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Chapter 19

Brain Mechanisms and Behavior

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During the past 20 years there have been some remarkable and intriguing developments in the study of the brain and behavior. These advances have been made at every level in psychobiology and most of them are described in this book. In the following, what I would like to set forth is some of the data and brain theory that has emerged from the neuropsychological examinations of both animals and man. It is unavoidably a selective and personal view of the field. In particular, a brief review of the studies on commissurotomy will serve as a point of departure for considering the problems of the cerebral distribution of mental functions, the extent of cortical reorganization possible following brain damage, and the problem of relating cerebral mass to cognitive capability.

BRAIN BISECTION: A GENERAL REVIEW

The interhemispheric commissures have fascinated neurologists and psychologists for years. As recently as 1950, however, Lashley wrote the structures off as not serving any important neurological or psychological function in the mammalian brain. He cited Akelaitis' (1941, 1943,

1944) work as revealing that section in whole or in part produced no striking changes in behavior.

It was in this climate that Myers and Sperry (1953) performed their classic experiment on the cat which showed that visual discriminations trained to one hemisphere of a callosum-chiasm section cat could not be performed by the other (see Sperry, 1966). This work was extended and developed in the 1950s to include monkeys and even chimpanzees. Myers' and Sperry's series of studies were truly dramatic and stood in marked contrast to the Akelaitis series in the 1940s carried out in man.

In the early 1960s, Dr. Joseph Bogen, encouraged by a critical review of the Akelaitis reports, began a study of a new limited series of patients along with Dr. P. J. Vogel (1962). The opportunity to study these patients from a neuropsychological view originally fell to R. W. Sperry and this author at Cal Tech. It was an exciting time and over a 5-year period the patients were intensively examined on sensory, motor, and general

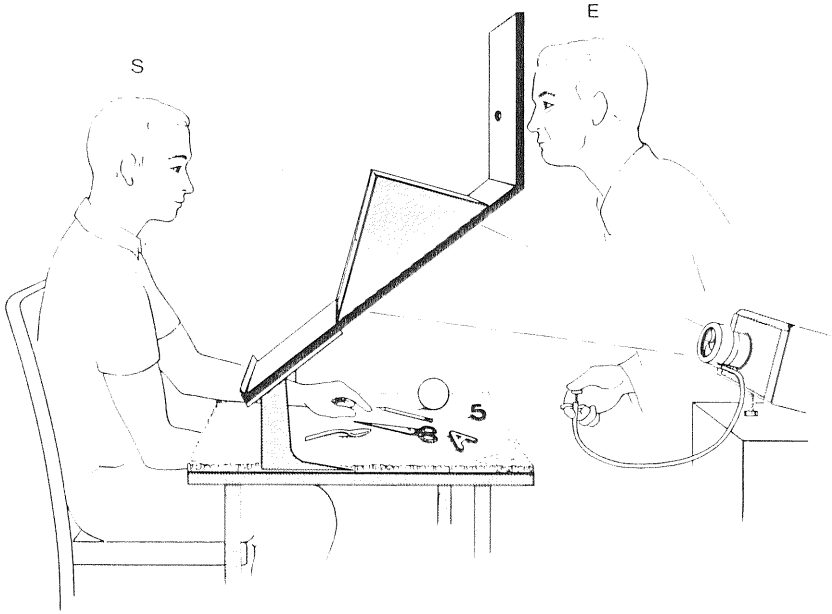

Figure 1. General testing apparatus originally used in testing of split-brain patients. I would monitor the subject's fixation and, when the eyes were on target, would flash a picture no longer than 100 msec into one or both visual fields. The subject was then free to choose with either hand an object that matched the stimulus, be it a word or a picture. Because stereognostic information from the left hand projects exclusively to the contralateral right hemisphere, a complete transaction can take place in a visual-tactile matching test without the left half-brain knowing what had occurred. (Adapted from Gazzaniga, 1970.)

cognitive functions (Gazzaniga, Bogen, & Sperry, 1962, 1963, 1965, 1967; Gazzaniga & Sperry, 1967; Bogen & Gazzaniga, 1965).

These studies have continued on the Bogen series of patients both at Cal Tech and elsewhere and have yielded a variety of insights into brain function (Milner, Taylor, & Sperry, 1968; Levy–Agresti & Sperry, 1968; Nebes & Sperry, 1972; Trevarthen & Sperry, 1969; Gazzaniga, 1970; Gazzaniga & Hillyard, 1971; Gazzaniga & Hillyard, 1973; Gazzaniga, 1967). In brief, the thrust of this work demonstrates there is a sharp breakdown in communication between the hemispheres of visual, somatosensory, motor, and cognitive information. Information presented to the left hemisphere was normally named and described while information presented to the right went nameless and the left hemisphere was unable to say what the right hemisphere was seeing or doing (Figure 1). Development of nonverbal response tests, however, made possible the demonstration that the right perceived the nature of those tasks and could execute an appropriate response. The studies went on to show that there were suggestions of marked differences in the way the hemispheres processed information with the left handling the verbal information and the right the visual-spatial tasks (Gazzaniga *et al.*, 1965; Bogen & Gazzaniga, 1965). More recent work suggests the intriguing possibility that problems that can be solved by either mode are handled by quite different cognitive strategies as a function of which hemisphere works on the task (Levy, Trevarthen, & Sperry, 1972; Nebes, 1971).

PARTIAL COMMISSUROTOMY AND CEREBRAL LOCALIZATION OF FUNCTION

Animal Studies

Of the variety of questions raised by split-brain studies, none is more important than determining the effects of partial commissurotomy on interhemispheric integration tasks. Animal work has suggested there is a discrete specificity of function within the forebrain commissures. The posterior or splenial areas subserve visual transfer as does the anterior commissure (Downer, 1962; Black & Myers, 1964; Gazzaniga, 1966; Sullivan & Hamilton, 1974). The area slightly anterior to the splenium is responsible for somatosensory transfer (Myers, 1962). The functional significance of the rest of the callosum remains largely unknown although there is a strong suggestion that it helps, among other things, to maintain a motivational equilibrium between the two hemispheres (Gibson, 1972).

Perhaps the most improbable and intriguing results from the partial section studies come from a series of reports by Hamilton and his col-

leagues (Hamilton & Brody, 1973). They have shown that split-brain monkeys, with small segments of the callosum anterior to the splenium left intact, are able to perform an interhemispheric match-to-sample on a pattern discrimination, while at the same time being unable to transfer pattern discriminations interhemispherically. Thus, a "+" versus "0" discrimination will not transfer through the callosum to the untrained half-brain while the animal can match a "+" or a "0" flashed to one hemisphere with a "+" and "0" sample presented to the other. This remarkable dissociation shows there is not, contrary to Lashley's (1950) opinion, a total equivalence within a sensory system.

One interpretation of these data is that, as visual information proceeds into the brain, it is constantly being recoded into new forms such that "X" becomes "X'." On the match experiments, the recoded "X'" transfers and as such is recognized by the opposite hemisphere which has performed the same operation on its "X." Thus, the match is possible. In a straight transfer experiment, however, "X'" is transferred but as such is of no assistance to the learning and memory mechanisms of the opposite brain which has had no meaningful experience with "X'." In some sense, the untrained hemisphere has the answer in the form of "X'" continually available to it but doesn't know what the question is. In a neurological vein, these data suggest that the learning and memory processes are initiated early in the primary visual system itself.

Human Studies

In humans, there are some classic accounts of neuropsychological deficits with partial callosal section as well as later reports (Geschwind & Kaplan, 1962; Gazzaniga & Freedman, 1973; Gordon, Bogen, & Sperry, 1971; Gazzaniga *et al.*, 1974a). In the late 1930s, Maspes (1948) and Trescher and Ford (1937) described cases where a partial posterior callosal lesion resulted in a breakdown in the interhemispheric transfer of visual information. Indeed, Maspes reported that while his patients were unable to read in the left visual field, they were able to describe various objects presented in the left visual field.

A striking breakdown in the interhemispheric transfer of visual information following splenial section was recently studied by Gazzaniga and Freedman (1973). The patient who was left-handed, with speech in the right hemisphere, was easily able to report verbally left-field visual information of all kinds while being unable to report identical stimuli presented to the right visual field. In this patient, there was no breakdown in interhemispheric tactile communication. This contrasts markedly with Geschwind and Kaplan's (1962) patient who had a dramatic breakdown in tactile function but no interhemispheric visual deficits. Their patient had tumor involvement in the anterior portions of the corpus callosum. Side-by-side comparisons of clinical data such as these allow the determination of where in the corpus callosum various sensory functions are transferred.

In further testing of our patient, we ran a modification of the Hamilton experiment on interhemispheric matching. We found some evidence that the subject could perform a match as to whether two geometric shapes were the same or different, no matter whether they were placed in the same or different visual fields. In this test, geometric shapes such as a square, triangle, and circle were flashed in pairs with both appearing in the same visual field or with one presented to the left of fixation and one to the right. The subject was able to judge correctly whether the two were the same or different, no matter where they were flashed. Yet, he tended to make errors when verbally describing the stimuli in the right visual field on the "different" trials. In other words, the right hemisphere speech system could not recognize the transferred information in the form it came over but could judge it was different from what was being processed in the right. This state of affairs would allow for a correct response of a "same or different" judgment but would not afford the patient's right hemisphere information as to "what" was different about the stimuli.

At quite another level, this same kind of finding was seen in other studies. Engrams laid down in the right hemisphere in the absence of speech and language as the result of the left unilateral injection of amytal cannot be accessed by the language system upon its return to normal functioning (Gazzaniga, 1972). Again, it would seem information stored in one form or neural mechanism is not easily accessible to another form or mechanism such as the language system.

MAPPING THE FLOW OF COGNITIVE INFORMATION WITH COMMISSUROTOMY

One of the powerful uses of partial commissurotomy as outlined in the preceding discussion is its application in the examination of where in the corpus callosum information transfers. Since the area of the projection of the callosal fibers is usually known, this gives good hints as to what part of the brain is involved in a particular task (Figure 2). It also allows examination of the question of how much backtracking there is in the cerebral flow of information. For example, if the visual

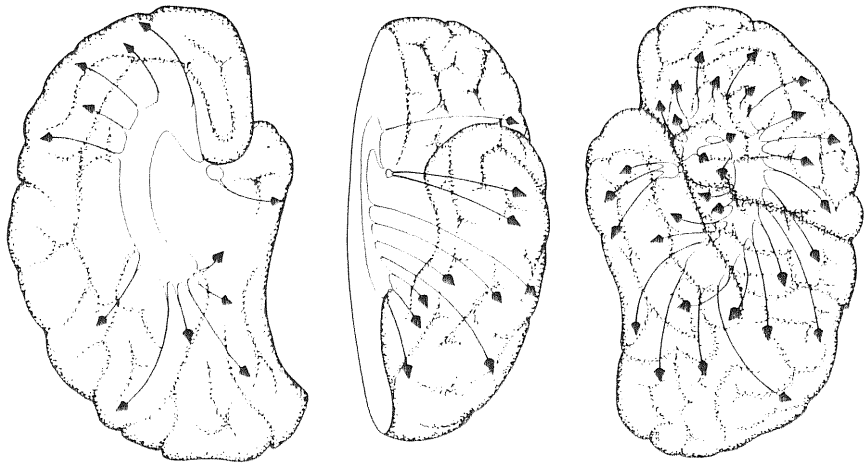

Figure 2. Indicates area of callosal projections in man as drawn from anatomical studies in animals. Surgical disconnection of the posterior or splenial region produces a visual split-brain syndrome but leaves other sensory functions, such as touch, intact.

areas are disconnected through a splenial section, can a visual–tactile match occur when the stereognostic information is presented exclusively to the hemisphere opposite the one receiving the visual stimulus? Or, conversely, can partial commissurotomy be used to explore the questions of whether lateralized mental duties carried out by specific structures, such as, for example, the right frontal or temporal lobes, can be carried out by the left hemisphere following frontal or temporal callosal disconnections? Likewise, can olfactory discriminations presented to the right hemisphere be known to the left following anterior commissure section?

These questions and more have been asked of a series of patients, most of whom have been operated on by Dr. Donald Wilson of Dartmouth Medical School (Wilson, personal communication, 1973). Dr. Wilson, using a new surgical approach he developed, has operated on several patients with the aim of limiting the interhemispheric spread of epileptic seizures. Encouraged by the medical results of the Bogen series as well as the Lussenhop *et al.* series (1970), Wilson has carried out both complete and partial sections of the callosal and anterior commissure fibers. This new series of patients is currently under investigation, and some of these results will be discussed later in this chapter.

Visual–Tactile Matches and Vice Versa

In the splenial section case previously described (Gazzaniga & Freedman, 1973), the patient was unable to cross-communicate visual information, but visual–tactile matches were easily performed when tactile information was placed in one hand and visual information was presented in either visual field. Since the match was made with split sensory input and since the visual information per se did not transfer in this subject, we must conclude the tactile information transferred over to the hemisphere viewing the stimulus. It is not possible, of course, to say in which domain the actual judgment is made, that is whether the tactile information is made available to the visual system or vice versa. A less simplistic interpretation, of course, would be that the information is funneled into another brain system within the hemisphere for final processing.

In a patient from the Wilson series where we have concluded that a portion of the splenial area remained intact while the rest of the forebrain commissures have been sectioned, tactile information could not transfer interhemispherically whereas visual information could. In this case, visual–tactile matches which required interhemispheric integration were also easily carried out. Here, it must be assumed, the visual information transferred for processing to the hemisphere exclusively holding stereognostic information.

This kind of data, of course, underlines how important it is to keep in mind the multiple channels that are available to the interexchange of information in the brain. Block one, and yet another remains that can do the job. Also, one cannot help but observe that it should not be too long before this kind of analysis could allow for even greater specificity in determining the nature of the interhemispheric codes. Namely, could a lesion that allows the interhemispheric transfer of recoded visual information, as in Hamilton's experiments, be able to perform a visual–tactile match? Answers to questions such as these ought to shed more light on the extent to which neurally recoded information is functionally available to other brain systems.

Lateralized Lobular Functions

Milner (1963) has elegantly shown striking dysfunctions following left and right frontal lobe lesions. Specifically, lesions of the right and left frontal lobes produce perseveration revealed by the inability easily to shift conceptual hypotheses on the Wisconsin Card Sorting Test. Moreover, left frontals, as opposed to right frontals, have marked deficits in word fluency and spontaneous speech.

To one patient with anterior callosal and anterior commissure disconnection we administered the Card Sorting Test in two forms—the normal approach and one where the stimuli were lateralized and quickly flashed onto the left or right visual field. The patient showed absolutely no

hesitancy in responding to either test and performed well within the normal range. Another patient, however, where it is believed some splenial fibers remained, showed a deficit on the Card Sorting Task. However, since defects were also observed on the word fluency test, the presence of an overall general frontal decrement is suggested. Still another patient, completely split, but who had suffered from cerebral palsy since the age of five, showed no deficit.

These preliminary data suggest that the proper synchronous function of the frontal lobes is not disrupted following the interhemispheric disconnection of the frontal callosal projections. This evidence contrasts markedly, of course, with the observations on the basic sensory systems of vision, touch, and possibly also olfaction, where the appropriate callosal section does block interhemispheric transfer. The model that can be entertained here, of course, is that the superordinate regulating mechanisms in behavior, such as those involving the frontal lobes, diffusely influence many brain systems that extend way beyond the boundaries of frontal callosal projections. It would seem that most of the cerebral mantle has access to and makes use of the processed output of the frontal lobes and, as such, can communicate it to the opposite half brain in a meaningful way, through a variety of callosal channels.

A similar point could be made on another observation of ours where we again followed up a study carried out by Dr. Milner. We recently administered to the Wilson series the tactile–spatial match-to-sample test that Milner and Taylor (1972) gave to the Bogen (Bogen, Fisher, & Vogel, 1965) patients. Milner and Taylor found a dramatic right hemisphere superiority on this task with the left being essentially unable to perform the task. In our test on the partially sectioned patients, the left proved easily able to do the task—even in the case where only splenial fibers remained intact but with the interhemispheric somatosensory communication system disconnected. Here again, the data suggest that a superordinate function specialized to one hemisphere can be contributed to the other over almost any callosal channel.

Summary

Revealing basic brain mechanism through studying the partially commissure-sectioned case appears to be a most promising enterprise. The animal work of Hamilton and others that appears to be teasing out psychological-brain process heretofore not imagined just hints at what the potential seems to be. Study of the partially disconnected patient seems equally revealing and productive in showing how many

high-level cognitive activities are managed in the cerebral flow of information.

With respect to the issue of localization of function, it would seem clear that those cerebral areas clearly involved in the immediate processing of raw sensory information can be selectively and specifically isolated and disconnected. In other words, the informational products of the long axonal Type I cells of Golgi, which Jacobson claims are the brain cells under strict genetic control, can be isolated, whereas the products of more complex and integrative mental activities which are managed by the more mutable Golgi Type II cells seem not to be so specifically disposed. Thus, these data suggest the lateralized specialities of the various left and right brain areas can make their contribution to the cerebral activities of the opposite hemisphere through almost any callosal area no matter what its size and location. Indeed, this interpretation suggests to me that the long-standing issue of the extent of localization could be better understood by considering the dichotomy in genetic specification as offered by Hirsch and Jacobson (see Chapter 4 in this book). Those cerebral processes that develop because of the mutability potential of Golgi Type II cells are hard to localize because of their ubiquitous nature whereas those tied to specific genetically determined systems are not.

CEREBRAL DYNAMICS AND MENTAL FUNCTIONS

Inherent in the discussion of the cerebral basis of mental functions is the foregoing problem of the nature and extent of cerebral localization. Most clinical data suggest that the brain is not a homogeneous system with every part equally involved with every function. Figure 3, for example, summarizes a variety of classic observations on the dominant hemisphere which argue for the view that cerebral lesions in particular areas give rise to more or less specific dysfunctions. To some extent, however, these descriptions, made by neuropsychologists and neurologists through the years, of behavioral disorders resulting from specific brain lesions were a direct function of the psychological views on language and cognitive behavior current at the time of testing. This phenomenon has been dramatically recounted by Bogen (1969) who listed various dichotomies of behavior and how, through the years, they have been assigned to either the left or right cerebral hemispheres. In the long run, this may say more about man's propensity to correlate any two dichotomies than how neurological systems subserve behavior.

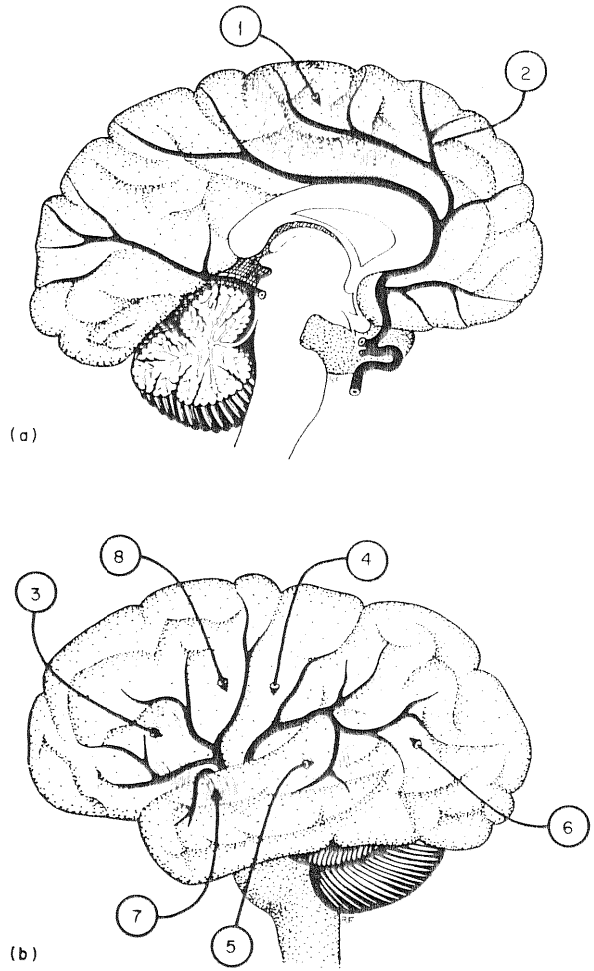

Figure 3. Lesions affecting language and speech processes.

(1) Area supplied by the anterior cerebral artery—involves fronto-parietal region and the corpus callosum with only transient loss of speech as a result of inclusion of the supplementary motor area.

(2) Supplementary motor area of either hemisphere—stimulation of which produces arrest of ongoing speech and initiation of repetitive, nonvoluntary vocalizations (similar to epileptogenic lesions in the left hemisphere of that area). Lesions result in abnormalities in initiation, continuation, and inhibition of speech.

(3) Broca's area—lower part of the pre-motor zone—typically produces agrammartism, poor articulation, and abnormal writing of events required both for pronunciation of words and fluent speech.

(4) Retrocentral area—lesions results in apraxia of the lips and tongue, leads to disintegration of speech as a whole.

(5) Temporal region—lesions affect the ability to generalize and differentiate phonetic sounds, cause disintegration of phonetic hearing. It always produces abnormal speech production and poor reading and writing.

(6) Temporo-parieto-occipital region—lesions do not change the external articulated speech, but prevent mental integration of separate elements (disturb simultaneous synthesis). Leads to disintegration of rational speech and to disturbance of the understanding of logical, grammatical constructions (semantic aphasia).

(7) Bilateral lesion of the temporal lobe, posterior $\frac{2}{5}$ of the first and second temporal convolutions, plus posterior half of the Isle of Reil, extending to the interior parietal lobe—shows word deafness, severe motor aphasia, more muteness than paraphasia.

(8) Near Broca's in the motor area of the lateral side of the left hemisphere—electrical stimulation results in perseveration of speech.

In recent years, the psychological processes involved in language and speech have been analyzed in more sophisticated and complex ways than ever before. Realizing that language behavior is not the simple output of a discrete system in the brain, the neuropsychologist finds himself looking for a set of different correlations regarding brain damage and verbal behavior. Instead of the old dichotomy of receptive and expressive language, of verbal and nonverbal processes, and the like, the neuropsychologist is finding that left hemisphere damage in the classic language and speech areas leaves the patient with enormous syntactic and semantic capacity that can be realized through other response systems (Gazzaniga, Velletri, & Premack, 1971; Glass, Gazzaniga, & Premack, 1972). Imagery and language have received wide attention (Paivio, 1969; Bower, 1972) and some studies suggest that this assisting cognitive system to language behavior is managed in quite different cerebral sites than the classic language area (Seamon & Gazzaniga, 1973). Word-match capability as well as other mental duties are also functions not performed in the left dominant hemisphere (Gibson, Dimond, & Gazzaniga, 1972; for review, see Gazzaniga, 1973). What emerges from these data is a picture of brain function which is quite different from that generally held in the past. This new view is that various cerebral functions managed in discrete areas throughout the brain are thought to be in a dynamic relation with other cerebral sites. While the idea that there are specific cerebral centers specialized for particular cognitive functions is not directly challenged here, it is maintained that a variety of spheres of influence in the brain, some with functions that overlap those of others, are all interacting in a dynamic way to produce a final integral behavioral response.

RECOVERY OF FUNCTION

There seems to be, in part, a swing back to older views of basic central nervous system maintenance and growth principles. Prior to Sperry's long series of studies emphasizing the presence of a high degree

of neurospecificity, the wildest claims had been made about the extent of functional recovery possible, following either central or peripheral nerve damage (Sperry, 1966). For years, it was these studies, as well as Harlow's (1971) at a psychological level, that put a halt to the runaway interpretation that function precedes form. However, many other studies—for example, the work on visual deprivation (Hirsch & Spinelli, 1971; Blakemore & Cooper, 1970)—have focused attention on the question of the degree of plasticity of the central nervous system (CNS) (see Chapter 4 by Hirsch and Jacobson). These studies have shown us how discrete visual experience during rearing modifies the basic organization of the primary visual system. In addition to this work are the studies of Schneider (1973), Raisman (1969), Moore, Bijorland, and Stenevi (1971), and others which detail the extent to which new neural growth is possible following central neural lesions. As a result, the idea in everyone's mind is that we may now have a grasp of the physical basis of recovery in the CNS—not to mention the insights such work affords us on the broader question of the physical basis of learning and memory.

Indeed, Hirsch and Jacobson, as previously pointed out, argue that adaptive behavior, in general, is the product of changes in the microneurons or Type II cells of Golgi. These cells, it is believed, remain adaptive while the long axon cells responsible for the major transmission of information into and out of the CNS are under early, and exacting, genetic control and specification. How long this state of flexibility obtains for the microneurons is not known. It supposedly extends into the teens in humans, a supposition that supports the speculation that it is the mechanism responsible for the kind of speech and language recovery seen in the rehemispherization of these processes following early brain damage. It could also explain why the relocalization of speech and language rarely occurs after 12 years of age. In this connection, it is worth noting the studies of bird song which Nottebohm (1970) conducted using canaries. He has shown that up to the age of 1 year, the song can be taught to birds that have not heard the song before. Birds deprived for longer periods cannot be so trained. Yet, if the birds are castrated when young, thus altering the testosterone level, they are able to learn the song well into the second year. Here, we see an exciting model for the experimental manipulation of how and why the CNS at some time "wires out" adaptive changes in communicative behavior.

In my view, however, all of the fascinating basic work in neural development does not directly bear on the question of recovery of function in the CNS as the term is normally used in a clinical sense. Before proceeding, however, let us look at the status of clinical functional recovery.

Clinical Recovery

There are various claims concerning the mechanisms and extent of nervous system recovery. Luria *et al.* (1969) feel that temporarily depressed areas can be "deinhibited" both by training and with the aid of pharmacological agents such as atropine and neostigmine. Yet most neurologists are skeptical of applying these methods to patients and, in general, believe the extent of long-term recovery from a lesion is a function of the individual's own capacity to recover and has little to do with external therapy. In studies, for example, examining the value of rehabilitation on motility and other sensory-motor functions on stroke patients, it has been concluded that no more improvement resulted than if the patient had been left alone (Stern, McDowell, Miller, & Robinson, 1971). The same case can be made for speech and language rehabilitation following stroke (Sarno *et al.*, 1971). Indeed, in the clinical setting it is hard to improve upon von Monakow's concept of diaschisis, where recovery is viewed as the reestablishment of temporarily impaired neural systems—not the vast reorganization of neural systems through substitution or retraining, or as the result of new growth. There have been, in recent years, both physiological and metabolic studies that support von Monakow's ideas. Recordings from cortical areas distant from cerebral lesions, for example, find the areas transiently depressed followed by return to normal levels of firing (Kempinsky, 1958). In stroke, it is observed that there is a marked transient decrement in metabolic rate in the brain areas opposite the lesions (Hoedt–Rasmussen & Skinhoj, 1964).

Yet, even if the basic ideas of von Monakow prove correct, some clinical instances of recovery involving the higher cognitive processes following massive brain damage probably come about through other mechanisms and involve neither deinhibition nor actual structural changes. In what follows, instances of recovery of function will be reported which can be brought about quickly after a brain lesion, by prelesion prophylactic measures; and that can be obtained long after diaschistic processes are thought to be active by the use of proper behavioral training routines.

In general, all of the data to be reported lead one to the view that recovery in the adult, arising from nonphysiological improvement, is the result of preexisting behavioral mechanisms not necessarily previously routinely involved in a particular act now covering for the mental activity under question. For instance, it will be maintained that the implicit functional syntactic mechanism present and active in decoding a meaningful pictorial array is probably able to come to the assistance of the

organism when the syntactic mechanism for language has been destroyed through stroke or lesion. But before getting into the clinical work, let me lay a broader base for this view with some recent work in animals.

Animal Research

We believe that the behavioral dysfunction supposedly resulting from discrete lesions in the brain can frequently be quickly circumvented by changing the environmental or behavioral contingencies (Gazzaniga, 1973b). For example, we recently pursued this idea in one of the most exhaustively studied systems in physiological psychology, the lateral hypothalamic syndrome. Bilateral lesions here, of course, produce an adipsic animal who will neither drink nor eat, and, if left alone postoperatively, would die (Figure 4). Such animals are nursed for an extended period of time and, with enough coaxing, some will eventually be able to sustain life postoperatively. We, however, observe that within a few days after the lesions, most rats will have a higher probability of running than they have of drinking. Thus the adipsic rat will show essentially no probability of taking a lick from a water spout but within a half-hour period will run between 100 and 150 seconds. We then made these

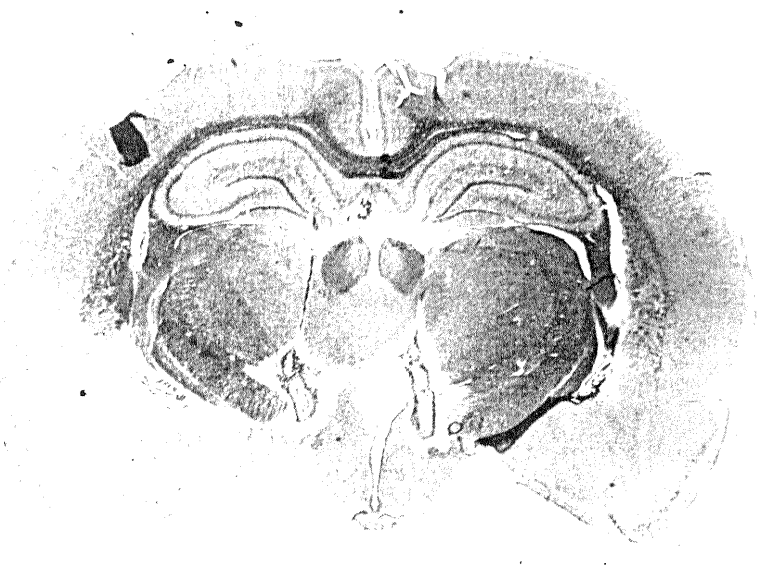

Figure 4. A bilateral lesion in one of the rats used in the study described. While the animal would not drink spontaneously, it would drink in order to have the opportunity to run.

two behavioral events contingent such that if the animal wanted the opportunity to run, he had to drink, which in turn released a brake on a wheel that allowed the animal to run. Dramatically, the adipsic rats immediately began to drink in order to have the opportunity to run.

Or, consider the inferotemporal lobe syndrome. Clark and Gazzaniga (1974) have recently extended the kind of insight afforded in the preceding experiment into discrimination problems trained to animals undergoing inferotemporal lesions. In the beginning, we assumed caged monkeys were like rats and would relish the opportunity to run. Instead, we seemed to have discovered the phylogenetic origin of "don't rock the boat." Here, when the animal has the opportunity to run, a preferred response turned out to be to adopt a vertical spread-eagle position so as to minimize movement in the wheel! This required a change in contingencies such that if the monkey made a correct choice, the wheel would be locked so no movement was possible.

Specifically, three monkeys were trained on a pattern discrimination for food reward on a discrimination panel that was placed inside of a large activity wheel. When the discrimination was learned, an added contingency was introduced. The wheel, driven by a motor, would automatically start to turn at the onset of the stimulus. As described, if the correct choice was made, the wheel locked during the intertrial interval. The animals, under these conditions, decreased their latency in making their responses and immediately made a perfect score even after all food reward was withdrawn.

All animals then underwent bilateral inferotemporal ablation. To our great surprise, the animals were instantly able to perform perfectly the discrimination to a food reward alone, as well as, of course, to the not-to-run contingency. Our expectation was that we would see a dissociation of performance between the food condition and the not-to-run contingency.

It would appear from this that the training of a visual task with two explicitly different kinds of rewards insulates the organism from showing the classic impairment following bitemporal lesions. It is as if the preoperative dual training encouraged the organism to use a number of conceptual strategies to solve the problem, creating a cerebral redundancy such that impairment to one part of the brain could in no way do exclusive damage to all of the paths used in problem solution. Indeed, the well-known beneficial effects of preoperative overtraining on postoperative scores may be the result of a similar mechanism. During the long overtraining period, the animals may well decide to solve the problem through a different kind of strategy than the one originally

used. This, of course, could never be delineated by the present experimental design. At the same time, this kind of interpretation is commonplace in complex discrimination training in humans where it is shown, using other testing methods, that both children and adults are constantly changing their hypotheses along the way as they learn a particular visual discrimination (Levine, 1966). In short, the old analysis of learning phenomena which urged simple behavioristic interpretations with the corresponding simplistic neurological models won't do any more, for the data are giving way to the view that distinctly separate mental processes are active during even the simplest kind of discrimination training.

Cognition following Stroke

The problem of determining the amount and kind of cognitive function remaining after severe brain damage to the left dominant hemisphere is difficult and, in the past, little credit has been given to what the right hemisphere is capable of in this regard. Encouraged by our earlier studies on the cognitive capacity of the right hemisphere, as described in the foregoing (Bogen & Gazzaniga, 1965; Gazzaniga *et al.*, 1967; Gazzaniga & Sperry, 1967; Gazzaniga, 1970), we undertook a series of studies on the severely left-brain-damaged patient in an effort to determine what, in fact, the cognitive limits were. We predicted that, with the right behavioral testing technique, much more extensive behavioral capacity would be evident than is usually claimed, and this has indeed been our experience. Using Premack's (1971) language training system which he developed for the chimp, we ran a series of tests on global aphasic patients and quickly discovered these patients could learn to perform many language-like operations (Glass *et al.*, 1972).

Before beginning language training, a viable social relationship must be established between the patient and the trainer. The importance of this phase cannot be overemphasized for if the motivational setting is inappropriate, no learning will occur. In psychological parlance, if a patient is emotionally flat and shows no preference, then it is impossible to arrange a contingency where manipulating and learning *X* will produce desired reward *Y*. Indeed, it would seem fair to say that all too frequently neuropsychological assessment procedures ignore this factor. Tests are designed, norms are established on a normal population, and the relation all this has to testing a brain-damaged patient who surely is in a complex ever-changing motivational state is frequently remote.

Using paper cut-out symbols, errorless training procedures were administered in the initial training. For example, in teaching "same versus different," two similar objects, say two erasers, were placed on a table in front of the patient. Placed in between was another symbol, a question marker, which comes to mean "missing element." The subjects learned to slide the question marker out from between the two test objects and insert in its place the symbol meaning "same." At first, this is the only response allowed. Subsequently, an eraser and a screwdriver are placed in front of the patient and the patient must remove the question marker and insert the symbol meaning "different." Following this training, the two symbols are both available on each trial and the subject must now make the correct response to the two varying, "same" or "different," stimuli. When the stimuli used in training are then changed, it is observed the subjects can use the symbols correctly no matter what test objects are used by the examiner.

These procedures then enable one to teach any of a number of language operations to the global aphasic patient. The negative, yes, no, the question, and simple sentences were all successfully mastered by the patient (Figure 5). Before teaching the sentences, the patient's lexicon was increased by teaching him a few nouns, verbs, and personal names.

Figure 5. After the examiner stirs some water in a glass, as opposed to pouring it or stirring Tang or pouring it, the subject must describe the act by arranging three of the six symbols correctly, which in effect says "Mike stirs water."

Each of these words was taught by associating a symbol with an object, action, or agent in the context of a simple social transaction. An object was placed before the patient along with the symbol for the object and the patient was required to place the symbol on the writing surface, after which he was given the object.

It is of interest to note that training in the use of symbols referent to actions (verbs) was consistently much more difficult than training in the use of symbols referent to nouns. Noun symbols were learned in a few trials whereas verbs sometimes took weeks to learn. To some extent, of course, this is not too surprising. To know a verb is to know the whole context, subject and object, whereas to know a noun is simply to know a single object. The difficulty we experienced in training the patient to use symbols referent to actions is also reminiscent of the finding that the right hemisphere of the split-brain patient was unable to process natural language verbs.

These data clearly suggest that the severely left-brain-damaged patient can perform a wide variety of conceptual tasks. Because of the large extent of left damage, it would seem likely that the intact right hemisphere is surely involved in many of these tasks. We know from other studies that the right hemisphere has enormous cognitive power (Gazzaniga & Sperry, 1967; Bogen & Gazzaniga, 1965; Levy *et al.*, 1972; Milner & Taylor, 1972) and, indeed, the imagery mechanism associated with language behavior appears to be a right-hemisphere process (Seamon & Gazzaniga, 1973).

In other studies, use was made of Sternberg's (1966) serial processing model of short-term memory processes. In brief, he found that as a memory set increased in size—for example, from one item to three items—a probe examining whether a word or letter was part of the set took longer to yield an answer the larger the memory set size. Seamon reasoned that if the instructions to a subject were varied, different response patterns would be evident. Instead of asking the subject to keep repeating the instructions verbally, as is usually the case in the Sternberg design, he told them to create, with the memory set words, an interactive image where all the words in the set "touched" one another in the image (Seamon, 1972). Thus "tree" and "bird" should find the bird in the tree, not flying by it. Changing the instructions in this way resulted in equivalent response times no matter how large the memory set.

This remarkable observation encouraged us, of course, to examine the possibility that there may be a left–right difference here. For years, we had felt that it was the right hemisphere that was specialized for handling the visual abilities of mental life and, in this context, we investigated whether different response times would function as a feature of

both our instructions for encoding the original material and the visual-field hemisphere first receiving the probe.

Results of the study clearly showed it is the right hemisphere that is specialized for the image process and the left for verbal directions (Figure 6).

For present purposes, these studies indicate how a cognitive system working in parallel with the language system could be helpful following left-brain damage. In addition, and perhaps more importantly, we see how, by manipulating the encoding instructions, wholly different brain systems are called upon to process information. In a sense, then, one can "shunt" around a brain lesion by setting up the environmental contingencies differently and, thereby, requiring a different part of the brain to be used in the solution of a problem.

Summary

For the present, we are faced with the problem of how to account for clinical improvement in terms of recovery of function. Does it reflect a process where the central and dominant language processing systems have recovered to the extent of allowing the observed behavior? Or, are these cognitive talents the product of other existing behavioral strate-

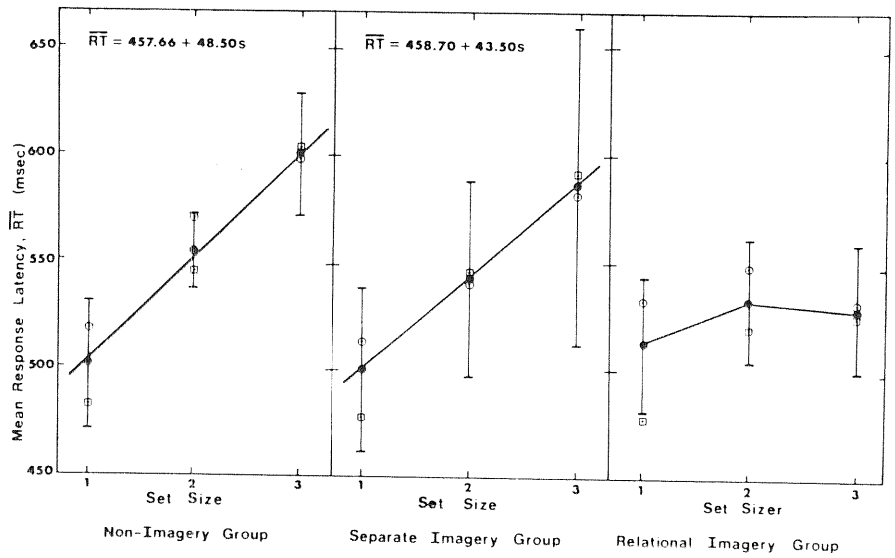

Figure 6. The right hemisphere proves superior in the normal in processing imagery information while the left excels at instructions emphasizing a verbal rehearsal strategy. (After Seamon and Gazzaniga, 1973.)

gies that are capable of handling the job but have previously been involved in other more supportive roles? With the latter view, the recovery period becomes more the time needed to allow for the realignment of these cognitive processes than the time needed for physical repair.

CORTICAL MASS AND COGNITIVE CAPABILITY

One of the most intriguing problems facing the neuropsychologist is to understand how the amount of brain tissue correlates with cognitive capability. The old approach of correlating brain weight with intelligence quotient (IQ) and the like has given way in recent years to a more approachable question—namely, is one-half of a split brain as competent as a whole brain? Put differently, what is the cost to the organism, if any, for having the brain split?

A number of studies on cats (Sechzer, 1970; Meikle, 1964; Voneida & Robinson, 1970) and dogs (Mosidze, Rizhinashvili, Totibadze, Kevanishvili, & Akbarolia, 1971) report that split-brain mammals show cognitive deficits compared to normals. Standing in contrast, however, are three studies on discrimination learning in monkeys documenting learning times, which reveal no differences between splits and normals (Hamilton & Gazzaniga, 1964; Myers, 1965; Gazzaniga, 1966).

In humans with commissurotomy, early studies suggested there were no major cognitive deficits resulting from hemisphere disconnection (Gazzaniga *et al.*, 1965, 1967). On the other hand, short-term memory (STM) studies suggested each hemisphere was below normal in its information-handling capacity (Gazzaniga, 1968). Yet, when both hemispheres were working together, the scores fell into the normal range. The study by Milner and Taylor described earlier, which reported that the split-brain patient is better in the right hemisphere than in the left hemisphere in carrying out a spatial–tactile STM task, also showed that on the whole a half brain performs inferiorly to normals or brain-damaged cases.

Using their test, we examined the three patients in the Wilson series described previously. The results clearly showed that when the callosum is not completely sectioned, the general deficits seen in the fully commissure-sectioned patient are not present. Moreover, either hemisphere can perform the problem equally well. Even in the case where only splenial fibers remain, there was no sign of a decrement in performing this task by the left hemisphere.

Still, since previous work has not clearly resolved these questions, as well as the more general question of the callosal contribution to intellectual function, we have begun a series of experiments on monkeys

to clarify the effects of commissurotomy on learning and memory. The following study examines the effects of commissurotomy on STM using a multiple delayed matching paradigm (Nakamura & Gazzaniga, 1974).

Short-Term Memory and Multiple Delayed Matching to Sample

In brief, the subjects were six rhesus monkeys. One had undergone section of the anterior commissure, corpus callosum, hippocampal commissure, and optic chiasm prior to testing. The other five began as normals, two of which were split in the course of the study. At the beginning of training, all monkeys were conditioned to perform a single color-matching task with no delay. A red or green light would appear at a top screen until it was turned off by the monkey's pressing on the screen. Immediately, the red and green choice colors would appear at two screens placed just below. A press on the screen of the color matching the earlier presentation would be rewarded with water. Subsequently, a delay period was introduced between the initial response of the monkey and the projection of the choice colors. As the animals met criterion performances, the delay was increased up to 18 seconds. On the initial condition, both eyes were open and the monkeys were tested on the delayed matching task until average weekly performance peaked.

Figure 7 shows the averaged data comparisons for splits versus nor-

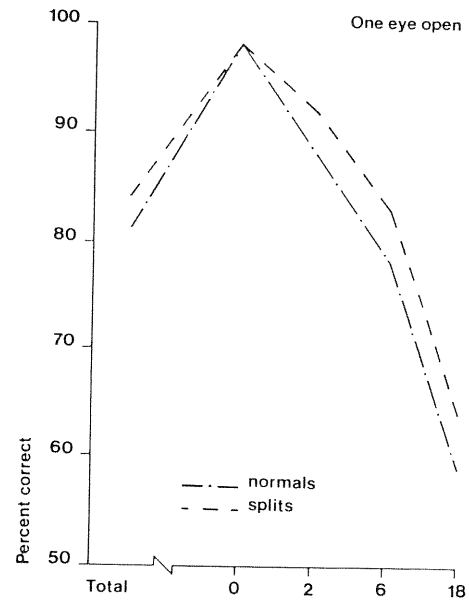

Figure 7. Average data comparisons for split versus normal monkeys on the multiple delay match-to-sample task. Note that splits do better than normals at all delays though this was not a significant difference.

mals. Each of the points to the left showing total percent correct is the result of at least 800 trials per animal and the points of the various delays denote, in turn, at least 200 trials per animal. The splits do better than normals at all delays, though this difference is not significant. There was also no significant interaction between operative condition and delay. Thus, split-brain animals are not worse than normals at any delay.

We have, then, a clear indication that the performance level following complete forebrain commissurotomy does not result in inferior behavior. Indeed, there was a suggestion that the performance had improved. Further work will, hopefully, make clear how acquisition of information might be affected by disconnection of the two half brains.

Cognitive Specialization and Motivation

When lateral cognitive specialization is apparent in the split brain, the question remains how much of the difference can be attributed to motivation? This strikes us as important because we have successfully manipulated the motivational state of animals unilaterally through brain lesions (Gibson & Gazzaniga, 1972; Gibson, 1972). With measurable differences here, in behavior such as eating, differences would clearly be forthcoming in the effectiveness of learning and performing cognitive tasks (Nakamura & Gazzaniga, 1974). These animal studies raise the question as to how much left–right differences could reflect left–right differences in motivation rather than in cognitive capability.

Summary

The overriding issue which cuts through so much of the foregoing is the question of the nature and extent of localization of function of the nervous system. While tying structure to function is one of the long-standing activities of neuropsychology, it still seems to be an elusive enterprise. The reasons are many and, in part, have to do with the problem of determining what it is that is supposed to be localized in a particular brain area. It would seem clear that even the simplest behavioral act is the result of a multitude of overlapping mental activities, such that destruction or impairment in one domain can often find the organism performing as if nothing had happened. What does seem to emerge from the studies reviewed here is that those informational systems in the brain which are involved in conducting primary input (and output) messages are susceptible to dramatic breakdowns in function and these can be easily localized and detected. When, however, the behavior in question is a superordinate process which involves interactions with cognition and motivational states, such as concept formation, or visual–spatial analysis, or logical capability, and the like, all processes which surely involve the small cortical cells, then it is extremely difficult to isolate through which channels such information can be mediated.

It seems to me that neuropsychology, instead of needing less complicated models to help us in the analysis of brain processes, needs a far more sophisticated set of concepts and ideas if it is to penetrate the sheath of mystery surrounding the problem of brain and behavior.

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Chapter 20

On the Origins of Language*

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INTRODUCTION

Consider two main ways in which you could benefit from my knowledge of the conditions next door. I could return and tell you, "the apples next door are ripe." Alternatively, I could come back from next door, chipper and smiling. On still another occasion I could return and tell you, "a tiger is next door." Alternatively, I could return mute with fright, disclosing an ashen face and quaking limbs. The same dichotomy could be arranged on numerous occasions. I could say, "the peaches next door are ripe," or say nothing and manifest an intermediate amount of positive affect since I am only moderately fond of peaches. Likewise, I might report, "a snake is next door," or show an intermediate amount of negative affect since I am less shaken by snakes than by tigers.

For simplicity, consider that everything of interest is next door, making locational information irrelevant. The question to be answered therefore is always, What is it? never, Where is it? Also, for simplicity, assume

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