W. L. (1966) Alterations in pattern equivalence following inferotemporal and lateral striate lesions in rhesus monkeys. *J. comp. physiol. Psychol.*, **61**, 309-312
- Butter, C. M. and Hirtzel, M. (1970) Impairment in sampling visual stimuli in monkeys with inferotemporal lesions. *Physiol. Behav.*, **5**, 369-370
- Butter, C. M., Mishkin, M. and Rosvold, H. E. (1965) Stimulus Generalization in Monkeys with Inferotemporal and Lateral Occipital Lesions. In Mostofsky D. I. (Ed.) *Stimulus Generalization*, Stanford University Press, Stanford
- Chow, K. L. (1951) Effects of partial extirpations of the posterior association cortex on visually mediated behavior. *Comp. Psychol. Monogr.*, **20**, 187-217
- Chow, K. L. (1952) Further studies on selective ablation of associative cortex in relation to visually mediated behavior. *J. comp. physiol. Psychol.*, **45**, 109-118
- Chow, K. L. (1954a) Effects of temporal neocortical ablation on visual discrimination learning sets in monkeys. *J. comp. physiol. Psychol.*, **47**, 194-198
- Chow, K. L. (1954b) Lack of behavioral effects following destruction of some thalamic association nuclei in monkey. *Arch. Neurol. Psychiat.*, **71**, 762-771
- Chow, K. L. (1961) Anatomical and Electrographical Analysis of Temporal Neocortex in Relation to Visual Discrimination Learning in Monkeys. In Delafresnye, J. F., Fessard, A. and Konorski, J. (Eds.) *Brain Mechanisms and Learning*, Blackwell Scientific Publications, Oxford
- Chow, K. L. and Orbach, J. (1957) Performance of visual discriminations presented tachistoscopically in monkeys with temporal neocortical ablations. *J. comp. physiol. Psychol.*, **50**, 636-640
- Chow, K. L. and Survis, J. (1958) Retention of overlearned visual habit after temporal cortical ablation in monkey. *AMA Arch. Neurol. and Psychiat.*, **79**, 640-646
- Cowey, A. (1967) Perimetric study of field defects in monkeys after cortical and retinal ablations. *Quart. J. Exp. Psychol.*, **19**, 232-245
- Cowey, A. and Gross, C. G. (1970) Effects of foveal prestriate and inferotemporal lesions on visual discrimination by rhesus monkeys. *Exp. Brain Res.*, **11**, 128-144
- Cowey, A. and Weiskrantz, L. (1963) A perimetric study of visual field defects in monkeys. *Quart. J. Exp. Psychol.*, **15**, 91-115

- Cowey, A. and Weiskrantz, L. (1967) A comparison of the effects of inferotemporal and striate cortex lesions on the visual behavior of rhesus monkeys. *Quart. J. Exp. Psychol.*, **19**, 246-253
- Dalby, D. A., Meyer, D. R. and Meyer, P. M. (1970) Effects of occipital neocortical lesions upon visual discrimination in the cat. *Physiol. Behav.*, **5**, 727-734
- Dewson, J. H., III, Nobel, K. W. and Pribram, K. H. (1966) Corticofugal influence at cochlear nucleus of the cat: some effects of ablation of insular temporal cortex. *Brain Res.*, **2**, 151-159
- Dewson, J. H., III, Pribram, K. H. and Lynch, J. (1969) Effects of ablations of temporal cortex upon speech sound discrimination in the monkey. *Exp. Neurol.*, **24**, 579-591
- Ettlinger, G. (1957) Visual discrimination following successive unilateral temporal excisions in monkeys. *J. Physiol. (London)*, **140**, 38-39
- Ettlinger, G. (1959) Visual discrimination following successive temporal ablations in monkeys. *Brain*, **82**, 232-250
- Ettlinger, G. (1962) Relationship between test difficulty and the visual impairment in monkeys with ablations of temporal cortex. *Nature*, **196**, 911-912
- Ettlinger, G. and Gautrin, D. (1971) Visual discrimination performance in the monkey: the effect of unilateral removals of temporal cortex. *Cortex*, **7**, 317-331
- Evarts, E. V. (1952) Effect of ablation of prestriate cortex on auditory-visual association in monkey. *J. Neurophysiol.*, **15**, 191-200
- Gerbrandt, L. K., Spinelli, D. N. and Pribram, K. H. (1970) The interaction of visual attention and temporal cortex stimulation on electrical activity evoked in the striate cortex. *Electroenceph. clin. Neurophysiol.*, **29**, 146-155
- Gross, C. G. (1972) Visual Functions of Inferotemporal Cortex. In Jung, R. (Ed.) *Handbook of Sensory Physiology*, **7**, part 3B. Springer-Verlag, Berlin
- Gross, C. G. Inferotemporal Cortex and Vision. In Stellar, E. and Sprague, J. M. (Eds.) *Progress in Physiological Psychology*, Vol. 5, Academic Press, New York (in press)
- Gross, C. G., Bender, D. B. and Rocha-Miranda, C. E. (1969) Visual receptive fields of neurons in inferotemporal cortex of the monkey. *Science*, **166**, 1303-1305
- Gross, C. G., Cowey, A. and Manning, F. J. (1971) Further analysis of visual discrimination deficits following foveal prestriate and inferotemporal lesions in rhesus monkeys. *J. comp. physiol. Psychol.*, **76**, 1-7
- Humphrey, N. K. and Weiskrantz, L. (1967) Vision in monkeys after the removal of the striate cortex. *Nature (Lond.)*, **215**, 595-597
- Humphrey, N. K. and Weiskrantz, L. (1969) Size constancy in monkeys with inferotemporal lesions. *Quart. J. of Exp. Psychol.*, **21**, 225-238
- Iversen, S. D. (1970) Interference and inferotemporal memory deficits. *Brain Res.*, **19**, 277-289
- Iversen, S. D. and Weiskrantz, L. (1964) Temporal lobe lesions and memory in the monkey. *Nature*, **201**, 740-742
- Iversen, S. D. and Weiskrantz, L. (1967) Perception of redundant cues by monkeys with inferotemporal lesions. *Nature*, **214**, 241-243
- Iversen, S. D. and Weiskrantz, L. (1970) An investigation of a possible memory defect produced by inferotemporal lesions in the baboon. *Neuropsychologia*, **8**, 21-36
- Iwai, E. and Mishkin, M. (1968) Two Visual Foci in the Temporal Lobe of Monkeys. In Yoshii, N. and Buchwald, N. A. (Eds.) *Neuropsychological Basis of Learning and Behavior*, Osaka University Press, Osaka, Japan
- Iwai, E. and Mishkin, M. (1969) Further evidence on the locus of the visual area in the temporal lobe of the monkey. *Exp. Neurol.*, **25**, 585-594
- Jones, B. and Mishkin, M. (1972) Limbic lesions and the problem of stimulus-reinforcement associations. *Exp. Neurol.*, **36**, 362-377
- Klüber, H. (1936) An analysis of the effects of removal of the occipital lobes in monkeys. *J. Psychol.*, **2**, 49-61

- Kluver, H. (1941) Visual functions after removal of the occipital lobes. *J. Psychol.*, **11**, 23-45
- Kluver, H. (1942) Functional significance of the geniculo-striate system. *Biol. Symp.*, **7**, 253-299
- Kluver, H. and Bucy, P. C. (1937) 'Psychic blindness' and other symptoms following bilateral temporal lobectomy in rhesus monkeys. *Amer. J. Physiol.*, **119**, 352-353
- Kluver, H. and Bucy, P. C. (1938) An analysis of certain effects of bilateral temporal lobectomy in the rhesus monkey, with special reference to 'psychic blindness'. *J. Physiol.*, **5**, 33-54
- Kluver, H. and Bucy, P. C. (1939) Preliminary analysis of functions of the temporal lobes in monkeys. *Arch. Neurol. Psychiat.*, **42**, 979-1000
- Lashley, K. S. (1950) In Search of the Engram. In *Physiological Mechanisms in Animal Behavior*, Society for Experimental Biology (Great Britain), Academic Press, New York
- Manning, F. J. (1971) Punishment for errors and visual discrimination learning by monkeys with inferotemporal cortex lesions. *J. comp. physiol. Psychol.*, **75**, 146-152
- Manning, F. J. (1971) The selective attention 'deficit' of monkeys with ablations of foveal prestriate cortex. *Psychonomic Science*, **25**, 291-292
- Manning, F. J. (1972) Serial reversal learning by monkeys with inferotemporal or foveal prestriate lesions. *Brain Res.*, **8**, 177-181
- Manning, F. J., Gross, C. G. and Cowey, A. (1971) Partial reinforcement: effects on visual learning after foveal prestriate and inferotemporal lesions. *Physiol. Behav.*, **6**, 61-64
- Meyer, D. R., Harlow, H. F. and Ades, H. W. (1951) Retention of delayed responses and proficiency in oddity problems by monkeys with preoccipital ablations. *Amer. J. Psychol.*, **64**, 391-396
- Milner, B. (1968) Visual recognition and recall after right temporal-lobe excision in man. *Neuropsychologia*, **6**, 191-209
- Mishkin, M. (1954) Visual discrimination performance following partial ablations of the temporal lobe: II Ventral surface vs. hippocampus. *J. comp. physiol. Psychol.*, **47**, 187-193
- Mishkin, M. (1958) Visual discrimination impairment after cutting cortical connections between the inferotemporal and striate areas in monkeys. *Amer. Psychol.*, **13**, 414 (abstract)
- Mishkin, M. (1966) Visual Mechanisms Beyond the Striate Cortex. In Russell, R. (Ed.) *Frontiers of Physiological Psychology*, Academic Press, New York
- Mishkin, M. (1972) Cortical Visual Areas and Their Interaction. In Karczmar, A. G. and Eccles, J. C. (Eds.) *The Brain and Human Behaviour*, Springer-Verlag, Berlin
- Mishkin, M. and Hall, M. (1955) Discriminations along a size continuum following ablation of the inferior temporal convexity in monkeys. *J. comp. physiol. Psychol.*, **48**, 97-101
- Mishkin, M. and Pribram, K. H. (1954) Visual discrimination performance following partial ablations of the temporal lobe: I. Ventral vs. lateral. *J. comp. physiol. Psychol.*, **47**, 14-20
- Mize, R. R., Wetzell, A. B. and Thompson, V. E. (1971) Contour discrimination in the rat following removal of posterior neocortex. *Physiol. Behav.*, **6**, 241-246
- Orbach, J. and Fantz, R. L. (1959) Differential effects of temporal neocortical resections on overtrained and non-overtrained visual habits in monkeys. *J. comp. physiol. Psychol.*, **51**, 126-129
- Pasik, P., Pasik, T., Battersby, W. S. and Bender, M. B. (1958) Visual and tactual discrimination by macaques with serial temporal and parietal lesions. *J. comp. physiol. Psychol.*, **51**, 427-436

- Pasik, T., Pasik, P., Battersby, W. S. and Bender, M. B. (1960) Factors influencing visual behavior of monkeys with bilateral temporal lobe lesions. *J. comp. physiol. Psychol.*, **115**, 89-102
- Pasik, T. and Pasik, P. (1971) The visual world of monkeys deprived of striate cortex: effective stimulus parameters and the importance of the accessory optic system. *Vision Res.*, Suppl. 3, 419-435
- Pribram, K. H. (1954) Toward a Science of Neuropsychology: (Method and Data) In Patton, R. A. (Ed.) *Current Trends in Psychology and the Behavioral Sciences*, University of Pittsburgh Press, Pittsburgh
- Pribram, K. H. (1958) Neocortical Function in Behavior. In Harlow, H. F. and Woolsey, C. N. (Eds.) *Biological and Biochemical Bases of Behavior*, University of Wisconsin Press, Madison
- Pribram, K. H. (1959) On the neurology of thinking. *Behav. Sci.*, **4**, 265-287
- Pribram, K. H. (1960) A review of theory in physiological psychology. In *Annual Review of Psychology*, Vol. 11, Annual Reviews, Palo Alto
- Pribram, K. H. (1960) The Intrinsic Systems of the Forebrain. In Field, J., Magoun, H. W. and Hall, V. E. (Eds.) *Handbook of Physiology, Neurophysiology II*, American Physiological Society, Washington
- Pribram, K. H., Blehert, S. R. and Spinelli, D. N. (1966) The effects on visual discrimination of crosshatching and undercutting the inferotemporal cortex of monkeys. *J. comp. physiol. Psychol.*, **62**, 358-364
- Pribram, K. H. (1967) Neurophysiology and Learning: Memory and the Organization of Attention. In Lindsley, D. B. and Lumsdaine, A. A. (Eds.) *Brain Function and Learning*, University of California Press, Berkeley
- Pribram, K. H. (1969) The Amnesic Syndromes: Disturbances in Coding? In Talland, G. A. and Waugh, N. C. (Eds.), *Pathology of Memory*, Academic Press, New York
- Pribram, K. H. (1971) *Languages of the Brain*, Prentice-Hall, Englewood Cliffs, New Jersey
- Pribram, K. H. and Bagshaw, M. H. (1953) Further analysis of the temporal lobe syndrome utilizing frontotemporal ablations in monkeys. *J. comp. physiol. Psychol.*, **99**, 347-375
- Pribram, K. H. and Barry, J. (1956) Further behavioral analysis of the parietotemporo-precipital cortex. *J. Neurophysiol.*, **19**, 99-106
- Pribram, K. H. and Mishkin, M. (1955) Simultaneous and successive visual discrimination by monkeys with inferotemporal lesions. *J. comp. physiol. Psychol.*, **48**, 198-202
- Pribram, K. H., Spinelli, D. N. and Reitz, S. L. (1969) Effects of radical disconnection of occipital and temporal cortex on visual behavior of monkeys. *Brain*, **92**, 301-312
- Raisler, R. L. and Harlow, H. F. (1965) Learned behavior following lesions of posterior association cortex in infant, immature, and preadolescent monkeys. *J. comp. physiol. Psychol.*, **60**, 167-174
- Reitz, S. L. and Gerbrandt, L. K. (1971) Pre- and post-trial temporal lobe seizures in monkeys and memory consolidation. *J. comp. physiol. Psychol.*, **74**, 179-184
- Riopelle, A. J. and Ades, H. W. (1953) Visual discrimination performance in rhesus monkeys following extirpation of prestriate and temporal cortex. *J. Genet. Psychol.*, **83**, 63-77
- Riopelle, A. J. and Churukian, G. A. (1958) The effect of varying the intertrial interval in discrimination learning by normal and brain-operated monkeys. *J. comp. physiol. Psychol.*, **51**, 199-215
- Riopelle, A. J., Harlow, H. F., Settlege, P. H. and Ades, H. W. (1951) Performance of normal and operated monkeys on visual learning tests. *J. comp. physiol. Psychol.*, **44**, 283-289
- Rosvold, H. E., Mishkin, M. and Szwarcbart, M. K. (1958) Effects of subcortical lesions in monkeys on visual-discrimination and single-alternation performance. *J. comp. physiol. Psychol.*, **51**, 437-444

- Schilder, P., Pasik, T. and Pasik, P. (1971) Extrageniculostriate vision in the monkey. II. Demonstration of brightness discrimination. *Brain Res.*, **32**, 383-398
- Schwartzkroin, P. A., Cowey, A. and Gross, C. G. (1969) A test of an 'efferent model' of the function of inferotemporal cortex in visual discrimination. *Electroenceph. Clin. Neurophysiol.*, **27**, 594-600
- Semmes, J. (1972) Somesthetic Effects of Damage to the Central Nervous System. In Jung, R. (Ed.) *Handbook of Sensory Physiology*, Springer-Verlag, Berlin
- Stamm, J. S. and Knight, M. (1963) Learning of visual tasks by monkeys with epileptogenic implants in temporal cortex. *J. comp. physiol. Psychol.*, **56**, 254-260
- Stamm, J. S. and Pribram, K. H. (1960) Effects of epileptogenic lesions in frontal cortex on learning and retention in monkeys. *J. Neurophysiol.*, **23**, 552-563
- Symmes, D. (1965) Flicker discrimination by brain-damaged monkeys. *J. comp. physiol. Psychol.*, **60**, 470-473
- Sperry, R. W. (1959) Preservation of high-order function in isolated somatic cortex in callosum-sectioned cats. *J. Neurophysiol.*, **22**, 78-87
- Vaughan, H. G., Jr. and Gross, C. G. (1969) Cortical responses to light in unanaesthetized monkeys and their alteration by visual system lesions. *Exp. Brain Res.*, **8**, 19-36
- Weiskrantz, L. (1963) Contour discrimination in a young monkey with striate cortex ablation. *Neuropsychologia*, **1**, 145-164
- Weiskrantz, L. (1967) Central Nervous System and the Organization of Behavior. In Kimble, D. P. (Ed.) *The Organization of Recall*, The New York Academy of Sciences, New York
- Weiskrantz, L. (1970) Visual Memory and the Temporal Lobe of the Monkey. In Whalen, R. E., Thompson, R. F., Verzeano, M. and Weinberger, N. M. (Eds.) *The Neural Control of Behavior*, Academic Press, New York
- Weiskrantz, L. (1972) Behavioral analysis of the monkey's nervous system. *Proc. R. Soc. Lond. B.*, **182**, 427-455
- Weiskrantz, L. and Cowey, A. (1963) Striate cortex lesions and visual acuity of the rhesus monkey. *J. comp. physiol. Psychol.*, **56**, 225-231
- Weiskrantz, L. and Cowey, A. (1970) Filling in the Scotoma: A Study of Residual Vision After Striate Cortex Lesions in Monkeys. In Stellar, E. and Sprague, J. M. (Eds.) *Progress in Physiological Psychology*, Vol. 3, Academic Press, New York
- Weiskrantz, L. and Mishkin, M. (1958) Effect of temporal and frontal cortical lesions on auditory discrimination in monkeys. *Brain*, **81**, 406-414
- Wilson, M. (1957) Effects of circumscribed cortical lesions upon somesthetic and visual discrimination in the monkey. *J. comp. physiol. Psychol.*, **50**, 630-635
- Wilson, M. (1968) Inferotemporal cortex and the processing of visual information in monkeys. *Neuropsychologia*, **6**, 135-140
- Wilson, M. and Kaufman, H. M. (1969) Effect of inferotemporal lesions upon processing of visual information in monkeys. *J. comp. physiol. Psychol.*, **69**, 44-48
- Wilson, M., Kaufman, H. M., Zieler, R. E. and Lieb, J. P. (1972) Visual identification and memory in monkeys with circumscribed inferotemporal lesions. *J. comp. physiol. Psychol.*, **78**, 173-183
- Wilson, M., Rothblat, L. and Kirsten, E. (1968) Frequency and recency of reward and inferotemporal lesions. *Psychonomic Science*, **11**, 237-238
- Wilson, M., Wilson, W. A., Jr. and Sunenshine, H. S. (1968) Perception, learning and retention of visual stimuli by monkeys with inferotemporal lesions. *J. comp. Physiol. Psychol.*, **65**, 404-412
- Wilson, W. A., Jr. and Mishkin, M. (1959) Comparison of the effects of inferotemporal and lateral occipital lesions on visually guided behavior in monkeys. *J. comp. physiol. Psychol.*, **52**, 10-17