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The Role of Cortico-Cortical Connections

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THE PROBLEM

At the end of a conference such as this, in which the flow of data was almost inundating, it would be foolish to try to "summarize" the reports. What I wish to do instead is to address a problem central to all of the reports: How do the cerebral commissures in particular, and cortico-cortical connections in general, function? In order to discuss this problem I will focus on two presentations: briefly on that of Maryse Lassonde, and at greater length, the one by Mortimer Mishkin.

First, a few words about Lassonde's beautiful presentation, which made a most convincing case for the proposition that the corpus callosum functions as an excitatory and not as an inhibitory pathway. This proposition received ample support from several of the other presentations given over the following days. However, I wish to point out that excitation may well function to produce inhibition, as shown by Lassonde's own data, which constituted her doctoral thesis [1977]. She performed an experiment in which she investigated the effects of electrical stimulation of the basal ganglia and cerebral cortex on the organization of receptive fields of single neurons in the primary visual cortex. She found, among other results, that contralateral cortical stimulation, irrespective of location (frontal or posterior), decreased the size of the receptive field. No direct test was made as to whether the effect of stimulation was mediated by the corpus callosum. Nonetheless, there was no callosal excitation evident as an end result in these experiments.

I mention this because I believe that statements regarding the inhibitory or excitatory functions of the commissures and cortico-cortical connections in general need to be qualified. There may be in fact an overall inhibitory or excitatory effect of commissural or other cortico-cortical activity. Often, however, as in the Lassonde physiological experiments, excitation leads to inhibition at the microneurological (receptive field, dendritic) level as an end result. The effects on behavior and on perception of such changes would not appear simply as inhibition or excitation, but as changes in *patterns* of rocessing. It is the organization of these processing patterns that I next ant to discuss.

DISCONNECTION SYNDROMES IN MONKEYS

Within the framework of this conference, the theme of my presentation nay seem misplaced: I will focus on some intrahemispheric connections as vell as on the interhemispheric. In part, this is because my expertise lies in he distinctions in functions between the frontal and posterior cortex, and he relationship between the frontal cortex and the limbic forebrain. At the ame time, I am no stranger to studies using callosotomy to solve specific roblems—although my name has not appeared on these studies, since they vere performed primarily by graduate and postdoctoral students in the aboratory. Some have not been published. The first of the experiments was eported by Ettlinger [1959b]. Mishkin and I helped design the experiment nd carried out the surgery. It is this line of research that Mishkin has ursued in the work reported here.

Another use made in the laboratory of the "split-brain" preparation has een to ascertain whether the effects of amygdalectomy are more related to he processing of sensory input or to a defective response mechanism [Minurn, 1952; Barrett, 1969]. The results were in accord with the theme of this onference: When using the amygdalectomized hemisphere, the monkeys ailed to utilize information gained by using the other, normal hemisphere, ut were able to learn visual discriminations normally. Thus the effect of mygdalectomy (e.g., taming, oral behavior) was inferred to influence a *re*decisional or relatively independent (parallel) stage of visual processing. This result, as will become evident below, runs counter to Mishkin's proosal for the serial operation of a striate → prestriate → temporal cortex → mygdala circuit.

In still another set of experiments with callosectomized monkeys [Reitz-Blehert, 1968] additional difficult-to-explain findings resulted that make vorthwhile a reevaluation of the entire program of experiments so ably erformed and described here and elsewhere by Mishkin. So please bear vith me while I delve into the problems raised by disconnection syndromes, hose produced by severing intrahemispheric cortico-cortical tracts as well s interhemispheric commissures.

ALTERNATIVE MODELS OF HIERARCHICAL PROCESSING SYSTEMS

Mishkin has presented a carefully documented brain model of visual rocessing, pointing out not only the evidence in support of his model but lso points where the model runs into some difficulty. I now want to make a case for an alternative that had its inception one evening more than 30 ears ago when Mishkin, Lashley and I were discussing how the sensory node specificity of the inferotemporal (and in fact much of the posterior intrinsic "association") cortex of monkeys comes about. We had discovered these sensory mode-specific functions some years earlier [Blum et al., 1950; Pribram and Bagshaw, 1953; Mishkin and Pribram, 1954; Pribram, 1954, 1958a,b; Pribram and Barry, 1956; Dewson et al., 1969] and Evarts [1952] had made extensive removals of the prestriate cortex with no lasting effect on visual discrimination learning and performance, such as that which follows resections of the inferotemporal cortex. There is no known direct input to the inferotemporal cortex from the primary visual cortex or from the lateral geniculate nucleus of the thalamus, so how does the inferotemporal cortex receive the visual information necessary to allow the monkey to make visual discriminations when the indirect paths through the prestriate cortex have been removed?

I suggested that perhaps visual input was not the critical factor in visual discrimination learning and performance; that instead, it was the output from the inferotemporal cortex to the visual system that is critical. Neither Lashley nor Mishkin thought much of the suggestion, dismissing the issue as being the result of incomplete removal of prestriate tissue. Thus the model that Mishkin presented here is a result of many years of effort to trace visual input to the inferotemporal cortex. Meanwhile, I pursued the possibility that the visual specificity of the inferotemporal cortex could be due to its output rather than to its input characteristics.

Some Evidence

First I had to establish the fact that more complete resections of the prestriate cortex would still leave the monkeys able to perform the visual discrimination tasks. Several experiments accomplished this [Pribram et al., 1969; Ungerleider et al., 1977; Cardu et al., in preparation]. All of these monkeys were able to perform visual discriminations, most without deficit despite deep cuts into the optic radiations that course just below the prestriate cortex, cuts that resulted in considerable degeneration of the lateral geniculate nucleus with resulting scotomata and often long periods of postoperative blindness. The important consideration has been to delay postoperative testing until the effects of geniculostriate damage has been overcome. Sometimes this takes as long as 6 months, during which the monkeys are trained to respond to peanuts suspended by a thread and dangled within the remaining functional visual field. If this is done, performance on formal tests has shown surprisingly little if any effect of the lesion (except as noted below, in size constancy).

There was still the possibility of an indirect visual input from the lateral geniculate nucleus to the pulvinar and then to the inferotemporal cortex. This possibility was ruled out by Mishkin [1973], who made large pulvinar lesions in some 27 monkeys and found no effect on visual discrimination behavior. (More recently Lindsley [1984] has found such effects but only when the cues are presented tachistoscopically.) Charles Gross [1973] pointed out that the possibility still remained that either the direct cortical or the indirect thalamic route could function in the absence of the other. This last alternative was also ruled out in a study in which both extensive prestriate and pulvinar lesions were made without impairing visual discrimination performance [Ungerleider et al., 1977].

Next, the possibility that there were in fact corticofugal pathways from the inferotemporal cortex to the visual system had to be explored. Tracts ending in the lateral geniculate nucleus would have solved our problem, but silver stains failed to show any input from the inferotemporal cortex to thalamus except to the pulvinar, from which the corticopetal fibers to the inferotemporal cortex arise. Instead, the deeper layers of the superior colliculus and the pretectal region turned out to be the prime corticofugal targets [Whitlock and Nauta, 1956].

More surprising was a heavy projection from the inferotemporal cortex to the putamen, which was demonstrated both by anatomical and electrophysiological techniques [Reitz and Pribram, 1969; Pribram, unpublished]. How these connections influence the visual system remains to be determined, but I have some preliminary evidence that the pathway—putamen to globus pallidus to reticular nucleus to the thalamus—might be critical. What is known is that cross-hatching of the inferotemporal cortex results in no deficit in visual discrimination learning or performance, while undercutting this cortex or making lesions in the neighborhood of the tail of the caudate nucleus and putamen do [Pribram et al., 1966; Buerger et al., 1974].

A Cortico-Subcortical Hierarchy

Despite these differences, there are many similarities between the models that Mishkin and I have developed. In an invited address at the Eastern Psychological Association Meetings in 1954, I pointed out that the sensorimotor systems must be hierarchically organized in the sense that resections of each succeeding processing stage leave more and more of the sensory-guided behavior intact. This was not a novel idea. Henry Head and Carl von Monikov, among others, had made the point previously, and Alexander Romanovitch Luria has emphasized it more recently. In my own writing, the idea was central in "The Intrinsic Systems of the Forebrain," my contribution to the *Handbook of Physiology* [1960].

This contribution also made the point about which Mishkin and I are at odds. The subtitle to that chapter was "An Alternative to the Transcortical Reflex," but unfortunately the editors decided to delete it, perhaps for the same reason that Lashley and Mishkin felt uncomfortable with the proposal. Let me therefore once again describe the data that make me challenge the transcortical model, with which, by the way, I would also feel most comfortable were there not so much evidence against it.

The hierarchical model is based on the fact that excision of the eyes leaves the organism totally blind, while after resections of the primary visual cortex there remains considerable residual vision [see Weiskrantz and Cowey, 1970; Weiskrantz et al. 1974]. And as has been pointed out, resection of the prestriate cortex leaves the monkey still more intact. However, this does not mean that no visual deficit occurs: size constancy is impaired; the monkeys respond to retinal image size, ignoring the cues that ordinarily relate size to distance [Ungerleider et al., 1977].

Inferotemporal resections also leave the organism with considerable visual skills. As Mishkin pointed out, the relation of the visual system to space is carried out cortically in proximity to the somatosensory systems in the parietal lobe [Pribram and Barry, 1956; Wegener, 1968; Wilson, 1975; Mountcastle et al., 1975]. Only visual form (and color) discrimination is impaired after bilateral resection of the inferior portion of the temporal lobe [Blum et al., 1950; Chow, 1951; Mishkin and Pribram, 1954]. This deficit is proportional to the difficulty of the task: easy discriminations such as color and three-dimensional objects are discriminated, albeit always with some deficit in the number of learning or retention trials when compared with control performance.

In natural settings the discrimination deficit is hard to observe. Monkeys with inferotemporal lesions will track moving objects such as gnats and appear to respond normally to food, their conspecifics, and to foreign intrusions [Reynolds and Pribram, unpublished observations]. Even in the laboratory, when choice is not involved, the monkeys can track changes in luminance [Ettlinger, 1959a].

Sensory-Mode-Specific Regions Within the Posterior Cortical Convexity

The deficit in visually guided behavior following resections of the inferotemporal cortex becomes manifest whenever choices among stimuli that have a consistent reinforcement history are required. This deficit is restricted to the visual modality; resections of other portions of the parieto-temporal-preoccipital convexity impair somatosensory, gustatory, and auditory discriminations [Blum et al., 1950; Bagshaw and Pribram, 1953; Pribram and Bagshaw, 1953; Pribram and Barry, 1956; Dewson et al., 1969]. Within the visual mode, the deficit depends on a variety of factors. Some are sensory, e.g., size or luminance [Mishkin and Hall, 1955]. Other factors are situational, however, and have little to do with visual sensory input per se. As an example, a monkey can show excellent discrimination between an ashtray and a tobacco tin when these are presented simultaneously. When, however, the same cues are presented successively and it has to make differential responses in the absence of the second cue, it fails miserably. The monkey shows that it is able to tell the difference between the two cues (in the simultaneous situation) but that it is unable to apply this ability to the somewhat harder successive task [Pribram and Mishkin, 1955].

The Non-Sensory Aspect of Modal Specificity

The finding that the visual impairment following inferotemporal resections is not always related to visual sensory factors, per se, alerts us to the possibility that the essence of the deficit may lie elsewhere than in visual input. On the other hand, the fact that visual generalization gradients are flattened [Butter et al., 1965], that the monkeys with such lesions process fewer features of the cues to be discriminated [Butter, 1968], or fewer of the cues of a set that needs to be discriminated [Pribram, 1960], indicates that whatever the impairment might be it impinges critically on the visual process.

Mishkin has handled this dilemma by subdividing the inferotemporal cortex into posterior and anterior parts, and has shown that the more posterior resections result in sensory-perceptual difficulties, while anterior lesions interfere with the memory-based performance aspects of these tasks [Iwai and Mishkin, 1968, 1969]. Furthermore, he has made a good case that the anterior lesions produce their effects because the pathways to such limbic structures as the amygdala and hippocampus are destroyed [Mishkin, 1982]. This recourse to hierarchy flows naturally from the earlier, less-refined conceptualizations.

The Limbic Connection: Some Problems

Though attractive and perhaps partially correct, Mishkin's formulation runs into severe difficulties. If, indeed, visual learning and performance are dependent on amygdala and hippocampal function, then resections of the medial temporal region (i.e., of the amygdala and hippocampus) should result in deficits when such tasks are given. This is not the case. Mishkin and I showed, in our early work together, that visual discrimination performance remains intact after such resections and that original learning of a visual discrimination is only slightly affected [Mishkin and Pribram, 1954; Pribram and Mishkin, unpublished results]. More recently, Mishkin has shown that a deficit in recognition tasks can be produced by medial temporal resections [Mishkin, 1982]. But these tasks employ trial-unique stimuli, which change them into one-trial learning tasks, more akin to delayed alternation and delayed response than to the discrimination tasks affected by inferotemporal lesions [Jacobsen and Nissen, 1937; Nissen, 1951]. And one-trial learning tasks are well known to be affected by medial temporal and other frontolimbic lesions [Pribram et al., 1952; Mishkin and Pribram, 1954; Pribram et al., 1962].

A word about such one-trial recognition tasks. They are highly sensitive to distractors, especially spatial distractors and to those which produce retroactive and proactive interference. Malmo [1942], Pribram [1961], Douglas and Pribram [1969], Grueninger and Pribram [1969], and Anderson et al. [1976] have presented a considerable body of evidence to this point. While resections of various frontolimbic formations make monkeys more sensitive to such changing cue presentations, performance after inferotemporal lesions is actually enhanced by changing presentations [Brody et al., 1977].

These facts do not detract from the importance of the finding that medial temporal lobe resections interfere with the performance of recognition tasks presented in this fashion [Gaffan, 1974; Mishkin, 1982]. The results of such experiments on monkeys have gone a considerable way to relating the work with nonhuman primates to that on humans with such lesions in whom Milner [1958] has described a particular memory deficit restricted to recall of events which have occurred since surgery, but which does not involve immediate short-term memory. However, once again I would emphasize the fact that short-term memory is intact in these patients until distraction intervenes, at which point interference disrupts the coding necessary to proper retrieval [Weiskrantz and Warrington, 1975]. Susceptibility to interference rather than recognition, per se, characterizes the medial temporal lobe deficit, since events that occurred preoperatively are readily recognized, and furthermore, perceptual and motor skills are readily mastered postoperatively. Thus, if one applies a behavioral, instrumental indicator, task recognition remains intact.

The Basal Ganglia

Mishkin [Mishkin et al., 1984; Mishkin and Petri, 1984] in two recent reviews handles the sparing of visual discrimination performance following medial temporal resection by a proposal that there are at least two different processes leading to retention in memory. As is pointed out in the reviews, similar proposals have also been made by Hirsh [1969], Gaffan [1974], Kinsbourne and Wood [1975], Huppert and Piercy [1976], O'Keefe and Nadel [1978], Cutting [1978], Olton et al. [1979], Wickelgren [1979], Cohen and Squire [1980], Cormier [1981], Stern [1981], Hirst [1982], Warrington and Weiskrantz [1982], and Graf et al. [1982].

Further, Mishkin suggests that the incentive form of retention necessary to trial-unique learning is mediated limbically, while choices among stimuli with consistent reinforcement histories depend on the integrity of the basal ganglia. These proposals are consistent with those that I and my laboratory colleagues, including Mishkin, have put forward over the past 30 years [Pribram, 1954, 1958a; Kimble and Pribram, 1963; Douglas and Pribram, 1966; Douglas, 1966; Hirsh, 1969; Kimble, 1969; Pribram, 1969; Pribram, 1977; Pribram, 1984]. For instance, evidence for the idea that the limbic formations are involved in learning based on incentive is presented in Douglas and Pribram [1966] (though the term "impellence" rather than "incentive" was used). As noted by Mishkin, he adopted Hirsh's nomenclature, which he developed in his Stanford doctoral thesis. In a paper entitled "The Amnestic Syndromes," the distinction between two types by retention was made by Pribram in a contribution to a volume by Talland and Waugh

[1969]. The importance of the basal ganglia to the functions of inferotemporal cortex was delineated in an address entitled "New Dimensions in the Function of the Basal Ganglia" [Pribram, 1977]. The difficulty with Mishkin's otherwise superbly illuminating formulation comes when the trial-unique type of process is identified with "recognition." In neurology and ordinary discourse, the term "recognition" is used to denote what in psychology is called "identification." In psychology, the term "recognition" is used to denote what in ordinary discourse and neurology is called "familiarity." Furthermore, for me, the distinction made by Tulving [e.g., Tulving and Donaldson, 1972] of episodic vs. semantic processing, or that of Olton [e.g., Olton et al., 1979], which teases apart the processes of working from reference memory, are more cogent. [But this is a matter of terminology, not of substance. These findings and their immediate interpretation seems securely established.]

A CORTICO-SUBCORTICAL, SENSORIMOTOR RECIPROCITY MODEL

The outlines of an alternative to the transcortical model are as follows: image processing and the perception of objects are sharply distinguished, and these in turn are differentiated from categorizing. Image, object, and category stand in hierarchical relationship to one another. The hierarchy is characterized by a progressive loss of detail in the patterns being processed. Thus, the model is, in a nontrivial sense, the reverse of the "initial sketch pad" theory proposed by David Marr [1982] and his MIT colleagues, [Marr et al., 1978]. However, the model is consonant with the psychophysical observations of S.S. Stevens [1951] and the neurophysiological proposals made by Horace Barlow [1961].

Image processing is a function of the primary retinogeniculostriate system. By contrast, object perception depends on interactions between the geniculostriate system and a set of visual motor mechanisms located in the prestriate-superior collicular connectivity. Categorizing is a function of operations of an inferotemporal-pretectal system, as it influences geniculostriate and/or prestriate-collicular activity. In this model, therefore, the operations that lead to both object perception and categorizing are preprocessing the input so that image, object, and category are simultaneously perceived.

The mechanisms of retinal, geniculostriate, and prestriate processing have been detailed in three other manuscripts by Pribram and Carlton [Carlton, 1985; Pribram and Carlton, 1985a,b]. Essentially, the first of these papers presents evidence for the formation of a retinal space-time image by the pupil-lens system, which performs a Fourier transform on the distributed incident spectrum of electromagnetic energy. The second paper addresses the functional microstructure of the striate cortex. While the gross overall organization of receptive fields reflects the topology of the space-time image of the retina, the output of each single neuron responds to the

Gabor transform of its receptive field. The Gabor transform is a Fourier transform that is essentially limited by a Gaussian envelope. Thus the distributed pattern which, were it produced by a Fourier transform, would reach infinity, becomes restricted to the boundaries of the dendritic receptive field of the neuron, most likely by way of lateral inhibition. Distributed processing has the advantage that correlations are readily achieved.

Correlations become the critical operation to achieve object constancy. These correlations are formed when eye movements scan an object to establish a center of symmetry from which the Fourier descriptors (the outlines) of the object can be computed. Input from the striate to the prestriate cortex becomes segregated to some extent according to features (e.g., color, shape) and figure-ground relations are enhanced by the stopped (hypercomplex) and opponens (and double opponens) nature of the receptive fields, which reflects an increase in the amount of lateral inhibition. Feature segregation aids in establishing centers of symmetry, which serve as foci for the eye movement patterns, which are organized by the pathways from the prestriate cortex to the superior colliculus. The correlations that are computed on the basis of the scan of the object then form a local context that is imposed on the striate cortex, and therefore on image processing, by collicular-striate connections.

The Inferotemporal System

According to this model, the functions of the inferotemporal system are another step in abstraction that segregates portions of the image from one another. However, the rules of operation of segregation are different from those that function in object perception. Categories are established on the basis of generalization gradients that differentiate among inputs. Butter et al. [1965] have shown that generalization gradients are dramatically flattened after bilateral resections of the inferotemporal cortex, and Martha Wilson [1975] has presented evidence that such resections interfere with categorizing. She proposes that the impairment is due to an interference with the formation of separate adaptation levels to each of the features or objects to be segregated. Roger Shepard (personal communication) is developing a multidimensional scaling approach that takes into account both adaptation level and generalization. Shepard distinguishes between dimensions of an image that are "integral" and those which are "separable." I have suggested that the rules for combining integral dimensions are those that lead to object perception, while the rules governing separability are those that lead to categorizing [Pribram, 1985].

The quantitative mathematical operations involved in categorizing will be detailed in another manuscript [Pribram and Carlton, in preparation]. Here, I want to address the neuroanatomical and neurophysiological evidence that makes the model plausible. I have already described the evidence for an inferotemporal cortico-collicular (and pretectal) pathway that could be responsible for the operation of segregation of image dimensions. In this instance, eye movements cannot have a role since electrical stimulation of the inferotemporal cortex does not result in eye movements. What must be occurring instead is a succession of computations of relationships among large portions of the visual field that are at any moment processed in parallel. In a sense, these momentary image patterns occurring in the striate cortex are put on temporary hold to operate as linear spatial filters which can be superimposed on one another. Much as IBM punch cards or the averaging techniques used in recording event-related electrical brain activity, successive superpositions allow commonalities among patterns to be enhanced, while irrelevancies (noise) are suppressed. Averaging is therefore one technique (perhaps the simplest) that can result in the production of adaptation levels. When more than one peak appears in the pattern, more than one generalization gradient, the several peaks become progressively more differentiated as more and more samples are processed.

Electrical stimulation of the inferotemporal cortex alters the receptive field properties recorded from neurons in the lateral geniculate nucleus and in the striate cortex: surround is enhanced with respect to center and effective receptive field size is diminished [Spinelli and Pribram, 1967; Lassonde et al., 1981]. These results can be interpreted to mean that the striate cortical microstructure has taken on a finer grain which allows sharper differentiation among the separable dimensions of the filter, the processing pattern. At the same time, the portion of the visual field being processed is relatively large: receptive fields recorded from the inferotemporal cortex are large and often extend across the midline [Gross, 1973].

Limitations of the Model

The weakness of the model as developed thus far lies in the fact that it does not account for the presence of visual receptive fields in the inferotemporal cortex; the fact that these fields are primarily visual, dependent on the integrity of the geniculostriate system and the forebrain commissural connections [Rocha-Miranda et al., 1975; Gross et al., 1977]; and the fact that in many cases neurons in the temporal cortex respond best to objects or other specific integral types of stimulation. These are the very data that support Mishkin's theory of the transcortical basis for hierarchy. The model under consideration must therefore take these data into account.

The receptive field properties of neurons are prime indicators of function. When that function is shown to be sensory-mode specific, it is reasonable to assume a fairly direct input from that particular sense. The transcortical connectivity to the inferotemporal cortex from the striate cortex involves at least two neurons—one to area 18 and another from area 18 to 19—before the final step from area 19 to 37 is completed. Even if one of these steps can be skipped, as perhaps is the case from the portions of the striate cortex that receive the most peripheral retinal projections [Ungerleider and Mishkin, 1982], the route remains an indirect one. In fact, one could trace an input to the inferotemporal cortex from the primary auditory cortex [see Pribram and MacLean, 1953; Dewson et al., 1969], the primary taste cortex [see Bagshaw and Pribram, 1953], and even the primary somatosensory cortex (see e.g., a pathway via area 7, Mountcastle et al. [1975]) in as few steps as those taken by the visual transcortical mechanism. Were the path from the peripheral retinal projection via the cortex on the medial surface of the monkey occipital lobe truly important, as Mishkin claims, this path would most likely feed into the cortical machinery involved in locating an object in space (the parietal cortex) and not the machinery involved in form and color discrimination.

Where, then, might a more direct input to the inferotemporal cortex originate? The short answer to this question is that I don't know. However, there are some leads that can be obtained from Gross et al.'s [1977] demonstrations of the dependency of the visual receptive field properties of the inferotemporal neurons on the integrity of the ipsilateral striate cortex and the forebrain commissures. They found that the latencies of response to visual stimuli were in the region of some 100 to 120 msec. (Striate cortex neurons respond at about 80 msec.) Resections of the occipital cortex and/or sections of the commissures were performed, and the monkeys were allowed a few weeks to recover. After unilateral occipital removal, inferotemporal units in both hemispheres responded only to stimuli in the hemifield contralateral to the intact striate cortex. After section of the corpus callosum and anterior commissures, inferotemporal units in both hemispheres responded only to stimuli in the hemifield contralateral to the recording site.

Some years back, I obtained some interesting results that may have a bearing on this issue. Using evoked potential techniques, experiments were carried out to determine the input to supplementary auditory cortical areas. In chronic experiments of the type used by Gross et al. [1969], I found that the input to the supplementary areas had disappeared. However, I obtained rather different results when I performed the experiments immediately after resection of the primary auditory cortex: potentials were evoked by auditory stimuli with only slight attenuation of amplitude. My conclusion was that in the chronic experiments, sufficient time had elapsed to allow degeneration of the medial geniculate input, and that the evoked potentials recorded from the supplementary auditory areas were dependent on the integrity of collaterals from the medial geniculate nucleus to these areas [Pribram et al., 1954].

It is possible that such collaterals also exist in the visual system and that some of them innervate the inferotemporal cortex. There is sufficient time for degeneration of the lateral geniculate to have occurred in Gross's and Mishkin's experiments [Chow and Dewson, 1966]. In the cat, all of what is now commonly called area 18 is innervated by the major projection of the lateral geniculate nucleus. This is not the case in the monkey, but the existence of collaterals has not been ruled out. Should they exist, they might well reach as far forward as the inferotemporal cortex.

An alternative route for a lateral geniculate input to the inferotemporal cortex would be via the pulvinar. The existence of massive geniculopulvinar connections is well established [Mehler, 1966], as is the existence of reciprocal connections between the inferior pulvinar and the inferotemporal cortex. Even this pathway is more direct than any known transcortical route.

But what, then, of the effects of section of the forebrain commissures? The role of the splenium of the corpus callosum in connecting the occipital cortices is well documented. Thus, the obtained effects of splenial section strengthens Mishkin's argument considerably. But this sectioning of the corpus callosum accounted for only half of the diminution of visual activation of inferotemporal neurons. What about the other half, which depends on the integrity of the anterior commissure? Are there fibers originating in the striate or prestriate cortex in the anterior commissure? I do not know of any. My guess, and at this time it is only a guess, is that the basal ganglia are involved, i.e., that a cortico-subcortical connection is important.

To summarize this section of my discussion: the hierarchical aspects of visual processing can be as readily attributed to systems of cortico-subcortical loops as to the operations of a transcortical mechanism. There is an abundance of evidence that cannot be easily subsumed under the transcortical theory. This evidence can be accommodated by reliance on a cortico-subcortical mechanism.

The Callosal Experiments

Within the framework of a cortico-subcortical hierarchical visual mechanism, what becomes of the results of the various elegant experiments detailed to us by Mishkin? He himself has pointed out some of the puzzling data that have emerged from his studies—but there is one fact that Mishkin rarely mentions. After all the extensive prestriate and inferotemporal resections and callosectomies, and chiasm and visual tract sections made in various combinations of laterality and order, the fact remains that many of these monkeys, after some prolonged period of difficulty, are able to perform the visual discriminations.

All of the transcortical pathways, and even much of the cortex that we have been discussing, are not *essential* to the performance of visual discriminations! In our published and unpublished experiments [Minturn, 1952; Ettlinger, 1959b; and especially Reitz-Blehert, 1968], we found this to be the case and Mishkin, in his review article [1966], notes in his second-to-last paragraph that parietal cortex (which Mishkin has relegated to spatial rather than to object vision) as well as prestriate must be removed in order for the deficit to appear.

Further, in our experiments we wondered if the recovery of function might be due to the prolonged period of testing, and that prolonged visual experience might in fact make the inferotemporal cortex inessential to the performance of the visual discrimination task. And we found just that. However, prolonged periods of testing, even with monkeys where resections in each hemisphere are performed in stages, ordinarily fail to impair the task when the resections become sufficiently extensive [Mishkin and Pribram, unpublished results]. We were therefore very surprised when our monkeys with huge bilateral prestriate and inferotemporal resections, unilateral optic tract and midline anterior commissure sections, *and* callostomy, performed readily and practically without deficit on visual pattern discriminations!

Our results immediately reminded us of James Sprague's [1966] fascinating experiments in which he was able to restore vision in a cortically produced hemianopic field by additional resection of the ipsilateral superior colliculus. As Hughlings Jackson had pointed out [1873], the several brain systems appear to be in balance and lesions often produce their effects by disturbing that balance. Sprague's remarkable experiments demonstrate that cortical-subcortical systems provide such a balance. Can this balance be restored as well by a procedure in which extensive visual training is provided between resections and transections which are performed in stages? It seems so.

The observations of Weiskrantz and Warrington [1975], and Warrington and Weiskrantz [1982] on blindsight in patients following unilateral occipital lobectomy also attest to the fact that a great deal of visual pattern processing occurs subcortically. The contribution of the cortex, per se, to each stage in the hierarchy of visual processes remains to be determined. Cytoarchitectural and receptive field considerations suggest that the cortex adds finer grain to whatever the subcortical mechanism is processing. The clinical observations suggest that, in addition to grain, reflective awareness of the resultants of the process depends on the integrity of the cortex.

My conclusion regarding the results of callosectomy in monkeys is therefore somewhat tangent to the interests of this conference. I am emphasizing the role of a hierarchy of precortical visual mechanisms (geniculate, collicular, pretectal) and suggesting that each of these mechanisms has a cortical component that improves grain and makes reflective awareness possible. It is, of course, the findings by Sperry, Bogen, Gazzaniga, Levy (see Levy, this volume) and their colleagues, of the role of the corpus callosum in reflective awareness that have proved so exciting. On this note I end my discussion.

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Epilogue

This symposium has brought together a wealth of information bearing on its title **"Two Hemispheres—One Brain: Functions of the Corpus Callosum"**, with some papers bearing only indirectly on its title as they deal with mechanisms of higher level integration of the function of the two hemispheres in perception, learning, and motor control. The corpus callosum and anterior commissure are obviously of critical importance in the bilateral integration of midline perceptual and motor functions, though interaction and coordinated activation through interconnections in the brain stem play an important role as well, in maintaining the unity of self-awareness and states of reactivity of the brain as a whole.

Specialized functions of each hemisphere, even with regard to speech and language, appear to be only relative, and not exclusive, even though verbal behavior and awareness may seem to depend almost exclusively on the left hemisphere in left dominant split brain human subjects. However, such preparations may give a false impression of functional specialization in the intact brain when information from the two hemispheres becomes available to each. As Sperry has expressed it so well in his letter: "the gesture, personal honor, and all will be most gratefully remembered in both of my hemispheres working together as a bilateral entity, the function of which supersedes that of either hemisphere alone."

Herbert H. Jasper