

PART VIII. HIGHER FUNCTIONS

CONSISTENCY AND DIVERSITY IN BRAIN ORGANIZATION*

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INTRODUCTION

The enormous diversity in cognitive as well as behavioral style in man is commonly attributed to either genetics, experiential factors, or both. Because of the complex problem of tracing the antecedent events or brain structures responsible for this huge variety in style, few answers have been forthcoming to these extremely general questions. While there have been some noteworthy and extremely fascinating exceptions¹ to this general ignorance, we feel that the problem of tying behavioral diversity to variations in brain organization is as intriguing as ever.

One does not have to look at man to observe the mystifying diversity of animal behavior within a species. Pigeons in fully environmentally controlled training boxes demonstrate a frustrating uniqueness in their response patterns to identical stimuli and reward schedules. While the experimenter ultimately has the power to extract a more or less consistent behavioral pattern, the route taken by the pigeon varies as it has been shown to vary in the adipsic rat.² Nonetheless, trying to correlate behavioral diversity with anatomic diversity is not yet possible. Karten³ has remarked that the consistency of brain organization in the pigeon is almost staggering, and working at both the gross and microscopic level yields no detectable variation.

The physical variation that must accompany behavioral variation might then conceivably be a product of which of a variety of inborn circuits an organism uses. This ordering or assigning of duty of differing circuits may be affected by experience, brain damage, or a variety of other influences to which the developing organism is subjected.

The question of relating physical variability to behavioral differences in man has rarely been traced down to specifics. While both the I.Q. argument, which at its core, deals with the problem, and modern personality theory, such as Mandler's intriguing analysis of the interactions of the mind and emotional systems, suggest that the origin of major behavioral differences is to be found in physical terms, the neurologic literature has barely touched the problem. This rather surprising fact has been obscured even more in recent years by the overpopularization of much of the basic data that Roger Sperry and I first reported some sixteen years ago. While follow-up studies from his laboratory have proffered a markedly different interpretation of the data than our own, neither of the formulations compare to the radical (and highly marketable) views of those not directly in-

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volved in split-brain research. These popular psychological interpretations of "mind left" and "mind right" are not only erroneous: they are also inhibitory and blinding to the new students of behavior who believe classic styles of mental activity break down along simple hemispheric lines. We truly live in an age of euphemism and cant!

Our approach to the problem of variability in brain organization has been to carefully study patients with identifiable discrete commissure lesions, as well as studying the separate functions of each hemisphere in a group of new patients. With the former approach one can determine whether or not particular commissural areas transfer different kinds of information, while with the latter method, the consistency of seeing particular psychological activities in a particular hemisphere can be analyzed.

In what follows, we will first show that a specific anatomic entity, the anterior commissure, can variably transfer visual and possibly also auditory information. Second, the enormous variation in the extent of right-hemisphere language will be demonstrated. Third, the variation in the extent to which the right hemisphere can carry out complex cognitive tasks will be examined. Fourth, the variation in the extent of specialized left versus right processes will be considered along with our recent findings that left versus right hemisphere differences are more a by-product of language developed in the left hemisphere rather than a reflection of true specialization of function in the right half of the brain.

In these new studies we have had the opportunity to carefully examine both pre- and postoperatively a series of patients operated on for intractable seizures by Dr. D.H. Wilson of the Dartmouth Medical School. In most cases the entire corpus callosum was sectioned with the anterior commissure being left intact. Each patient, of course, came to surgery with a widely different neurologic history. As we will describe, each "tests out" quite differently on a large battery of tests, most of which have been designed to investigate both the separate and integrated function of the cerebral hemispheres in man.^{4,5}

The studies reviewed below were carried out by a team of investigators including Joseph LeDoux, Gail Risse, and Sally Springer.

VARIABLE TRANSFER CAPACITIES OF THE ANTERIOR COMMISSURE IN MAN

We have recently been able to ascertain the varying functional role of the anterior commissure in the patients operated on by Wilson.⁶ The anterior commissure, which has been presumed to play a minor role in interhemispheric communication, was tested for the transfer of visual, auditory, and olfactory information. In several cases, Wilson spared the anterior commissure while carrying out complete section of the corpus callosum.

Most of the tests used were extremely simple in nature, and in general simply required the subject to give a verbal (left hemispheric) description of modality-specific information, exclusively presented to the right half of the brain. As with all of our tests, lateralization was accomplished by tachistoscopic presentation of visual items, single-nostril discrimination of common odors, and dichotic stimulation in the case of audition. The results of these tests showed there was specific interhemispheric transfer of at least one type of modality-specific information in each patient. In other words, while some patients transferred visual information, others did not. Some patients seemingly transferred auditory information, while others did not. Lastly, all the patients transferred olfactory information.

These data strongly suggest that fibers of the anterior commissure are capable

of transmitting diverse sensory messages. This conclusion is consistent with the anatomic distribution of the pathway, which implicates the phylogenetically older anterior limb in the exchange of information between paleochochordic olfactory regions and the more recent posterior limb in the transfer of visual and auditory impulses between temporal cortical areas. Although behavioral investigation with nonhuman primates has described limited visual transfer through the anterior commissure,^{7,8} the clinical data reported here indicate that complete visual exchange between the hemispheres is possible. Olfactory transfer, which has long been assumed to occur over this pathway, has also received confirmation in our work. Lastly, and perhaps most surprisingly, there is indication that interhemispheric fibers from auditory areas in the temporal lobe can sustain a functionally meaningful exchange of information.

When we look at these data another way, however, it becomes entirely clear that a particular neurologic structure can greatly vary in what it transfers; while the same structure in case A transfers visual information, it seems not to transfer visual information in case B. The same is apparently true for other modalities. Whether this variation is produced by early neurologic damage is not yet completely clear. What is clear, however, is that a particular neurologic structure can greatly vary in its functional role.

LANGUAGE IN THE RIGHT HEMISPHERE

Up until the mid-1960s, it was commonly believed that the right hemisphere in man was little involved in language processing in either the comprehension or expressive end. Penfield and others,⁹ for example, were only able to obtain language phenomena by stimulating language areas within the left hemisphere. While there were clear exceptions to this general rule, especially in left-handers, the predominant view was that language-processing was the business of the left hemisphere.

About that time, Sperry and I reported on a series of tests carried out on Bogen's split-brain patients.¹⁰ In our first set of studies we showed in some patients that the right hemisphere could comprehend some simple nouns. These patients, however, were totally unable at that time to process verbs, and they showed little evidence that they could grasp adjectives. Hillyard and I¹¹ reported on a series of linguistic tests later in the 1960s. Again, we showed that the right hemisphere was syntactically weak. It seemed to be able to recognize the negative, but could not make plurals, comprehend tense, and failed on a variety of other tests of syntactic ability. Other studies by Levy and Trevarthen¹² revealed that the right hemisphere could not rhyme, and they too came up with a rather disappointing picture of its language functions. In still other tests on Wilson's series of patients, Springer and I¹³ showed that the right hemisphere performed very poorly on tasks requiring phonemic analysis. These tests suggested that if the right hemisphere does understand simple spoken words, it must gain meaning from the whole sound of the word, and not from its phonemic elements. A similar report was made by Zaidel and Sperry on the California series of patients.

More recently, Zaidel and Sperry¹⁴ have reported that the right hemisphere in Bogen's patients seems quite adept at language. They attribute, in the main, this increased ability to process language to their improved methods of lateralizing stimuli, which in effect allows the subject more time to explore the nature of the stimulus. By chance we have been able to study a new patient in the Wilson series who is truly remarkable, and it is worth considering briefly here some of the language skills we have noted to date.¹⁵

In contrast to all of the patients I have seen in both series, case P.S., within a month after surgery, was able to show an incredible range of language skills in the right hemisphere. This was determined by means of standard tachistoscopic exposure procedures. In brief, the patient was able to rhyme, to recognize superordinate classes, and also probably be able to act on printed commands. Thus, when a word, ("pie", for example) was laterally projected to the right hemisphere, the patient would claim that he saw nothing, but then with the left hand was able to point to the correct word card (which had "pie" written on it). By means of similar procedures, the superordinate classes were managed. For example, when the word "judge" was flashed to the right hemisphere, the patient could choose from a series of cards the most appropriate matching word, "trial." Similarly, lateralized printed commands were correctly carried out.

This rather startling demonstration of right-hemisphere language in this patient underlines the general rule concerning right-hemisphere language in split-brain patients. In brief, the variation in the amount and kind of language in the right hemisphere is far greater than the consistency, and is most likely a function of the degree and place of early brain damage to the left hemisphere. In case P.S. it is known that there was most likely early brain injury to the left temporal-parietal region at the age of two. The consequence of this lesion must surely be to bilateralize the language process. In contrast to this language-rich case, we were unable in another case (J.H.) to demonstrate language of any kind in the right hemisphere.

Because of the varying degrees of language in the right hemisphere in split-brain patients, obvious questions are raised over the role the right hemisphere plays in language processing in the normal subject. We have just completed a series of tests that strongly suggest that the right hemisphere in the normal brain carries out little or no language processing. In these tests, which were carried out by John Niederbuhl and myself,¹⁶ we make use of the fact that when a word is flashed across the midpoint of the visual field, those letters appearing to the left of center go to the right hemisphere, and those appearing to the right of center go to the left.¹⁷ Thus, as a subject is fixating the midpoint of the word TYRANT, the first three letters, TYR, go to the right hemisphere, and the last three, ANT, go to the left. While it seems reasonable to assume that the entire six letters must be reassembled before the subject can read the complete word, we hoped to be able to pick up what the separate hemispheres can do linguistically with the three-letter word segments presented to it before the whole six-letter word was assembled.

In our first experiment, a large list of ordinary six-letter English words were generated. There were four types: Type 1 words, in which the first but not the last three letters formed a word, e.g., POTENT; Type 2 words, in which the last three letters formed a word, e.g., DESPOT; Type 3 words, in which both three letter groups formed words, e.g., TARGET; and Type 4 words, in which neither of the three letter groups formed words, e.g., FOSTER. The subject's task in this study was to press a small, vertically mounted lever held between the thumb and index finger of the right hand if either three-letter segment formed a word. If neither segment formed a word, the subject was required to refrain from pressing.

Again, this means that when a stimulus of Type 1 (POTENT) was presented, the left hemisphere initially received the nonword portion, and the right hemisphere the word portion. The reverse was true when stimuli of Type 2 were flashed. If the subject responded faster to stimuli of Type 2 than stimuli of Type 1, the result would suggest that the left hemisphere could make a judgment about part of the word before the entire word was assembled. On the other hand, if the

subject responded faster to stimuli of Type 1, where the three-word segment goes to the right hemisphere first, then the result would suggest that the word was assembled in the left hemisphere, and scanned from left to right. In other words, if the results took this turn, it would suggest that the right hemisphere does no processing of the information, but rather sends it over to the left for assembly and language analysis.

We found that indeed Type 1 stimuli were responded to approximately 300 msec faster than were Type 2 stimuli. Our interpretation of these findings is that the right hemisphere sends its information across to the left, where the entire word is assembled. After assembly, a scanning process, which normally goes from left to right, extracts from the three-letter segment the information necessary to make the correct response. These and other studies described in our original report suggest that the right hemisphere, no matter what its potential for linguistic analysis might be, does not, when normal English words are being read, contribute much to the reading process. The studies do not rule out the possibility that the right hemisphere *may* be capable of performing simple linguistic functions, but they do strongly imply that the right-hemisphere linguistic abilities are not heavily relied upon by callous-intact persons when they are reading ordinary prose.

When the clinical and abnormal data are taken together, they serve up a very important warning, which is that data obtained in the clinical setting are not necessarily applicable in the effort to understand normal cognitive processes, and vice versa. Thus, the variety and extent of language-processing in the right hemisphere of split-brain patients appear to be a function of early brain damage. At the same time, whatever the extent, it would seem that a normal person makes very little use of possible language skills existing in the right hemisphere.

COMPLEX COGNITIONS IN THE ABSENCE OF SPEECH

One of the problems that we continue to explore is the relationship between complex cognition and language processes. We initially became interested in this issue as a result of considering some of our older studies on intermodal associations that we discovered could be made by the right hemisphere in split-brain patients. Those results, along with a variety of others, convinced us that the right hemisphere had at least a basic logical capacity. Subsequently, working with Glass and Premack,¹⁷ we tried to ascertain how much a global aphasic patient could learn of a meta-language scheme developed by Premack¹⁸ for the chimpanzee. These results were extremely encouraging, and suggested that a global aphasic could indeed learn a communication system, presumably with his remaining intact and healthy right hemisphere.

More recently, in Wilson's series of patients, we have directly examined the amount and kind of cognitions that can go on in the mute right hemisphere. Specifically, we designed a test that allows one to escalate the conceptual complexity in a particular trial without ever changing the general response mode. In these tests, developed by Margery Pinsley and myself, the subject is shown a picture in either the right or left hemisphere, or both, by our normal quick-flash procedures. On each trial, a set of four choice cards is placed in front of the subject, and after the stimulus presentation the subject is required to point to a card that best relates to the stimulus. The task starts out very simply, and requires nothing but straight physical matching. As the task becomes more complex, however, each trial requires an efficient memory system and the ability to make

inferences, categorizations, new conceptualizations, and the like. For example: the claw of a chicken may be presented, and the most relevant choice among the cards would be an egg. We have run these tests on case P.S., and he was able to perform all of them perfectly, with either hemisphere.

These data, as well as many other studies carried out on aphasics (including some new work by Risse on the ability of aphasics to perform on a wide range of Pagetian-type conceptual tasks), continue to point up the complexity of thought that can exist in the absence of normal language. Here, too, there is wide variation in performance skills, clearly suggesting that what can be done by a remaining neural system greatly varies and is most likely a function of differing early experience.

MECHANISMS AND DYNAMICS OF CEREBRAL SPECIALIZATION

The superior performance of the right hemisphere of split-brain patients on a variety of spatial tasks has come to be viewed as evidence concerning the unique specialization of this hemisphere. However, in recent experiments carried out with Joseph LeDoux, we have shown that the right-hemisphere advantage on many of these tasks only exists so long as manipulative activities are involved in either the stimulus perception or response production. Experimental and clinical observations suggest that the probable neural substrate of these manipulospatial acts involves the inferior parietal lobule of the right hemisphere in humans. In the left hemisphere, however, linguistic functions occupy the inferior parietal lobule. This suggests that in acquiring language the left hemisphere may have sacrificed space and thus efficiency in mediating manipulo-spatial functions. Consequently, it is our view that the superior performance of the right hemisphere of split-brain patients on such tasks does not reflect the evolutionary specialization of the right hemisphere, but instead represents the price paid by the left hemisphere in acquiring language.

This point takes on even more significance when it is realized that nearly every demonstration of a right-hemisphere advantage in split-brain patients has involved manipulo-spatial activities.²⁰⁻²⁵ The outstanding exception to this situation is the study by Levy, Trevarthen, and Sperry²⁶ of the performance of split-brain patients on the bilateral chimeric stimulus task.

In the process of routinely examining one of the recent patients in Wilson's series²⁷ during the first postoperative month, we found that although he performed like a textbook split-brain patient on many of the classic tests, his performance on the bilateral chimeric task was quite unlike that previously reported.²⁸ Instead of showing the typical right dominance he selected the choices matching both the right- and left-hemisphere stimuli. Further testing during the later postoperative months revealed that right dominance gradually replaced the bilateral responding.

We feel that the emergence of right dominance is not indicative of the unique perceptual specialization of the right hemisphere, but instead represents a settlement between the hemispheres whereby it is discovered that less conflict is encountered if each half-brain controls performance for different classes of activities. By default, the left mediates verbal encoding and responding. In contrast, when a situation is resistant to verbal encoding or is amenable to perceptual encoding, then although both hemispheres form nonverbal percepts, the judication of interhemispheric conflict requires that the left defer control over the response mechanism to the right.

The argument that the hemispheres use different cognitive strategies in forming visual percepts is methodologically weak, and is also challenged by these data. If the left hemisphere is asked to describe a complex visual stimulus, its verbal description will of necessity be lacking, though it may well perceive the whole stimulus. In addition, if on a chimeric test, hemisphere performance is evaluated where the hemispheres use different response modes, it is not surprising that the hemispheres seem to do things differently. On our bilateral response trials, when each hemisphere was responding by the subject's simply pointing, we found no evidence that one side outperformed the other.

The manipulo-spatial and chimeric data presented here show how our theories and ideas are bound to our methods. Slight variations in the design of classic experiments change the previously unequivocal notions concerning the unique organization of the human brain and show how dubious interpretations can be perpetuated in the literature.

GENERAL DISCUSSION

The new series of patients, operated on by Dr. Donald Wilson, has offered us an opportunity to extend much of our earlier work, as well as the work of others, and to assist in shedding light on many of the continuing mysteries of brain organization. In particular, some of the principles that appear to emerge from the foregoing data are: (1) that a particular brain structure can vary greatly in its functional role; (2) that the brain areas involved in language are easily varied, probably as a result of early brain insult; (3) that complex logical analysis can go on without expressive speech; and, finally, (4) that right-hemisphere advantage is more a manipulative skill that appears as a consequence of the earlier emergence of language in the left hemisphere.²⁹

The implication of these general principles are many. From an evolutionary point of view these data raise fundamental questions concerning where the uniqueness of man lies. Starting with the last point first, it becomes more and more apparent that the right hemisphere's greater superiority for gestalt-like tests, as well as other perceptual, nonverbal tests, is frequently more apparent than real. Our view is not that the right hemisphere is specialized in some unique way in man. Rather, it continues to do what it does elsewhere in the phyla.²⁹ The surprise is that the left hemisphere, because of the early ontogenetic emergence of language, becomes filled up, synaptically speaking, and as a result has little remaining neural space available for those executing skills involved in manipulating items in external space, which mature later. In other words, language matures in the left, leaving the right principally responsible for acquiring these manipulative spatial skills in later life.¹⁵

Secondly, the level of cognitive analysis that can be carried out by a languageless aphasic or speechless right hemisphere, reminds us that thought processes are not hopelessly linked to the existence of natural language systems. The structure of our thought process, with out ability to grasp relationships, causality and all the rest, emerges out of a deep-core information-processing capacity that is probably in a continual state of evolution and is present in some form in the chimpanzee, monkey, and dog, as it is in us.

Lastly, the evolutionary imperative in man is not iron-clad in terms of what brain structures must underlie specific mental operation. While there is most likely a general framework set up by the genome, what a particular neural network does might be the result of subtle, organic as well as early environmental

influences impinging on the organism. As a consequence, it would seem extremely likely that variations in our physical structure account for our varied behavior.

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