INVESTIGATIONS ON LATERALIZATION OF FUNCTION IN THE DISCONNECTED HEMISPHERES OF MAN

Thesis by

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Abstract

The effect of long standing cerebral damage upon the pattern of functional lateralization revealed by division of the forebrain commissures was investigated in a young commissurotomy patient with birth injury to the somatosensory region of his left hemisphere. Results from a battery of sensory - motor tasks showed that, unlike previous commissurotomy cases, the major hemisphere of this subject had access to somesthetic information from the ipsilateral as well as the contralateral hand, thus allowing him to name objects out of sight in his left hand, and to use this hand to tactually find items, the pictures or names of which had been visually presented to only the left hemisphere. The most plausible explanation for these exceptional cross integrative abilities would be the presence of a left sided ipsilateral somesthetic projection, which, in compensation for the subject's early brain damage, has strengthened into a functional system. Additional evidence for compensatory reorganization in this boy was found in his minor hemisphere, which exhibited an enhanced capacity for expressive language, being capable of transcribing printed words into script, and, upon occassion, of writing the name of an object.

Further research into the lateralization of higher intellectual functions in man involved a study of the

psychological processes responsible for the superiority of the right side of the brain on certain perceptual activities. The minor hemisphere, in the several commissurotomy patients tested, was found to excell the major on tasks involving visualization, from incomplete or disjointed sensory data, of the total stimulus configuration; this was revealed by its supremacy on such problems as: judging from a tactual or visual inspection of an arc, the size of the circle from which it had come, or mentally reconstructing the contour of a geometric shape seen in a fragmented state, or perceiving the pattern inherent in a visual display due to the differential spacing of its components. Extension of this testing to normal persons established that competency in the handling part-whole relationships is, in some manner, correlated with handedness, as left handed individuals performed much worse than right handed ones.

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I. General Introduction

Behavioral testing of both animals and human beings in whom the neocortical commissures have been surgically divided has established to a large degree the role of these structures in unifying the higher processes of the two cerebral hemispheres (1,2,3,4). Section of these large interhemispheric fiber tracts has been found to abolish normal integration of the two halves of the sensory world, leaving each hemisphere aware only of the contralateral sensory field. The left hemisphere thus perceives visual stimuli only if they fall in the right half visual field, and tactual stimuli only if they contact the right side of the body. Since in most human beings the left hemisphere alone possesses language, following commissurotomy the patient is asphasic for those events occurring in the left sensory field; these stimuli are, however, perceived by the right hemisphere as can be demonstrated by various non-verbal tests. While later research (5,6,7) showing the underlying unity of the brain, especially in its primative orienting functions (8), has modified the above picture, the general conclusions as to the independence of higher functions, such as learning, memory, perception etc, in the separated hemispheres remains unchanged.

Knowledge as to the types of information which do not transfer between the two sides of the brain in the absence of the neocortical commissures allows the design of experiments to investigate problems such as compensatory reoganization and hemispheric specialization, in which separate testing of the two hemispheres is a distinct advantage.

Shifts in the laterality of various functions following early unilateral cortical damage would be easily detectable in the commissurotomized patient as a retention of unusual cross integrative abilities, or as a variation from the normal pattern of hemispheric dominance. Independent examination of each hemisphere might further reveal the form and strategy taken by such compensatory reorganization.

Human commissurotomy patients are also an especially fine preparation for investigating the lateral specialization of cerebral function. Most studies of this question have compared the performances of individuals with damage restricted to one or the other hemisphere. This produces grave problems in matching the two unilateral lesion groups for size and locus of lesion, as well as for age, sex, etc. By contrast, in commissurotomy patients both hemispheres are intact and available for independent testing, allowing comparison in a single individual of the two sides of the brain. Since both hemispheres are from the same person, factors such as education, age and sex are automatically equated. However, the most important advantage of commissurotomy subjects for this sort of investigation is the possibility of determining directly the competency of each of their hemispheres on a task. In studies involving humans with unilateral injury this competency is inferred from the patient's failure on a particular test. If, for example, subjects with right hemisphere damage do worse than those with injury to the left hemisphere, the right side of the brain is inferred to be more essential for that task than the left. This sort of reasoning can, however, prove dangerous as has been pointed out by Semmes (9). If both hemispheres are equally competent on a test, but the neural substrate involved is more focally organized on one side than the other, damage to that hemisphere will be more apt to cause a severe deficit, thus producing an appearance of superiority. This danger of "pseudo-dominance" does not exist with a commissurotomy patient, as it is the abilities of his two hemispheres that are compared rather than their disabilities following injury.

II. The Commissurotomy Syndrome in a Patient with Birth Injury to the Left Hemisphere.

A. Introduction

The commissurotomy syndrome, as established to date, has been based largely on several select cases with little pre-existent brain damage. While all commissurotomy patients have had severe epilepsy, and thus some brain disfunction, the reported cases showed, prior to surgery, no outstanding sensory or motor deficits which would obscure the pure symptoms of the the cerebral disconnection. The ways in which compensation for long standing brain injury might change the functional consequences of this surgery, thus have not been investigated.

The plasticity of the young mammalian brain in response to injury has been amply demonstrated in both sensory and motor systems. Large cortical lesions having devastating effects in the adult, produce in the young only transient, or mild permanent symptoms. Ablation of the motor cortex in a monkey aged nine months or younger causes defects only in his fine finger movements (10,11,12), while in the adult it results in permanent paresis and spasticity (13). Destruction of the striate cortex in the infant rat (14), cat (15), or monkey (16) leaves the animal with visual capacities far in excess of adults with similar lesions. Ablation of the somesthetic projection area in young kittens yields cats indistinguishable from normal in all but the most difficult tactual discriminations (17). More complex functions show a similar relation between time of injury and severity of the aftermath. Infant monkeys with damage to the posterior association cortex do not show the visual learning deficits seen in adults with an identical lesion (18). The same hold true for the frontal association cortex and delayed response performance (19).

In man, the compensatory reorganization which occurs after early injury to large areas of the cortex is revealed by hemispherectomy, where removal of an entire hemisphere atrophied from infancy produces few of the sensory or motor deficits seen to follow ablation of a hemisphere injured at maturity (20,21,22). Even the capacity for language, normally restricted to the left hemisphere of most right handers, can, if the major hemisphere is damaged before age 15, shift to the normally mute right hemisphere (23).

Cases of agenesis provide the most dramatic examples of compensation, for although a portion of the brain is missing at birth due to a developmental or genetic error, the person displays none of the symptoms which would follow loss of this structure as an adult. A man with agenesis of the cerebellum thus earned his living washing windows in high rise buildings (24), while a girl born without a corpus callosum failed to show any of the cross integrational deficits seen after surgical division of this structure (25).

The availability of a young commissurotomy patient with left hemispheric injury dating from birth made possible an investigation of the manner in which compensation had affected the deconnection syndrome as seen in earlier cases. These experiments were concerned mainly with manual functions, as the pre-existent damage was to the cortical representation of the patient's right hand. The language capacities of the minor hemisphere were, however, also of interest as any damage to the major hemisphere might cause some shift in laterality of the language processes.

B. Case History

A.A.'s birth was a difficult one, necessitating a forceps delivery fourteen hours after labor was induced because of toxemia. At the age of four months he had two convulsions associated with fever, but was thought to be developing normally until age five and one-half when generalized convulsions began to recur. These often started with "spasms" or a "drawing up" of the right arm. The EEG indicated generalized abnormalities more marked over the left hemisphere. The convulsions continued, and despite medical treatment became progressively worse over the next eight years. A fractured clavicle, and a number of head injuries were sustained in attacks during this period.

On October 14, 1964 at age fourteen A.A. underwent cerebral commissurotomy, performed by Dr. Philip Vogel and his staff at the White Memorial Medical Center in Los Angeles.

The operation included division of the entire corpus callosum and anterior commissure with presumed section of the hippocampal commissure. The massa intermedia was not visualized. The surgery was difficult, requiring interruption of two large bridging veins from the frontal cortex. Postoperatively, substantial right hemisphere edema occured, leaving the subject with a mildly spastic left leg and a positive Babinski sign. His left arm, however, showed recovery to approximately the preoperative level. Since the operation he has suffered occassional episodes of right arm numbness and incoordination often associated with speech arrest.

Preliminary testing two years after surgery revealed A.A.'s right hand to be subnormal in several respects. Not only was its two point threshold raised above that of the left hand which was normal, but also the direction in which the first joint of one of his right fingers was moved by the examiner was often reported incorrectly. There was no deficit in either hand in the discrimination of pressure as tested by the von Frey hairs. In simple tactile tests where the patient had to blindly retrieve from among many objects an item which he had been told to find, or which he had previously felt, the right hand was usually less successful than the left. Despite this sensory deficit A.A. was right handed for most activities.

The patient's mental capacities were generally subnormal, but he could, after careful instruction, competently perform fairly complex tasks.

C. General Procedure

The testing procedures were, in general, similar to those used for studying integrational deficits in previous patients with section of the forebrain commissures (1,2). Most of the tests were carried out in a standard set-up (Figure 1) in which the subject was seated at a table in front of a projection screen of translucent plexiglas that served also to shield from sight the top of the table, the examiner, and the testing equipment. In the center of the screen at eye level was a black spot upon which the subject centered his gaze during tachistoscopic presentation of visual material. The patient could reach under the screen through a fringe to perform various manual tasks hidden from sight. To minimize auditory cues during tactile testing, the stimuli were placed behind the screen on a thick towel. This experimental arrangement allowed for controlled lateralized testing of different sensory modalities, and for separate motor performance by the two hands with vision excluded.

Unless otherwise stated, the subject was allowed in advance of the actual trials to identify by sight and touch, and to name aloud, all of the objects, words, or pictures to be used in a given test. In the case of visual stimuli this involved a free view for several seconds of each slide. All

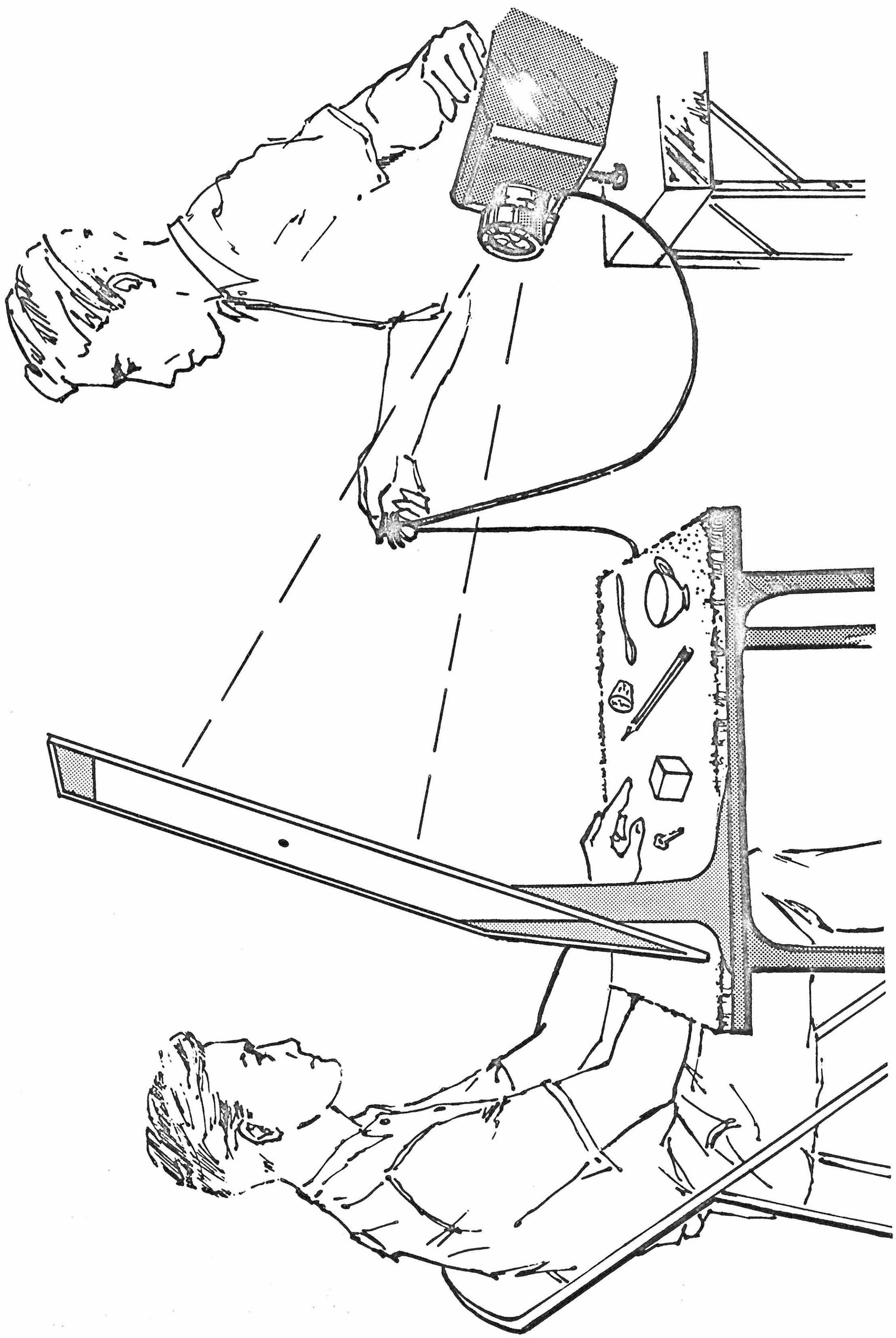


Figure 1. General Testing Set Up

of the projected images subtended a visual angle of approximately ten degrees.

In preliminary testing it was noted that, when required to identify stimuli in the left sensory field, the subject would often silently mouth, over and over, the names of the possible choices. To eliminate this as a source of peripheral cross cueing, mouthing was prohibited in the tests to be reported, even to the point of having the patient hold his tongue between his teeth.

Further procedural details for specific tests are described below in context.

D. Tests for Compensatory Reorganization of the Somesthetic System

1. Introduction

The main cortical representation for sensations of touch and kinesthesis from one half of the body lies in the contralateral hemisphere. The second order neurons from both the ventral spinothalamic tract, mediating coarse touch, and the dorsal funiculi, mediating discriminative touch and kinethesis, cross the midline and rise to the contralateral thalamus from which the third order neurons then project to the post central gyrus.

In view of the predominantly unilateral nature of the somesthetic projection it is not surprising that fine discriminative tactile and kinesthetic learning does not transfer between the forepaws of animals in whom the neocortical commissures have been cut (26,27,28,29). Commissurotomized humans show similar incapacities for cross localizing points on different halves of the body, and for reproducing with one hand, positions imposed by the examiner upon the other (30,31). The disjunction of the cortical representations for the two halves of the body is especially evident in the inability of the human patients to talk about somesthetic stimuli on their left side. The left, speaking hemisphere is thus ignorant of sensory events in the body half whose somatic representation is in the right hemisphere.

There is, however, behavioral evidence that somesthetic information is not totally restricted to the contralateral side of the brain. Respiratory responses conditioned to tactile stimulation of one paw of a split brain cat transfered to stimulation of the contralateral paw (32). A monkey could blindly coordinate his two hands so as to drop a grape from one to the other, even after division of the fore and midbrain commissures, and the cerebellum (6).

There is also substantial electrophysiological evidence for the representation in each hemisphere of ipsilateral as well as contralateral parts of the body. This is especially clear for the head and neck (33). In somatosensory area II evoked potential recordings have revealed also a bilateral mapping of the body's surface (34,35,36). The cortical potentials elicited by stimulation of ipsilateral body parts could be demonstrated even after total removal of the other hemisphere, and thus can not be attributed to an intercortical relay (37). In the cat two types of ipsilateral potential have been found. Although one of these is abolished by callosal section, the other, slower, one survives division of all forebrain and diencephalic commissures. This longer latency potential arrives simultaneously at both hemispheres, suggesting a bilateral projection system (38).

The active role played by the ipsilateral tactile representation in the normal functioning of the brain has recently been shown by an experiment in which ablation of the somatosensory cortex on one side of a monkey's brain caused a deficit in his performance on a tactual discrimination with the ipsilateral hand (39).

Since the ipsilateral systems have such a significant function in the normal brain, they undoubtedly would be of even greater value in compensating for early damage to the primary projection areas. The amount of sensation remaining after hemispherectomy depends to a great extent on the time of the original lesion. If an injury, such as a tumor, occurs at maturity, then following removal of an entire hemisphere the person usually has no sensation below the elbow in the contralateral arm (21). If on the other hand, the original lesion dates from birth, as in infantile hemiplegia, then after a right hemispherectomy the subject can describe coins, objects and even skin writing in his left hand (20). Since identification and naming require cortical processing it seems certain that the left hemisphere in these hemiplegics received tactual input from the left hand, probably through ipsilateral pathways.

The results of the following tests of somesthesis on a commissurotomy subject with early injury to the somatosensory region of his left hemisphere reveals a pattern of compensatory reorganization which would not have been evident with the commissures intact.

2. Results

a) Verbal Identification of Stimuli in the Left Hand. With his left hand screened from sight the subject was asked to feel and to verbally describe or name objects placed in his hand one at a time by the examiner. The simplest task involved stereognostic discriminations based separately on size, weight, or surface texture. For each of these tests a set of three cylinders was used. In the set varying in weight the cylinders were wood with lead inserts; all had the same height (2½") and diameter (1¼"), but weighted 100, 150, or 200 gms. The size discrimination involved three wood cylinders all 3" high but 1", 1½" or 2" in diameter. The subject was not allowed to lift these last stimuli in order that weight would not be a cue. For the texture discrimination, metal cylinders 2" by ½" with either a smooth, lightly or heavily knurled surface were used. In this task the cylinders were gently rubbed across the subject's finger tips by the examiner. In all of these tests the patient was shown, and allowed to feel the three stimuli before the actual trials began, and during the test had only to state how the cylinder out of sight in his hand compared to the other two of the given set. In size discrimination for example, he had only to say largest, smallest or medium. The subject's verbal reports for all three types of tactual discrimination made out of sight with the left hand were correct well above the chance level (Table I). When testing was extended to verbal identification of simple shapes (a round versus a square wooden rod, both 3½" long and 3/4" in diameter) A.A. correctly identified which one was in his left hand 22 of 24 times ($p < .001$).

Under conditions where he did not see or name the test items in advance, the subject was able to give good verbal descriptions of common household objects, such as a spoon, pencil or cup, placed in his left hand. He could describe these items in terms of their size, texture, material, etc. For example, he characterized a quarter as being "round, thin and made of metal". An oval bar of soap he called "smooth, hard, and rounded". A cotton glove was reported as "soft and made of cloth". In this test where the objects were totally unspecified in advance he was occasionally able to get the exact name of very simple items, such as a wooden

Table I.

Verbalization of Stimuli in the Left Hand

Three Cylinders of Different Texture	16/27	$p < .005$
Three Cylinders of Different Weight	24/30	$p < .001$
Three Cylinders of Different Diameter	13/13	$p < .001$
Two Common Objects	62/84	$p < .001$
Three Common Objects	103/129	$p < .0001$
Three Plastic Numbers	12/14	$p < .01$
Four Common Objects	59/74	$p < .0001$
Four Wooden Shapes	13/21	$p < .001$
Nine Common Objects	12/56	$p > .05$
Touch on One of the Five Fingers	30/70	$p < .001$

equilateral triangle, by describing aloud their tactile characteristics. His accuracy on this task was below that of his own right hand or of normal control subjects, but was well above that of the subordinate hand of other commissurotomy patients.

Since A.A. was generally unable to identify stimuli in his left hand when he had no prior knowledge of the objects to be given, experiments were conducted in which this information was provided. To discover the limits of his left hand naming capacities both the number and similarity of the stimuli were varied over several sessions.

Results of tests using from two to six choices demonstrated that A.A. could verbally identify well above chance which item the examiner placed in his left hand for tactual inspection (Table I). The somesthetic sensitivity possible under these conditions is seen in a series in which five centimeter high plastic letters (C,H,M,P,S,T) randomly presented to his left hand were correctly named 8 of 16 times ($p < .002$). When the number of items exceeded nine, even prior knowledge as to their identity was not sufficient to increase the subject's accuracy above the chance level.

The scores with his right hand on the preceding test were, as a rule, somewhat above those of the left, despite the right hand's sensory impairment.

b) Written Identification of Stimuli in the Left Hand. Since there existed some possibility of right hemisphere speech in this patient, his ability to identify in writing items felt by the left hand was examined. In these tests the subject was asked to write with his right hand the name of an object presented to the left hand, instead of speaking it aloud. Both the paper and the right hand were out of sight behind the screen. The written scores obtained under these conditions were quite similar to those for verbal reports of stimuli in the left hand. In detecting whether the rough or smooth metal cylinder had been lightly drawn across his left fingers, his written answers were correct 15 of 15 times ($p < .02$). When four wooden shapes (square, triangle, cross, and circle, with a diameter or side of 2" and a thickness of ½") were individually presented to the left hand in random order, he wrote the correct name 9 out of 18 times ($p < .02$). The identities of five common household objects (fork, pen, cup, comb, and key) randomly placed in his left hand were correctly written with the right hand 14 of 20 times ($p < .0001$). When the left instead of the right hand was used to write the answers in the preceding test, he was correct 8 of 11 times ($p < .001$). Six of the nine errors made by the two hands in this last test involved one object (the fork), all presentations of which were incorrectly identified. At the end of this session it was discovered that the subject had forgotten this particular stimulus was among the five choices. In these tests where written answers were used to identify objects in the left hand, A.A. was, as on those involving verbal reports, markedly superior to previous commissurotomy cases.

c) Verbal and Written Identification of Stimuli in the Left Visual Field. In order to determine whether under the present experimental conditions the subject's ability to name objects in the left sensory field was confined to the tactual modality, object pictures were presented by tachistoscopic flash to one or the other visual field, and A.A. instructed to say, or write out blindly with his right hand the correct name. Under these conditions he was able to name, either verbally or in writing, only those pictures presented in the right half field of vision. Neither the number of stimuli nor prior knowledge as to their identity made any difference in the results. His inability to identify stimuli presented in the left half visual field was quite comparable to other commissurotomy patients. In brief, A.A. was often able to say or write the names of test objects when they were presented tactually to the left hand, but not when the same objects were presented visually as pictures in the left half visual field.

d) Localization of Left Hand Stimulation. The subject extended his hands, palm upwards with fingers spread, underneath the testing screen, where, out of his sight, they were stimulated by the examiner with light pressure from a blunt plastic stylus. He could always report verbally the onset of contact with either hand, the pressure thresholds for the right and left hands not being noticeably different in this respect. When asked to say which of eight spots on his left arm and hand (lower arm, wrist, palm and the ends of the five fingers) had been lightly touched, his performance was well above chance (21/80, $p < .001$), as it also was when just the five fingers were tested (30/70, $p < .01$). The right hand scores on these latter tasks were somewhat better than those of the left, but were also subnormal (12/20, $p < .0001$).

In order to compare the ability of each hemisphere to cross localize touch, a test was given in which, with both hands screened from view, the subject was instructed to move the finger on his left hand that corresponded to the one touched by the examiner on his right, and vice versa. It was found that A.A. could perform this task from the left to the right hand but not in the reverse direction, from the right to the left. When a finger on his left hand was touched he correctly moved the corresponding finger on his right hand 21 of 49 times ($p < .001$). When, however, the right hand was stimulated, his performance with the left did not rise above chance (10/44, $p = .38$). A good deal of perseveration was also evident in this latter situation.

The observed ability of this subject to verbally localize points touched on the distal parts of his left hand and arm, though well below that of normals, was much better than has been demonstrated in any other commissurotomy patient. Previous patients also have not been able to cross localize touch in either direction.

e) Tactual Cross Retrieval. In this test an object was placed in one of the subject's hands for tactile examination, after which it was removed and scrambled among an array of other test items for retrieval by the opposite hand. This entire process was carried out with both hands screened from view, and with controls for auditory cues. Significant scores for cross retrieval in both directions were obtained for the three sets of cylinders described under verbal testing. When the right hand was required to retrieve from among the three cylinders of a set the one which the left hand had felt, the scores were 10/15 ($p < .01$) for size discrimination, 14/22 ($p < .01$) for weight discrimination and 11/15 ($p = .002$) for roughness discrimination. With left handed retrieval of cylinders felt by the right hand he was correct 10 of 15 times ($p < .01$) on the size, 14 of 24 times ($p < .02$) on the weight, and 13 of 18 times ($p < .001$) on the texture.

When common household objects were used or items, like wooden blocks or plastic letters, that varied only in their shapes, A.A. was not able to perform the cross retrievals with any significant success. Even with three objects (pen, key, and cork) varying markedly in their tactile qualities no reproducible positive results were obtained.

f) Visuo-tactile Matching. Since the results of visual testing with this subject were identical with those of previous cases, in that he was unable to verbally identify left field stimuli, it seemed reasonable to assume that each half field projected to only the contralateral hemisphere. This allowed independent testing of each hemisphere's ability to use tactile information from the right and left hands.

The patient was instructed to retrieve by touch from among an array of objects behind the screen the item that matched a picture flashed tachistoscopically to one or the other visual field. In early tests, pictures of 15 common household objects (key, spoon, pencil, cork, coin etc.) were used, with the articles themselves set in scrambled order behind the screen for tactual inspection. Under these conditions A.A., like previous patients, had no difficulty finding the correct items with the hand ipsilateral to the half field receiving the visual stimulus. When, however, required to use the hand contralateral to the field in which the picture appeared, the subject performed successfully in one direction but not in the other. While with his left hand he was able to find objects pictured in the right visual field, he could not locate with his right hand items seen in the left field (Table II.). Similar results were obtained when the printed names of articles rather than

Table II.

Visuo - Tactile Matching

	LVF-Left Hand		LVF-Right Hand		RVF-Right Hand		RVF-Left Hand	
	Picked	Named	Picked	Named	Picked	Named	Picked	Named
Pictures of	8/15	---	4/24	---	17/21	---	8/15	---
15 Objects	$P < .0001$	---	N.S.	---	$p < .0001$	---	$p < .0001$	---
Printed Names	6/15	---	4/23	---	13/22	---	13/23	---
of 15 Objects	$p < .002$	---	N.S.	---	$p < .0001$	---	$p < .0001$	---
Pictures of 15	13/15	2/15	2/16	2/16	12/14	12/14	14/15	14/15
Objects	$p < .0001$	N.S.	N.S.	N.S.	$p < .0001$	$p < .0001$	$p < .0001$	$p < .0001$
Pictures of 6	18/19	4/19	5/21	5/21	16/21	21/21	20/30	29/30
Wooden Shapes	$p < .001$	N.S.	N.S.	N.S.	$p < .0001$	$p < .0001$	$p < .001$	$p < .001$
Pictures of 6	6/7	3/7	1/7	1/7	8/11	10/11	5/10	9/10
Plastic Letters	$p < .001$	N.S.	N.S.	N.S.	$p < .001$	$p < .0001$	$p < .015$	$p < .0001$

LVF = Left Visual Field
RVF = Right Visual Field
N.S.= Non significant

their pictures were flashed to the two half fields. Here as before, the hand ipsilateral to the field of presentation was readily used to find the named objects, while in the cross retrieval situation the left hand alone could retrieve items named in the contralateral half field.

In further testing when the subject was requested after each retrieval to name aloud objects he had seen, A.A. correctly identified only those pictures flashed to the right visual field. Despite this inability to name objects in the left field he was, as in previous tests, able to find the correct stimuli with his left hand. Upon flashing the picture to the right half field he could retrieve the object with the left as well as the right hand, and could verbally name it (Table II.). The results of the foregoing naming and retrieval tasks were the same whether the stimuli were fifteen common objects, six wooden shapes, or six plastic letters. In these tests A.A., alone of the commissurotomy cases reported to date, has shown an ability to do crossed intermodal matching, using the left hand to find objects whose identity had been visually revealed to only the left hemisphere.

g) Visuo-visual Matching. In order to confirm the assumption made in the previous experiment that there was no crossing of visual information between the hemispheres of this subject, a test was given in which one of six geometric shapes was tachistoscopically presented in one or the other half visual field, followed three seconds later by the flash presentation in the same or opposite field of two of these shapes vertically arranged, one above and one below the level of fixation. One of these latter two stimuli was identical to that seen in the first presentation. The subject was asked to point to the place on the screen where the matching form had appeared, and then to name it. Only when both presentations fell in the same visual half field was he able to point out the correct shape above the chance level. He correctly named the figure solely on those trials where the first presentation was to the right visual field (Table III.). This failure to match stimuli between the two half visual fields is what would be expected from the previous results of tachistoscopic testing with commissurotomy patients.

Table III.

<u>Visuo - Visual Matching of Six Geometric Shapes</u>

	R.V.F. Then R.V.F.	L.V.F. Then L.V.F.	R.V.F Then L.V.F.	L.V.F. Then R.V.F.
Picked	15/20	18/20	4/20	5/20
(Chance= 1/2)	$p < .02$	$p < .001$	N.S.	N.S.
Named	3/20	19/20	5/20	20/20
(Chance= 1/6)	N.S.	$p < .001$	N.S.	$p < .0001$

R.V.F.= Right Visual Field
L.V.F.= Left Visual Field
N.S. = Not significant

3. Discussion

The combined results of cross integrational tests given this subject point to the presence in his left hemisphere of an unusually strong sensory representation of the left hand. Although the amount of useful somesthetic information received by A.A.'s major hemisphere from this hand was less than would be normally obtained across the callosum, it qualitatively exceeded that found in any other commissurotomy patient. This subject could describe both the location and somesthetic qualities of stimuli out of view in his left hand. This information as to size, weight, texture, material and shape was sufficient to allow actual identification of the object if the number of alternatives was limited, and their identities known to the subject beforehand. His lack of success with a larger number of choices could be due either to the crudity of the data with which the left hemisphere had to make its discriminations, or to the difficulty of remembering all the possible alternatives. If the major hemisphere identified these objects by reviewing its past left hand sensory experience with each choice, and matching this against present input, then the greater the number of alternatives the more likely some would be overlooked. When the identities of the test stimuli were not revealed to the subject in advance, this in effect multiplied the number of possible choices, and thus the difficulty of the task. In visual - tactile matching where the left hemisphere successfully distinguished up to 15 items through the left hand, a much smaller requirement was placed upon the ipsilateral system, as in this case the major hemisphere was provided with the item's identity, and had only to search with the left hand for a set of somesthetic characteristics it had previously learned was unique among the choices to that object.

While the above results suggest that the left hemisphere has access to tactual information from the left hand, there is no evidence that the minor hemisphere has a similar access to somesthesis from the right hand. Successful cross localization of touch occurred in one direction only, from the left to the right hand. This can be understood either as the right hemisphere possessing an exceptional amount of ipsilateral motor control not shared by the major hemisphere, or as the left hemisphere alone receiving tactile input from its ipsilateral hand. Similar undirectional results with visual-tactile matching, where only the left hemisphere - left hand combination was successful, settles this question in favor of an ipsilateral somesthetic system.

The only results inconsistent with the proposed model are those for tactual cross retreival. Although objects of varying size, weight or texture which were felt by one hand could be retrieved by the other, those differing in shape could not. This failure may be attributable to the subject's right hand sensory deficit, as tactual-tactual matching of shapes has been shown to be a more difficult task than is visual - tactile matching (40). Since A.A. could cross retrieve items varying in simple somesthetic qualities, his failure with shape, a stimulus characteristic more normally examined through vision, may reflect the difficulty of this type of matching for someone of such lowered tactile capacities.

There are several other possible interpretations for the data obtained from A.A., but none account for all the results as well as does the proposed left sided ipsilateral tactual system. Speech in the minor hemisphere while conceivably explaining the naming of objects in the left hand, can not be the basis of the cross localization of touch, or the increased intermodal matching. If peripheral or subvocal cross cueing of answers between the hemispheres were involved, then visual as well as tactual information should cross. This, however, was not the case as was shown by the failure of the subject to name left field stimuli, or to match shapes between the visual fields. This latter result demonstrates that the success of the left hemisphere - left hand combination in visual - tactile matching must be due to the major hemisphere receiving information from the left hand, and not to the right hemisphere learning the identity of the stimulus in the right visual field.

While there is evidence that one other commissurotomy patient, L.B., also possesses a functioning ipsilateral somesthetic projection, the amount of information his major hemisphere receives from the left hand seems to be substantially less than in A.A.. Although this patient could say aloud which of two shapes lay out of sight in his left hand, if asked to write the name, he performed at chance unless given feedback as to the correctness of his answers. It thus appears that his major hemisphere received sufficient information to distinguish the two shapes, but not enough to decide which was which without knowledge as to the accuracy of his replies (7). It should also be noted that L.B. was only thirteen when he underwent commissurotomy, and thus any ipsilateral abilities he possesses may, like A.A.'s, be a result of compensation. This possibility is strengthened by the failure of an adult commissurotomy patient to show any left hand naming on identical tests (7).

The main issue remaining concerns the course that compensatory readjustment has taken in this subject. Results obtained from lesions in immature animals would lead one to expect that A.A.'s right hand would gain an increased representation in the right hemisphere after its primary projection in the left had been injured. Exactly the opposite was found. In both visual -tactile matching and cross localization of touch the right hemisphere showed no ability to utilize tactual information from the right hand, but rather it was the damaged left hemisphere which exploited its ipsilateral hand. While this discrepency might be a result of subsidiary damage from head injuries or edema, it is more likely a reflection of basic brain organization, as it has been shown that, in man, the left hand has a higher probability than does the right of possessing a functional bilateral representation (41). Since compensation probably occurs through stengthening of existing pathways, this would predispose alteration in favor of a left sided system. Compensation would thus provide the left hemisphere with increased sensory information from the left hand offsetting the lose of tactual capacity caused by the birth injury.

This sort of reorganization would only be detected after division of the commissures allowed demonstration of cross manual abilities far above those seen in the typical commissurotomy patient.

E. Tests for Minor Hemisphere Expressive Language

1. Introduction

The association between right sided paralysis and aphasia has been known since biblical times-

> "If I forget thee O Jerusalem, let my right hand forget her cunning. If I do not remember thee let my tongue cleave to the roof of my mouth..."(42).

It is only within the last hundred years, however, that the neural basis of these symptoms has been localized, and language shown to reside almost entirely in the left hemisphere of right handed individuals. The capacity of the right hemisphere for expressive language, while proven for some left handers (43,44), remains unclear for those persons in whom the left hemisphere is dominant. A right handed adult whose major hemisphere was removed due to a tumor was capable of comprehending some written and spoken language, but not of producing any substantial amount himself (45.46). The right hemisphere of reported commissurotomy subjects show a similar capacity for comprehension, and incapacity for expression (47,48,49). There is, however, good evidence that the right hemisphere participates in the normal acquisition of expressive language in children, and has a potential for developing speech in the presence of left hemisphere damage (50). The earlier in life this injury to the major hemisphere occurs, the more likely is the right hemisphere to acquire verbal skills (23,51). Agenesis of the corpus callosum depriving the two hemispheres of their normal interaction also appears to induce the development of language in the minor hemisphere (52).

In view of these shifts in laterality produced by early cortical insult, the capacity of A.A.'s minor hemisphere for expressive language was investigated to determine how it might differ from that of the typical commissurotomy patient.

2. Procedure

Since tactile stimuli placed in A.A.'s left hand could not be assumed to be perceived by only his right hemisphere, tests for minor hemisphere expressive language were confined to tachistoscopically presented visual material. Earlier visual tests had demonstrated that, under the present experimental conditions, A.A. could not verbally identify stimuli in the left visual field, therefore in these tests he was required instead to blindly write out his answers. Before each session began all stimuli to be used, printed words or object pictures, were shown to the subject in free view, and he was asked to say their names aloud. The same stimuli were then exposed tachistoscopically with both the order of their presentation and the alternation between the visual fields randomized. After a stimulus had been flashed, the subject wrote his answer with one or the other hand on a pad of paper out of sight, behind the screen, and then named aloud the word he had written. In all cases A.A. spontaneously wrote in script rather than printing his answers.

3. Results

a) Writing to Printed Words in the Left Visual Field. In the first task, the visual stimuli were ten to fifteen short common printed nouns (cup, pen, key, et.). When these were projected to the right half visual field the results were similar to previous cases and to normals; the subject was able to write the correct word with either the right (18/22, $p < .01$) or left hand (16/24, $p < .01$), and could always name what he had written. When the stimuli were exposed in the left visual field his performance with the right hand exhibited the deficits seen in the other commissurotomy patients; the written answers were never correct (0/24), and his verbal responses always mirrored the written ones, thus demonstrating major hemisphere guessing. By contrast, his performance with the left, subordinate, hand was altogether different from previous subjects. Of the thirty-nine presentations of printed nouns to the left field, he wrote in script with his left hand the correct word twelve times. On ten of these occassions he then either could not name, or misnamed the word he had just written, suggesting minor hemisphere writing (Figure 2). The words correctly written but misnamed were : "cup", "comb", "dog", "key", "eye" (twice), "book" (twice), and "cat" (twice) (Figure 3 a & b). The responses by his left hand to the rest of the left field presentations consisted of incorrect answers which he could later always verbalize, indicating that in these instances the major hemisphere was doing the writing.

When the stimuli were printed verbs rather than nouns, again it was only the left field -left hand combination that yielded results divergent from the typical commissurotomy syndrome. Of the twelve presentations to the left field, the left hand wrote two possibly correct answers. In the first case the word presented with "lie"; he wrote "li", stopped, added "n", and said "run". In the second case the word was "sit"; he wrote "si", stopped, added "mp", and said "jump" (Figure 3c.). Both "jump" and "run" were known by

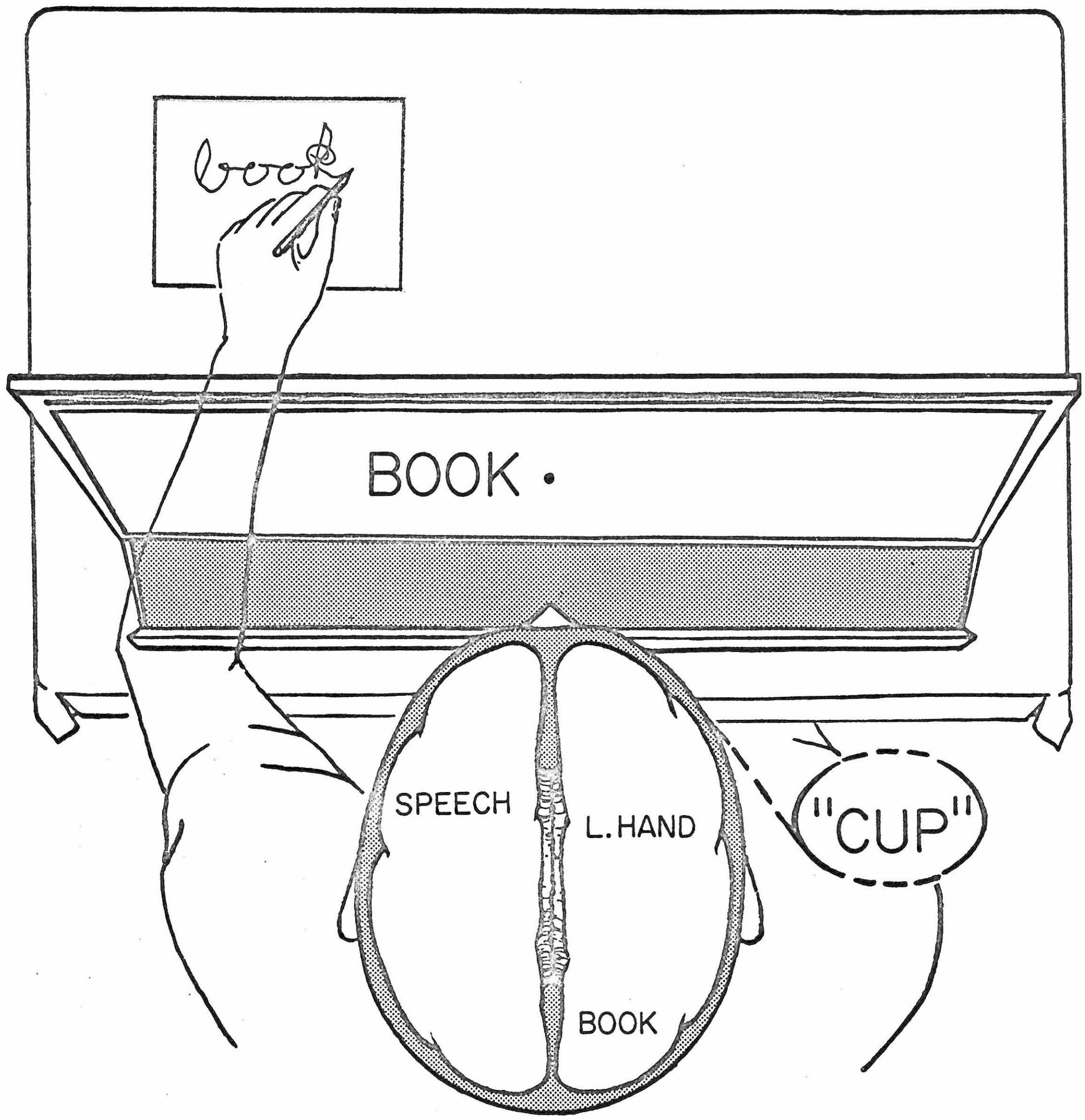


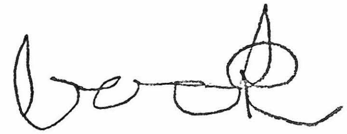
Figure 2. An example of left hand writing to a left field presentation, followed by incorrect verbalization of the answer given. The written word shown is an actual half size reproduction of the subject's answer.

a.

Word presented: DOG

Subject said: "I don't know, some word".

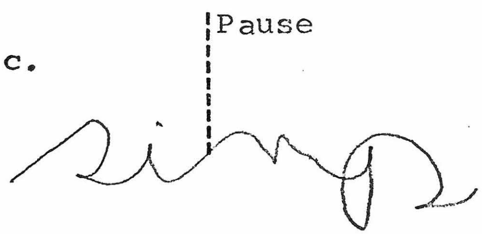
b.



Word presented: BOOK

Subject said: "Cup."

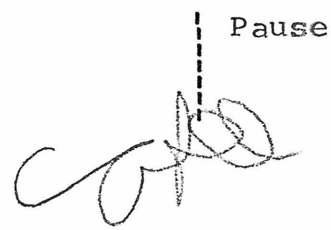
c.



Word presented: SIT

Subject said: "Jump."

d.



Picture presented: Cat

Subject said: "Bottle".

Figure 3. Illustrations of writing by the left hand after presentation of words or pictures in the left visual field.

the subject to be possible choices on this test. On the other trials the major hemisphere apparently dominated the left hand response throughout, and only incorrect answers, which he could later say, were obtained.

b) Writing to Object Pictures in the Left Visual Field. In this task A.A. was required to write out the names of fifteen common objects the pictures of which were flashed to one or the other visual field. Most of the pictures were of articles the printed names of which had been the stimuli in the first task. When these were flashed in the right field, as expected, he was very successful with either the right (16/16) or the left (38/43) hand. When the stimuli were introduced in the left half field the right hand wrote the correct answer only 2 of 15 times. Using the left hand, of 54 tachistoscopic exposures of pictures to the left visual field, the subject wrote the correct name six times, but on only two of these occasions did he then fail to name what he had written. Both of these exceptional successes involved a picture of a Siamese cat greatly resembling the family pet. The first time, when asked what he had written he tried to peer over the screen, and only after being prevented, admitted that he did not know. In the second case he wrote "cat", stopped, said "no that's wrong", added two loops (Figure 3d) and then said "bottle". On all other presentations to the left visual field he wrote an incorrect answer, and then verbally named the word he had written. Line drawings or pictures of other breeds of cat did not elicit a correct written response, however, major hemisphere interference was exceptionally great in these particular sessions.

4. Discussion

The preceding results demonstrate that A.A. could transcribe into script with his left hand printed words seen only by his minor hemisphere. The subject's inability to then verbally name the word just written by his own left hand makes it clear that the major hemisphere did not participate in this writing. These examples of minor hemisphere writing cannot be viewed as mere copying of visual shapes, for while the stimuli were printed, the subject's answers were always in cursive script. Rather, this performance required, on the part of the right hemisphere, both comprehension of the printed symbols, and an ability to transform them into an equivalent form.

The common tendency of the major hemisphere to supercede the minor's command of the left hand after a left field presentation can be seen in the frequent writing of incorrect words which could then be verbalized. Transfer of motor control from the minor to the major hemisphere occurred several times in the middle of an answer already correctly begun by the right hemisphere. Outward signs of this shift were a cessation of writing often accompanied by some exclamation of the effect that what he had written was wrong; the answer would then be completed with letters from an incorrect word which he could later verbalize.

Since all responses fully written by the minor hemisphere were correct, it seems reasonable to suppose that on those trials in which the right hemisphere was unsure of the word, or was hesitant in beginning to write, the major hemisphere seized control of the left hand and imposed its own guess.

The left hemisphere was even more intrusive when the visual stimuli were pictures of objects rather than their names. The only two examples of minor hemisphere writing under these conditions occurred with the picture of a cat resembling the patient's pet. The role of emotional ties in this performance is not clear as other pictures with emotional overtones elicited no right hemisphere writing. These two instances, however, were definitely not random responses, as the subject only once wrote "cat" to an inappropriate picture.

Due to interference by the major hemisphere it was not possible to obtain a true measure of the capacity of A.A.'s minor hemisphere for expressive writing. This, however, was not the sole limiting factor on its performance, but rather the language skills of his right hemisphere seemed basically inadequate to produce the name of a picture. While there was greater major hemisphere interference with pictures than with printed words, this is more likely a consequence of the right hemisphere's failure, than the actual cause of it.

There is no reason to believe the major hemisphere would have intruded more often with the one type of stimulus than with the other, unless the right hemisphere had shown itself particularly deficient in handling pictures.

While surpassing all previous commissurotomy cases, except for L.B. (53), by having the motor patterning necessary to write words, A.A.'s minor hemisphere fell short of infant left hemispherectomy cases in that it was unable to initiate writing of a name upon seeing the object itself. This deficiency seemed to be mainly one of ascertaining the correct word, since A.A.'s right hemisphere, like those of previous cases (50), could recognize and pick out the name of an object it had seen or felt. Therefore, this subject's right hemisphere knew how to write but not what to write, being incapable of itself creating the correct symbol.

In summary, while A.A. has, in his right hemisphere an increased aptitude for language, it is qualitatively less than is seen in cases in which the left hemisphere was totally damaged early in life. This is probably a reflection of the continued functional presence, in this subject, of the left hemisphere language centers, whose activity would tend to inhibit the development of language in his minor hemisphere, although not as totally as in the normal brain.

III. Minor Hemispheric Dominance for the Perception of Part - Whole Relations

A. Introduction

The role played by man's right hemisphere in complex mental activities was, until recently, greatly underestimated. The dramatic nature of the language deficits which follow left hemisphere damage, plus the verbal character of most of the testing procedures of the time contributed to the concept that the left hemisphere was the sole or dominant seat of all higher brain processes; the right hemisphere at best was an automaton possessing no special functions. The left hemisphere was even proposed to be the sole possessor of consciousness (54).

The development in the 1930's of test batteries such as the W.A.I.S. (55), which examined many diverse mental operations, demonstrated that, while left cerebral injury did affect verbal test scores, defects on nonverbal or performance tasks were more likely to follow damage to the right hemisphere (56,57). Since that time performance deficits such as dressing apraxia (58), some types of drawing disability (59,60,61), and constructional apraxia (62,63) have been associated with the right, rather than the left, hemisphere.

In the past ten years the interest of many investigators has turned to the perceptual aspects of hemispheric specialization. Their work has confirmed the relationship between the left hemisphere and verbal material , and has linked the right hemisphere to the perception of a large variety of non-verbal stimuli, such as visuospatial relations (64,65,66,67), faces (68,69,70), nonsense shapes (71,72,73), and incomplete figures (74,75,76). Even such widely divergent functions as stereopsis (77), visual hallucinations (78), and the recognition of melodies (79) have been said to reside mainly in the right side of the brain.

There have been several attempts to characterize the psychological properties common to these tests on which performance is effected more by damage to one hemisphere than to the other. The left hemisphere has been said to handle best tasks in which the stimuli are verbal, verbalizable (71, 74), or familiar (73), the right, those having nonsense, meaningless (72), or visually complex discriminanda (71).

Other hemispheric dichotomies have been based on postulated differences in the type of perceptual processing employed by the two sides of the brain. This distinction between the left and right hemispheres has been described as: symbolic versus visuospatial (80), associative versus apperceptive (81), propositional versus appositional (82), and analytic versus gestalt (83). All these classifications imply that the organization and processing of data by the right hemisphere is in terms of complex wholes, with a predisposition for perceiving the total rather than the parts. By contrast, the left hemisphere is postulated to sequentially analyze input, abstracting out the relevant details and associating these with verbal symbols.

If the minor hemisphere does concern itself mainly with the overall stimulus configuration, then it ought to excell on those operations necessary to form this type of percept, such as generating from incomplete data a concept of the whole, or detecting the organization present in an array due to the interrelationship of its elements. In order to test this prediction, tasks were designed to examine the relative abilities of the two hemispheres to perceive the whole inherent in the part or parts of a stimulus.

B. Subjects

The seven commissurotomy patients used in these studies were operated on from three to five years before testing in order to relieve epilepsy not controlled by medication. The surgery by Dr. P.J. Vogel and his staff at the White Memorial Hospital involved complete section of the corpus callosum, anterior and hippocampal commissures (84,85). Except for R.M. and C.C., these individuals now lead fairly normal lives in their own homes. Before surgery all seven patients considered themselves right handed. This was confirmed during the present experiments by the Harris Test of Lateral Dominance (86), which also revealed them to be, except for R.M., right eye dominant. None of these subjects had any significant abnormalities on brain scan, angiogram, or air study. The approach to the callosum in every case was accomplished by retraction of the right hemisphere. Evidence for preoperative brain damage in each individual is as follows:

A.A.'s case history was given in the previous section.

L.B.,a seventeen year old boy,presented prior to surgery, no lateralizing signs or symptoms, his EEG abnormalities always being generalized. Post-operatively, a few seizures restricted to the left side of the body occurred, indicating a possible right Rolandic lesion.

C.C., an eighteen year old boy, evidenced symptoms, including turning of the head to the right and speech arrest, characteristic of an anterior occipital focus in the left hemisphere.

N.G., a thirty-seven year old woman, had EEG indications of a left temporal focus; evidence for a right central lesion also existed, consisting of a one centimeter wide Rolandic calcification as well as a left side numbness preceding some of her preoperative convulsions.

R.M., a thirty year old man, had no reliable localizing signs either before or after surgery. He is the only patient whose generalized convulsions were not helped by this operation.

N.W., a thirty-nine year old woman, had preoperative seizures often involving turning of the head and flailing of the limbs first to the left and then to the right. Mild slowing of the right temporal EEG was present, as was an intermittent left hypesthesia. One year after her commissurotomy a ventriculo-jugular shunt was implanted through a right parietal burr hole. Revision of this shunt has been necessary three times.

R.Y., a forty-six year old man, suffered generalized seizures probably dating from a childhood head injury. A visual aura often preceded his attacks; according to Mullan and Penfield (78), the chances are ten to one that this represents a right hemispheric focus.

In all but A.A. and C.C., therefore, it is the right hemisphere which is more liable to disfunction from extra-callosal damage or from any residual subictal abnormalities.

In addition to the commissurotomy patients, some testing was carried out on a fifty-five year old man (H.D.) in whom the right occipital and posterior parietal lobes had been removed due to an abcess. Prior to surgery H.D. had been a draftsman, but in the year since his operation he has been unable to return to work due to left field blindness and an inability to recognize persons by their faces (prosopagnosia).

C. Arc-Circle Matching

1. Introduction

Previous studies of right hemispheric function in human beings have involved mainly visual stimuli, especially complex patterns. If, however, an actual dichotomy does exist in the strategies by which the two hemispheres organize and process perceptual data, it should be evident also in other sensory modalities; likewise complex stimuli should not be a necessity if the mental manipulations required are performed better by one side of the brain than the other.

The present experiment was designed to test the ability of individuals to handle simple part-whole relationships. Subjects were asked to judge from tactual or visual examination of an arc, the size of the circle from which it had come. Since the stimuli were arcs and circles differing only in their size, and thus in their rate of curvature, complicating factors such as novelty, complexity, and verbalizability should not obscure the part-whole nature of the problem.

Besides comparing the independent perceptual capacities for this task of the right and left hemisphere of commissurotomy patients, the present tests was also used to examine a prediction made by a recent theory of hemispheric specialization (87), to the effect that left handed normal subjects would be inferior to right handers on tests requiring minor hemisphere performance.

2. Methods

The stimuli for this experiment were made from plexiglas rings of four different sizes: 2", 1½", 1¼", and 1" in inner diameter (Figure 4). For each size there was a set consisting of a whole ring and four arcs of varying degrees

Figure 4

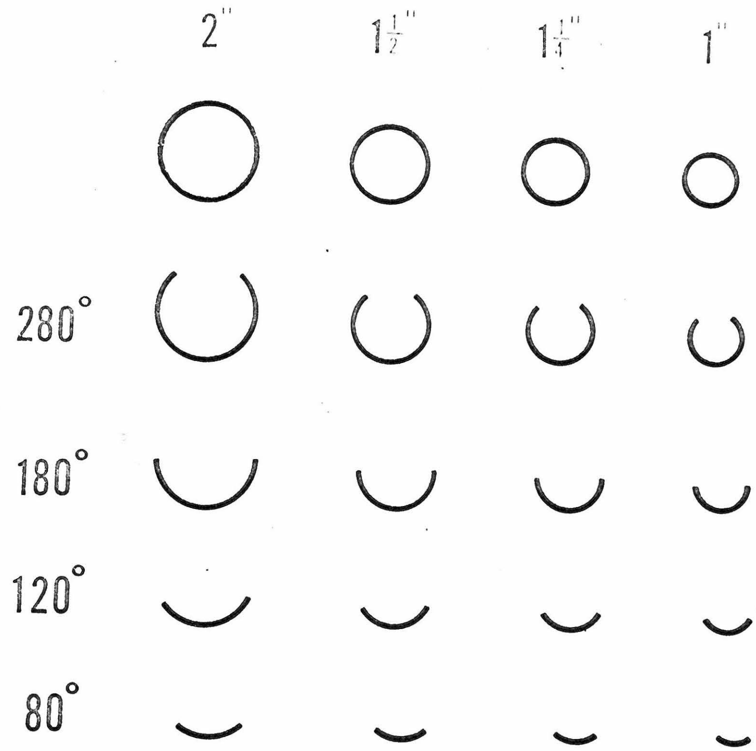


Figure 4. Stimuli for the Arc - Circle Matching Test

of completeness: 280°, 180°, 120°, and 80°; all had the same wall thickness (1/8") and height (1/8"). Each was individually mounted on a 3"x 3" card.

In the first session with each individual, special sets of stimuli (1 3/4" and 2¼") were used to demonstrate the geometrical relationship existing between the arcs and complete rings of the two sizes. The subject was encouraged to superimpose different arcs on the rings to see how they fit. It was emphasized that the length of an arc alone could not reveal the size of the circle from which it had come, but, rather it was the amount of curvature over the given length which was important. None of the subjects had any apparent difficulty grasping this concept.

The individual was next instructed that he would be presented with a series of arcs, and for each one he was to pick out the size of circle of which that arc was a segment.

Each person was given the test in three different forms. The first two of these required intermodal matching, as the arc was presented in one modality and the choices in another; the third was totally intramodal.

In the first form, Somesthetic - Visual, (Figure 5a) the subject reached beneath a screen and felt an arc, while simultaneously looking at three sizes of ring. When he had made his decision as to which one the segment was from, he withdrew his hand and pointed to it.

In the second form, Visual - Somesthetic (Figure 5b) the

Figure 5

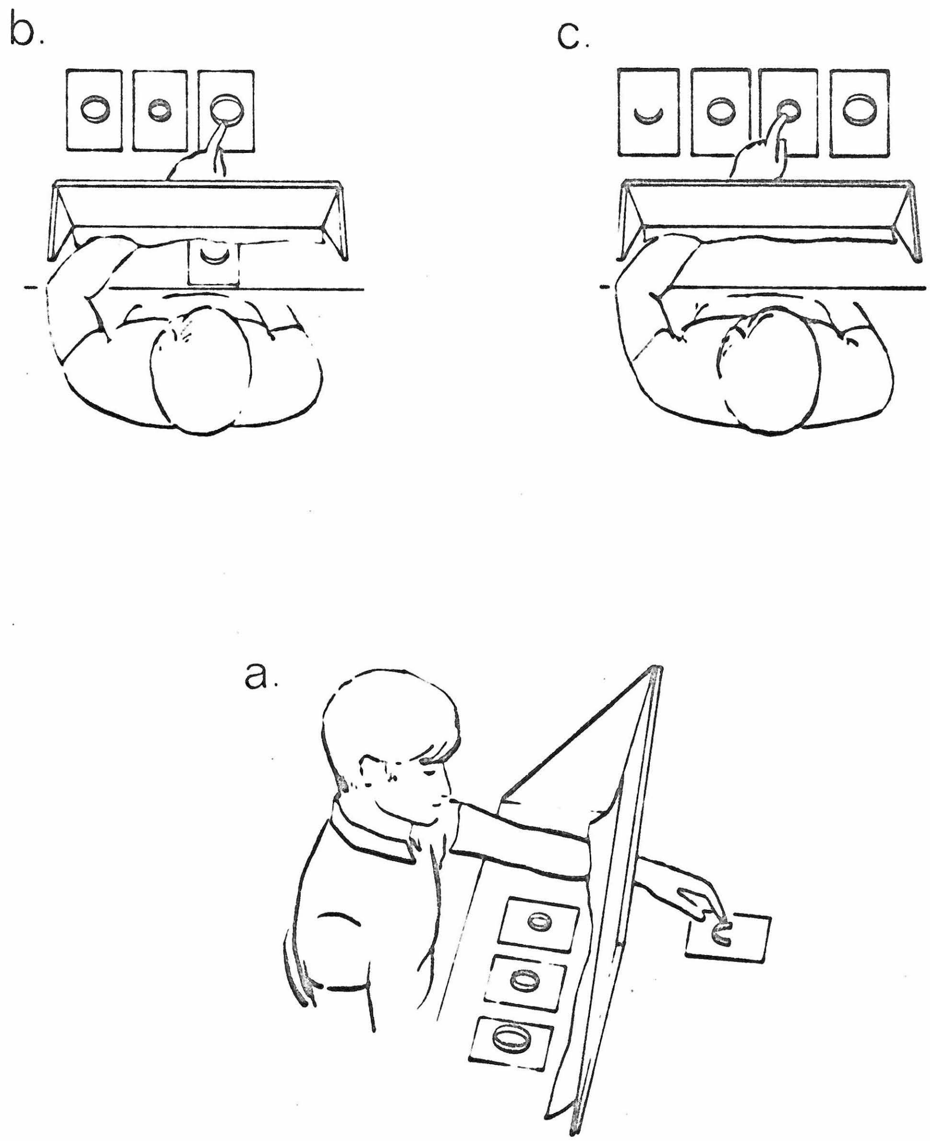


Figure 5. The Three Forms of the Arc - Circle Matching Test - a) Somesthetic - Visual, b) Visual - Somesthetic, c) Somesthetic - Somesthetic.

arc was presented in free view, while the rings were arranged behind the screen for tactual inspection. In this case the subject indicated his choice by tapping the correct ring.

The third form, Somesthetic - Somesthetic, (Figure 5c) had both the arc and the rings hidden from view, with no restriction on the number of times the subject could shuttle between them for comparison.

In the second and third forms of the test the arrangement of the choices was changed after every trial; the disposition, however, for any one arc was identical for the right and left hands. In all three test forms the various arcs were presented to both hands in the same predetermined random order.

The exact sizes of the rings used in the three forms of the test depended on each individuals ability. On the Somesthetic - Visual (S - V) and Somesthetic - Somesthetic (S - S) forms all subjects were given circles differing by one quarter inch - 1½", 1¼" and 1". In the Visual - Somesthetic (V - S) procedure both L.B. and R.Y. performed at chance with these sizes, and were, therefore, retested with rings varying by one half inch - 2", 1½" and 1".

In all forms of the test, somesthetic examination of the stimuli was limited to the index finger of either hand. The subject's arm rested on the table and only finger and some wrist movement was allowed. Before either hand was given any section of the test the subject was allowed to feel in free view with that hand the three choices to be used.

In addition to the experimental trials, there were, for each form of the test, two control series. In these controls the procedures were identical to the experimental tasks, except that instead of matching arcs to complete circles the subject now matched circles to circles or arcs to arcs.

In the first control (Circle matching) both the test stimuli and the three choices were complete rings of the same sizes as were used for each subject in the experimental trials. Thus with the S-V procedure the subject now felt a complete ring, and had to pick out the matching size from among the three rings lying in free view.

In the second control both the test stimuli and the three choices were arcs. Although these control arcs all had the same external circumference (1½"), they had been cut from the three ring sizes used in the experimental trials, and therefore differed in curvature.

These two controls were thus designed to measure the subject's ability to match with each hand sizes of circles or degrees of curvature under the same inter or intramodal conditions used in the experimental task of matching arcs to circles.

Another control test (Cross Matching) was given to determine whether there was any transfer of somesthetic information between the right and left hands. With both hands behind the screen, the subject felt a stimulus with one hand, and then tried to find it among three choices with the other. Each person was tested both with the complete rings and the control arcs for cross retrieval in either direction, left hand feeling the stimulus and the right hand retrieving it, and vice versa.

The experimental and control series were given to the brain operated subjects in the following order: S-V experimental, V-S experimental, S-V and V-S controls, more S-V and V-S experimental, more S-V and V-S controls, S-S experimental, S-S controls, more S-S experimental, more S-S controls, cross matching controls.

Control trials for the three forms were inserted between two sets of experimental trials to insure that any difference between the results of the experimental and control series was not due to experience. To further eliminate the effect of experience, the left hand was tested before the right on the first set of experimental trials, and after it on the second. The left hand was always tested last on the control series in order to elicit any superiority on its part in these situations.

The order in which the three forms were administered to the control subjects varied. Two of the normals had the same sequence as the commissurotomy patients, while of the remaining three, one had V-S, S-V and S-S, the second V-S, S-S and S-V, and the third S-S, V-S and S-V.

The complete battery of experimental and control tests was given to as series of brain operated patients as well as to a control group of five right handed normals. The brain surgery group consisted of five commissurotomy patients (L.B., N.G., R.M., N.W., R.Y.), and the right occipital lesion case (H.D.). The normals were five Cal Tech technicians (three females, two males) aged nineteen to forty.

Partial results were also obtained from another commissurotomy patient (C.C.) not available for the complete test series.

In addition to the above five normals, another twenty graduate students and postdoctoral fellows were given twenty-four trials with each hand on the experimental part of the S-V form. This last group was evenly divided between right handers and non-right handers, as established by the Harris test of Lateral Dominance.

The experimental and control scores for the two hands of each brain operated and control subject were compared in a 2 x 2 chi square contingency table using a Yates correction whenever an expected frequency fell below 11. A binomial expansion was used to determine whether each score was significantly different from chance.

3. Results

a) Commissurotomy Patients. The totals for the right and left hands of each individual, and of all the subjects combined are given separately for the three forms of the test in Tables IV, V, and VI. The top row of each table contains the data for the two hands on the experimental trials, the second and third rows the control results - Circle Matching and Arc Matching. Below each pair of scores is the chi square of their comparison, along with the probability of that chi square having arisen by chance. The experimental results are also given in graphic form in Figures 6,7 and 8.

The data show that in four of the five commissurotomy patients the left hand was significantly more accurate than the right in matching arcs to the correct size of circle, regardless of the modality of the stimuli. Generally thirty-six or less trials were sufficient to demonstrate this left hand advantage, and in no case were more than forty-eight trials with each hand required. The strength of the left hand's predominance varied between individuals, generally being strongest in N.G. and R.M., somewhat weaker in N.W. and R.Y., and altogether lacking in L.B. The combined scores for all five subjects on both the inter- and intramodal procedures reveal a highly significant disparity ($<.001$) in favor of the left hand.

An indication of the right hand's ineffectiveness on these tasks was its general failure to rise above chance levels, as designated in the tables by asterisks. Only in the V-S form did the right hand of any of the subjects beside L.B. attain a score above that possible by pure guessing.

Table IV

First Form SOMESTHETIC - VISUAL

		L.B.	N.G.	R.M.	N.W.	R.Y.	Totals
Experi-mental	Rh	17/36	13/36*	9/36*	16/36*	17/48*	72/192*
	Lh	14/36*	28/36	21/36	25/36	28/48	116/192
	X^2=	.70	12.68	8.21	4.56	5.05	31.48
	p	$<.05$	$<.001$	$<.005$	$<.05$	$<.025$	$<.001$
Circle Match-ing Control	Rh	24/36	24/36	21/36	25/36	32/48	126/192
	Lh	28/36	23/36	25/36	27/36	36/48	139/192
	X^2=	1.1 N.S.	<1 N.S.	<1 N.S.	<1 N.S.	<1 N.S.	<5 N.S.
Arc Match-ing Control	Rh	19/36	24/36	23/36	27/36	31/48	124/192
	Lh	22/36	27/36	27/36	27/36	34/48	137/192
	X^2	<1 N.S.	<1 N.S.	1.05 N.S.	0 N.S.	<1 N.S.	<5 N.S.

*Chance performance, Lh = Left hand, Rh = Right hand, N.S. = Not significant.

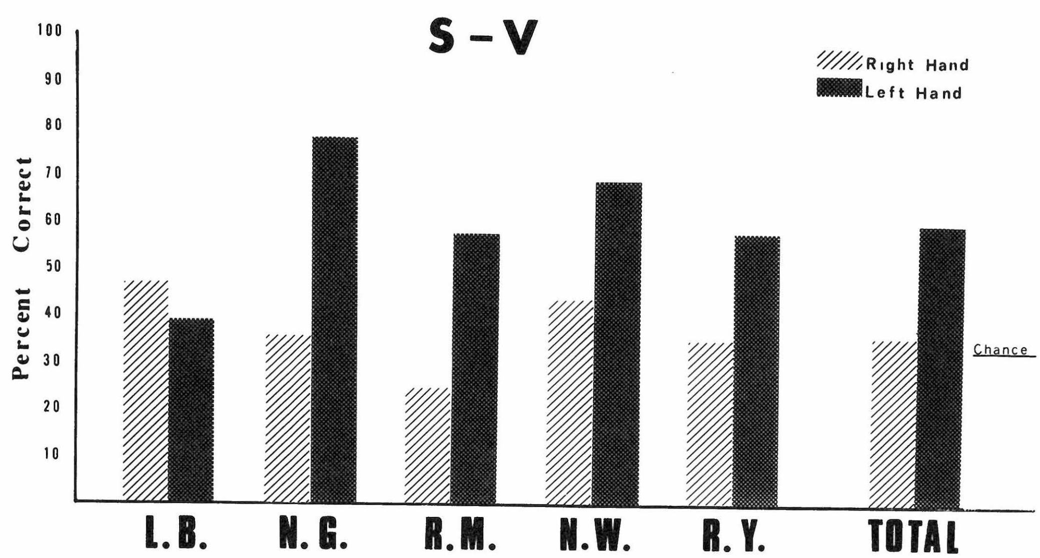


Figure 6. Experimental Results

Table V

Second Form VISUAL - SOMESTHETIC

		L.B.	N.G.	R.M.	N.W.	R.Y.	Totals
Experi-mental	Rh	20/24	18/48*	13/24	17/36	16/30	84/162
	Lh	17/24	29/48	22/24	29/36	25/30	122/162
	X^2	1	5.04	6.74	8.0	4.92	27.59
	p	$<.05$	$<.025$	$<.01$	$<.005$	$<.05$	$<.001$
Circle Match-ing Control	Rh	20/24	41/48	20/24	26/36	29/30	136/162
	Lh	21/24	43/48	21/24	29/36	28/30	142/162
	X^2	<1	<1	<1	<1	<1	<5
		N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Arc Match-ing Control	Rh	16/24	33/48	17/24	24/36	19/30	109/162
	Lh	11/24*	34/48	18/24	25/36	23/30	111.162
	$X^2=$	1.34	<1	<1	<1	<1	<5
		N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

*Chance performance, Lh = Left hand, Rh = Right hand, N.S. = not significant.

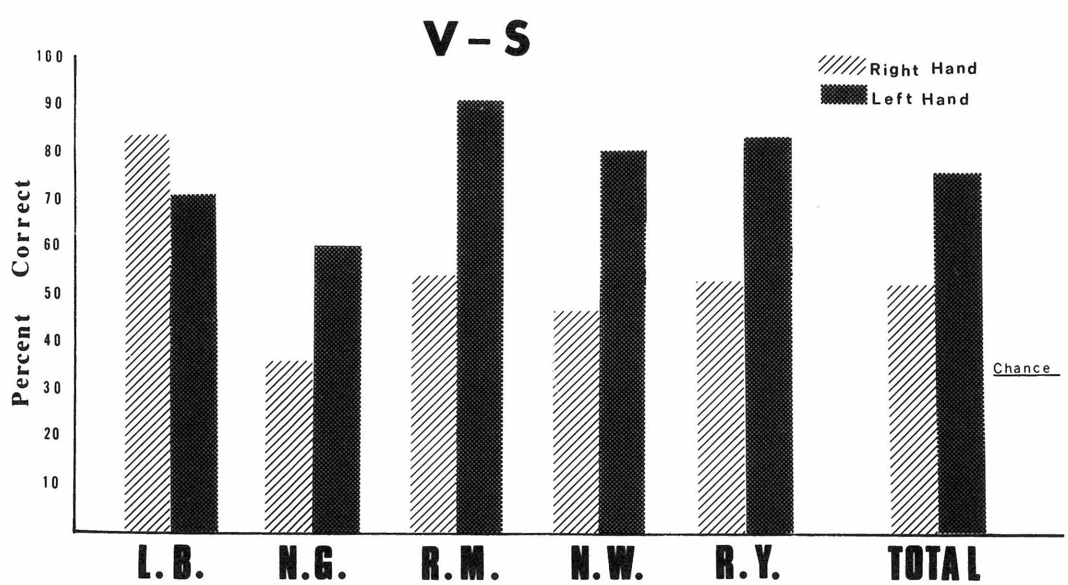


Figure 7. Experimental Results

Table VI

Third Form SOMESTHETIC - SOMESTHETIC

		L.B.	N.G.	R.M.	N.W.	R.Y.	Totals
Experimental	Rh	13/24	13/36*	8/24*	9/24*	10/24*	53/132*
	Lh	14/24	24/36	19/24	17/24	18/24	91/132
	X^2	<1	6.74	10.24	5.4	4.19	26.61
	p	<.05	<.01	<.005	<.025	<.05	<.001
Circle Matching Control	Rh	16/24	26/36	18/24	21/24	17/24	98/132
	Lh	19/24	26/36	21/24	20/24	16/24	102/132
	X^2	<1	=0	<1	<1	<1	<5
		N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Arc Matching Control	Rh	18/24	22/36	18/24	18/24	18/24	94/132
	Lh	17/24	20/36	21/24	17/24	16/24	91/132
	X^2	<1	<1	<1	<1	<1	<5
		N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

* Chance performance, Lh = Left hand, Rh = Right hand, N.S. = not significant.

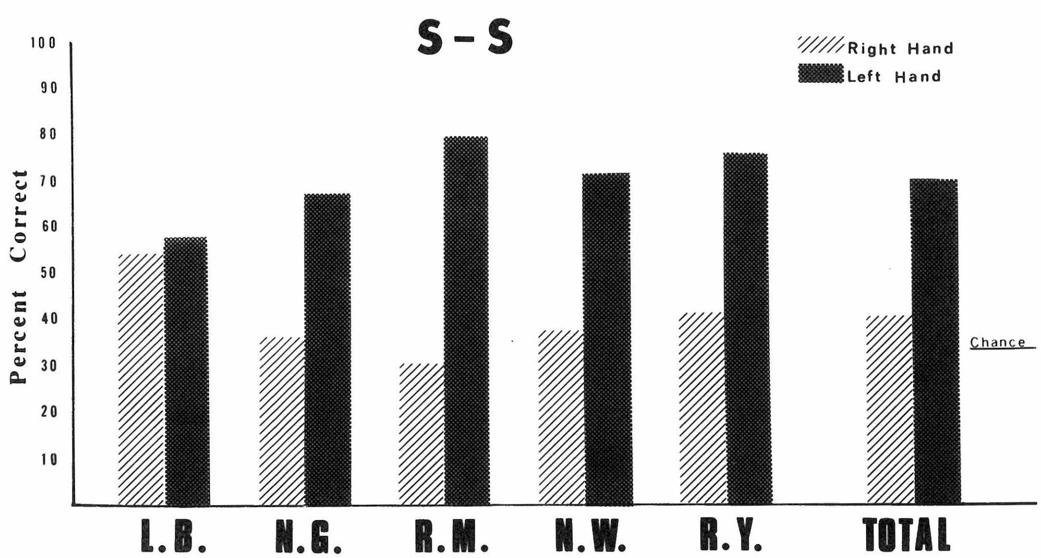


Figure 8. Experimental Results

In contrast to the experimental trials, the right hand's achievements on both control series were well above chance, and did not differ significantly from those of the left hand, the chi square generally falling below one. The size of the discrepancy between the right hand's performance on the experimental and control tasks, as seen in Table VII was quite large. While a few of the comparisons did not reach significance due to a low number of trials, or to the difficulty of the arc marching controls, in most cases the right hand was significantly worse at matching arcs to complete circles then it was at matching circles to circles or arcs to arcs.

In summary, four of the five commissurotomy patients tested performed far better with their left hands than with their right on the inter- or intramodal matching of arcs to circles. The right hand's incompetency was,however, limited to the part-whole procedure, and did not extend to the matching under identical conditions of sizes of circle or degrees of curvature.

The available data on yet another commissurotomy patient, C.C., give further evidence for the superiority of the left hand on these tasks. On the S-V form of the test, while C.C.'s right hand performed at chance (13/36), his left hand achieved a score of 22/36 ($X^2 = 4.47$, $p < .05$). On the V-S form his left hand was correct on 27 of 36 trials, his right on only 17 of 36, for a chi square of 5.82 ($p < .02$).

TABLE VII

Comparison of Right Hand Experimental and Control Scores

		SOMESTHETIC-VISUAL		VISUAL-SOMESTHETIC		SOMESTHETIC-SOMESTHETIC	
		Circle Matching	Arc Matching	Circle Matching	Arc Matching	Circle Matching	Arc Matching
L.B.	Exp.	17/36	17/36	20/24	20/24	13/24	13/24
	Cont.	24/36	19/36	20/24	16/24	16/24	18/24
		$X^2= 2.76$	$X^2<1$	$X^2=0$	$X^2=1$	$X^2=3.2$	$X^2=1.46$
		N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
N.G.	Exp.	13/36	13/36	18/48	18/48	13/36	13/36
	Cont.	24/36	24/36	41/48	33/48	26/36	22/36
		$X^2= 6.7$	$X^2=6.7$	$X^2=23.1$	$X^2=9.4$	$X^2=9.44$	$X^2=4.48$
		$p < .01$	$p < .01$	$p < .001$	$p < .001$	$p < .001$	$p < .05$
R.M.	Exp.	9/36	9/36	13/24	13/24	8/24	8/24
	Cont.	21/36	23/36	20/24	17/24	18/24	18/24
		$X^2= 8.2$	$X^2=10.9$	$X^2=3.48$	$X^2=3.8$	$X^2=8.38$	$X^2=8.38$
		$p < .005$	$p < .001$	N.S.	N.S.	$p < .005$	$p < .005$
N.W.	Exp.	16/36	16/36	17/36	17/36	9/24	9/24
	Cont.	25/36	27/36	26/36	24/36	21/24	18/24
		$X^2= 4.57$	$X^2= 6.56$	$X^2=4.66$	$X^2=2.76$	$X^2=10.72$	$X^2=5.4$
		$p < .05$	$p < .01$	$p < .05$	N.S.	$p < .001$	$p < .025$
R.Y.	Exp.	17/48	17/48	16/30	16/30	10/24	10/24
	Cont.	32/48	31/48	29/30	20/30	17/24	18/24
		$X^2= 9.36$	$X^2= 8.16$	$X^2=12.8$	$X^2=1.1$	$X^2= 3.04$	$X^2=4.19$
		$p < .001$	$p < .005$	$p < .001$	N.S.	N.S.	$p < .05$
Total	Exp.	72/192	72/192	84/162	84/162	53/132	53/132
Total	Cont.	126/192	124/192	136/162	110/162	98/132	94/132
		$X^2=31.59$	$X^2=32.52$	$X^2=44.04$	$X^2=15.06$	$X^2=31.9$	$X^2=23.91$
		$p < .001$	$p < .001$	$p < .001$	$p < .02$	$p < .001$	$p < .001$

N.S.= Not significant

The one subject not conforming to this general picture is L.B. His left hand did not excel his right in matching arcs to circles, nor did his right hand find the control tests any easier than the experimental. Both of L.B.'s hands were, in general, superior to the right hands of the other commissurotomy patients, and slightly inferior to their left hands.

L.B. also differed from the other patients in his manner of examining the arcs in the S-V or S-S forms of the test. While they repeatedly traced the inner surface of the segment, L.B. often employed such strategies as measuring the chord of the arc, or tracing in with his finger the arc's missing portion in order to get an idea of its completed size. Since these methods generally led to a series of mistakes their use was discouraged; the subject, however, often returned to them claiming that just feeling the curvature was too boring.

The results of the third control test served to further distinguish L.B. from the other four subjects. In this test for transfer of somesthetic information between the hands, only L.B. scored above chance (Table VIII). Thus, while the others showed the lack of cross integration typical of commissurotomy patients, L.B. could find with one hand an arc or ring felt by the other. This cross retrieval occurred equally well in either direction.

Although this last result suggests that in L.B. there is

Table VIII

Results of Cross Matching Between the Hands

	Complete Circles		Control Arcs	
	Rh to Lh	Lh to Rh	Rh to Lh	Lh to Rh
L.B.	13/20 p<.01	14/20 p<.001	12/20 p<.05	11/20 p<.05
N.G.	8/20 N.S.	7/20 N.S.	6/20 N.S.	8/20 N.S.
R.M.	8/20 N.S.	6/20 N.S.	6/20 N.S.	6/20 N.S.
N.W.	8/20 N.S.	7/20 N.S.	9/20 N.S.	8/20 N.S.
R.Y.	8/20 N.S.	6/20 N.S.	8/20 N.S.	5/20 N.S.

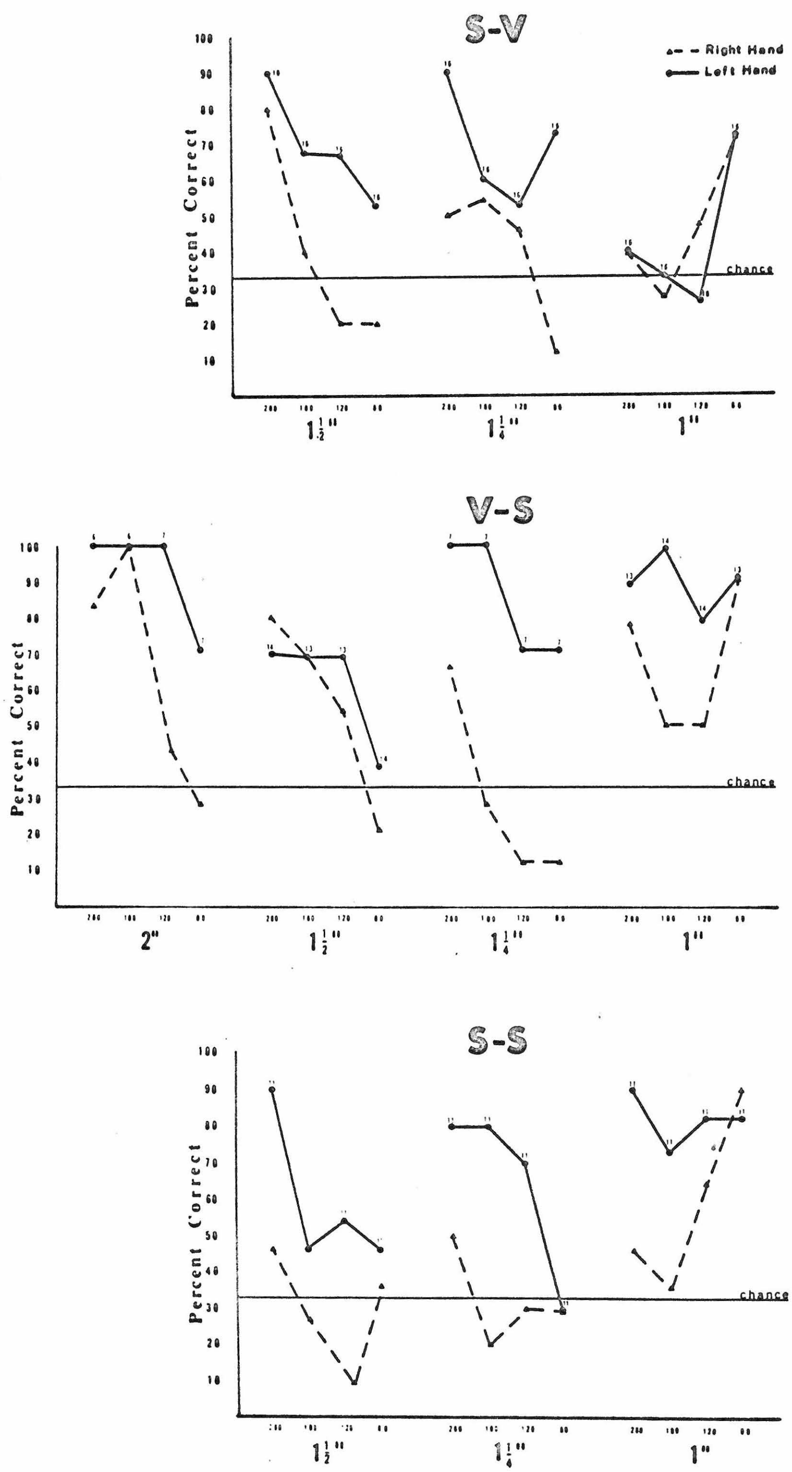
Rh= Right hand, Lh= Left hand, N.S.= Not significant.

considerable interhemispheric transfer of somesthetic information, his scores were included with the rest in the following analysis of the data, as preliminary plots showed they caused no major distortion of the results.

A series of scatter diagrams was made for each subject showing the answers given by his two hands on every stimulus in the experimental and control series. From these diagrams was extracted the data seen in Figure 9, which shows for the three forms of the test the percentage of correct answers

Figure 9

Experimental Results For Each Arc



made by the right and left hands of all subjects on each arc in the experimental series. Next to every point on the plot for the left hand is the number of trials it represents; the percentages for the right hand are based on equal numbers of trials.

Figure 9 reveals that the right hand's accuracy was generally greatest with the most complete arcs (280°), and fell off rather rapidly as the segments became smaller. With arcs of less than 180° the right hand usually performed at chance, the sole exception being the 80° arc of the 1" series, on which in all three test forms it showed a dramatic rise in accuracy. The reason for its success with this particular arc was found in the scatter diagrams, where it was obvious that the right hand was choosing the 1" circle for almost all 80° arcs regardless of which size circle they were actually from.

The left hand's performance was more stable than that of the right, not being so tightly linked to the completeness of the segment. The left hand was often as accurate on the 120° arcs as on the 280°; however, it too showed a drop on the 80° arcs of all but the 1" series.

Overall, the right hand's performance was greatly dependent on the amount of the segment present. The nearer the arc was to being a complete circle, that is, the closer the task was to the circle matching control, the more accurate the right hand became. By contrast, the left hand's performance tended to be equally good over a wide range of segment size.

Figure 10 shows right and left hand experimental scores arranged by circle size. In these graphs each point represents the combined scores on all arcs from that size circle.

The relative success of the two hands with the various sizes can be seen to be different in the first two forms of the test. In the S-V form, while the right hand performed best on the 1" series, the left hand found it to be the most difficult. In the V-S form there was a considerable discrepency between the comparative performances of the two hands on the 1½" and 1¼" series of arcs. The S-S form was the only one to give an identical pattern of difficulty for the two hands.

In contrast to the experimental tests, on the two controls (Figure 11) the right and left hands were very similar both in absolute scores and in the pattern of their success, each hand finding the middle size more difficult than either extreme.

Examination of the types of errors made by the two hands in both the experimental and control tasks revealed no striking consistency or pattern, but rather a considerable variation not only between subjects, but also between tests. The right hand especially seemed to make as many overestimates as it did underestimates. The left hand, while more apt to show a tendency towards one or the other type of error, was never significantly different from the right.

Figure 10

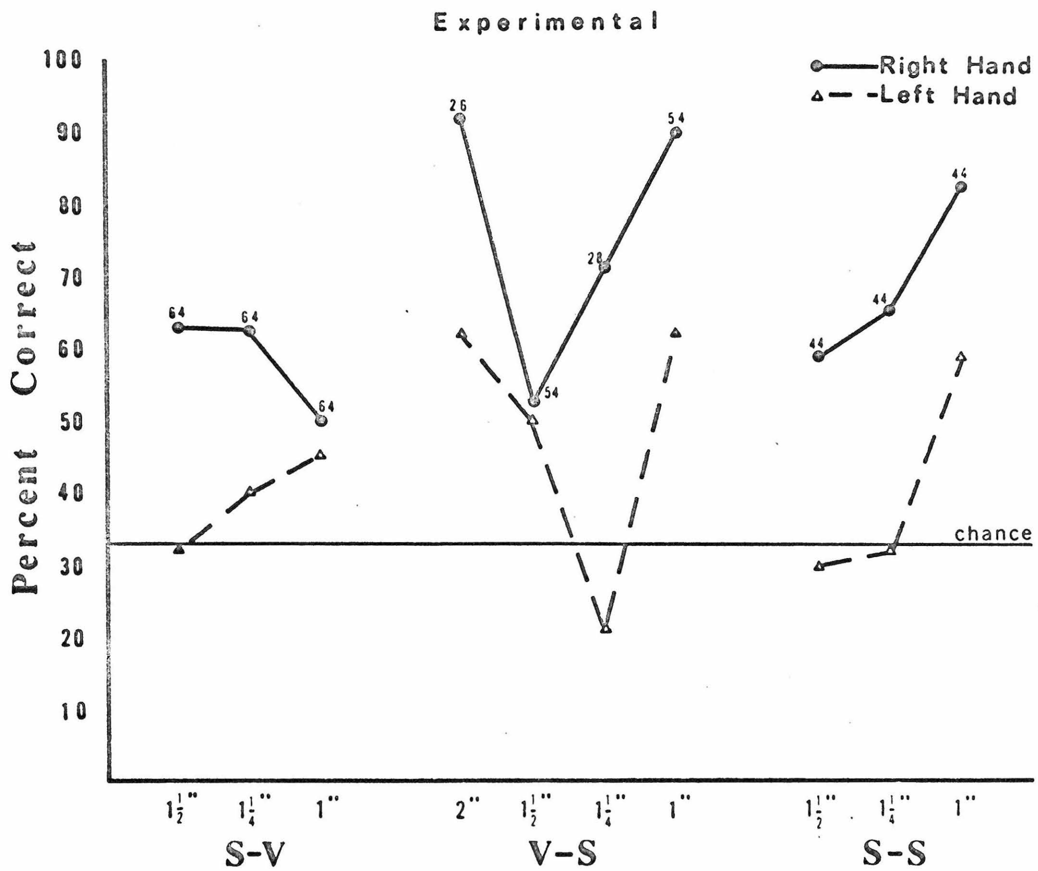
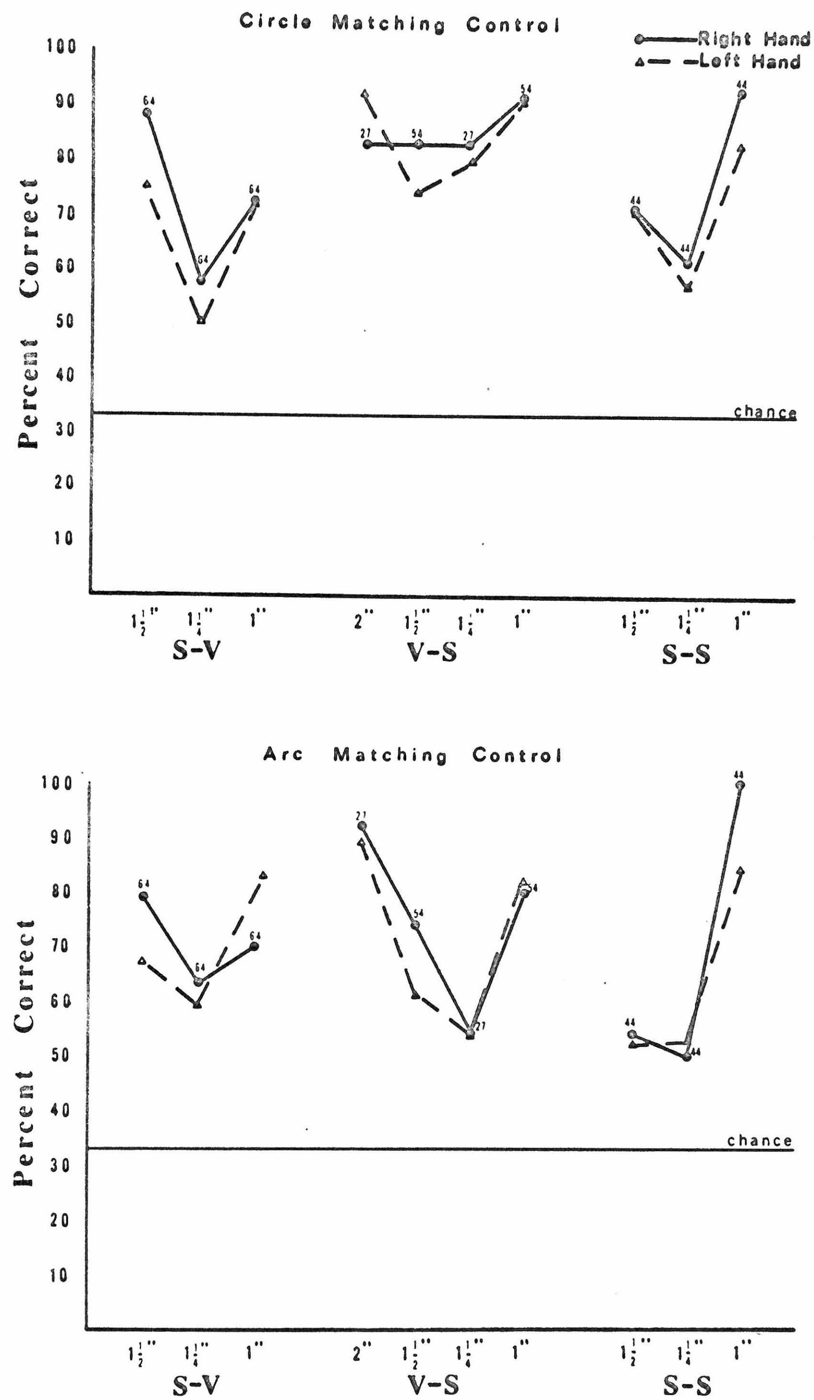


Figure 10. Experimental Results Organized by Circle Size. Each point represents the scores on all arcs from that size of circle.

Figure 11

Results For Each Circle Size



b) <u>Right Occipital Lesion Patient</u> In contrast to the commissurotomy cases, a man (H.D.) with right hemispheric damage performed worse with his left hand than with his right when required to match arcs to the appropriate size of circle (Table IX). This disparity between the two hands, however, was never large enough to reach significance even on the S-S form, where the left hand scored at chance. Like the commisurotomy patients, this subject was equally proficient with either hand on the two control tests. The findings with H.D. are discussed further in connection with the normal subjects.

Table IX

Right Occipital Lesion Patient

		Somesthetic-Visual	Visual-Somesthetic	Somesthetic-Somesthetic
Experimental	Rt. Hand	24/36	24/36	14/24
	Lt. Hand	18/36	17/36	7/24
Circle Matching Control	Rt. Hand	31/36	31/36	24/24
	Lt. Hand	31/36	34/36	24/24
Arc Matching Control	Rt. Hand	30/36	27/36	22/24
	Lt. Hand	28/36	28/36	21/36

c) <u>Normal Control Subjects</u>. The five right handed normals given the full test sequence had no significant differences between their two hands either on the experimental or control tasks. The average scores achieved by each hand over twenty four trials are given in Table X. The S-V form was found to be the most difficult regardless of the order in which the three forms were administered. Within each test form the circle matching control proved to be the simplest task, while the arc matching and experimental trials were equally demanding; only with the S-V procedure did normals have more difficulty matching arcs to circles, than they did arcs to arcs.

Further analysis of the data failed to reveal any variation in accuracy correlated either with the size of the circles or with the degree of completion of the segments. Control subjects were only slightly less accurate with the smaller arcs (120° and 80°) than with the more complete.

As expected, on the cross matching control all subjects were very proficient in matching between their hands both sizes of circle and degrees of curvature.

In order to compare control and brain operated subjects on the various tests, their scores were transformed into percentages. Since the totals for the two hands of the normals were not significantly different, they were averaged for use in Figures 12 and 13.

Figure 12 reveals that on the experimental task, although both hands of commissurotomy patients scored below normal, the left hand was down by only 10 to 15 percentage points, while the right was deficient by some 35 to 45 points. On

Table X

Average Scores for the Five Right Handed Control Subjects Over 24 Trials

	S-V	V-S	S-S
Experimental	Rh 17.6	Rh 22	Rh 20.2
	Lh 16.6	Lh 21.2	Lh 21.2
Circle Matching	Rh 20.6	Rh 24	Rh 23.2
	Lh 21	Lh 23.8	Lh 23.6
Arc Matching	Rh 20.4	Rh 22	Rh 21.2
	Lh 19.8	Lh 22	Lh 21.4

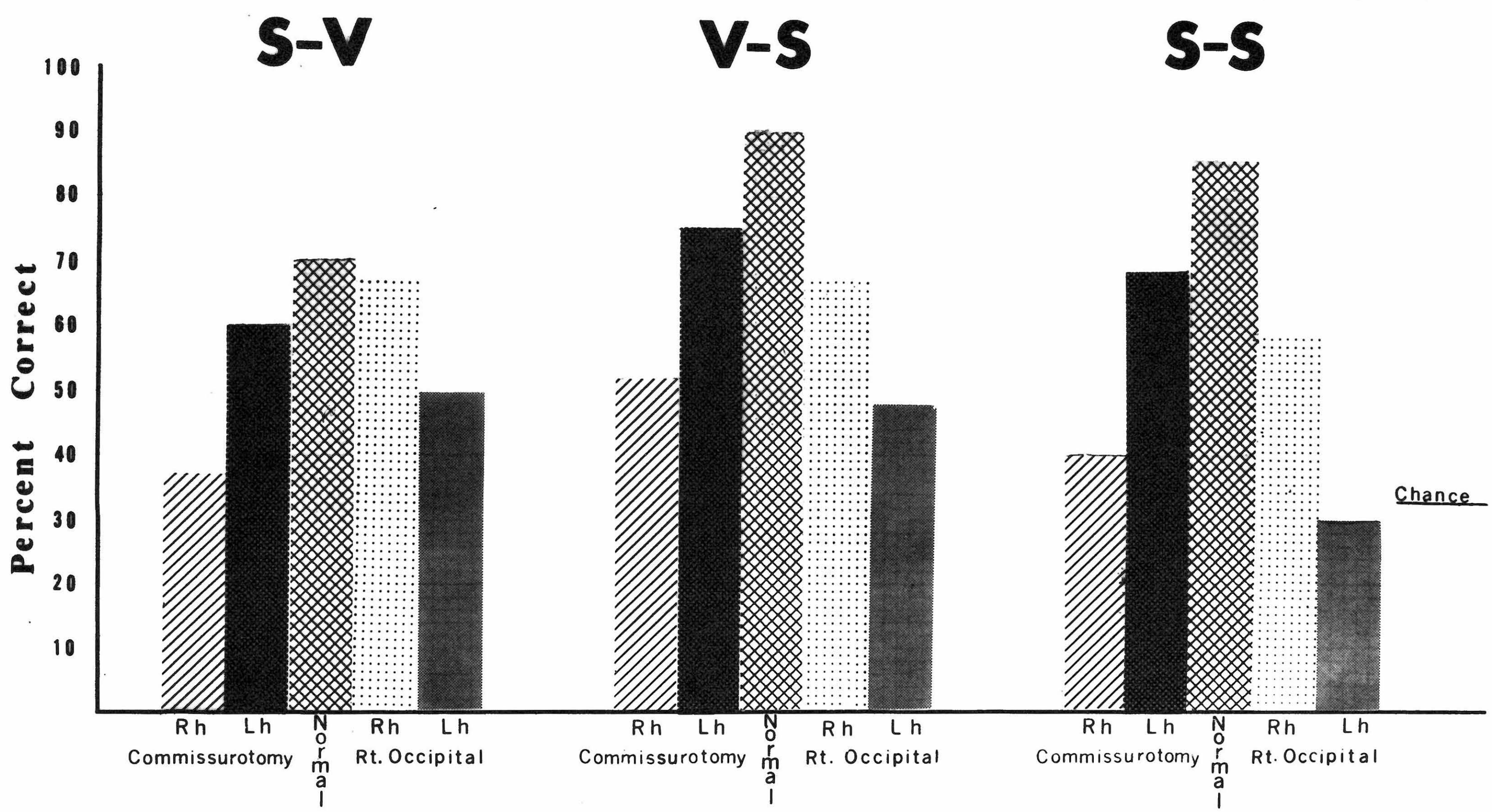
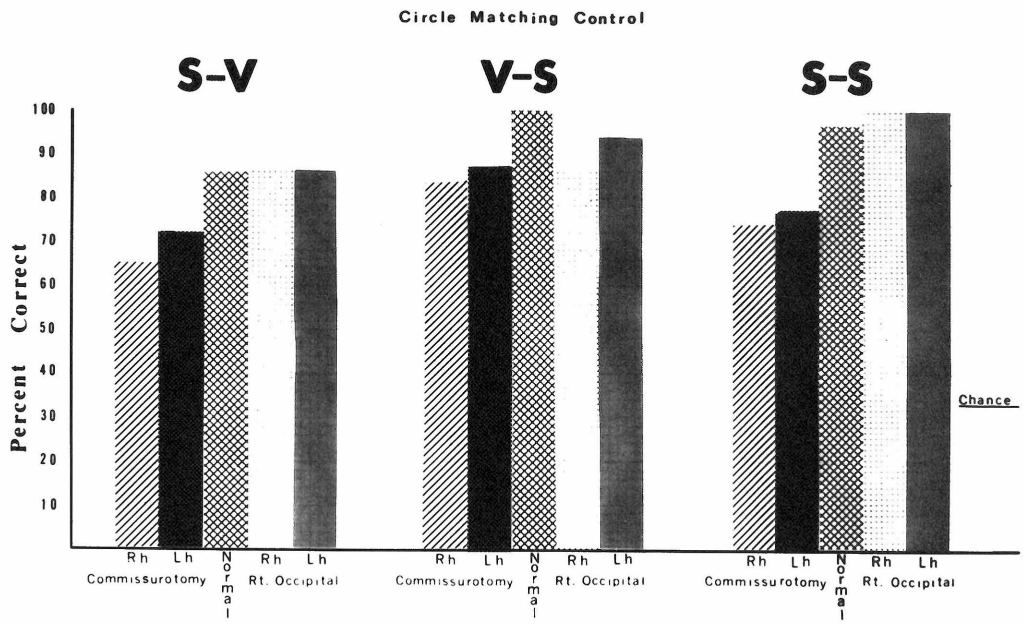


Figure 12. Comparison of Brain Operated and Normal Subjects on the Experimental Parts of the Three Forms of the Test.



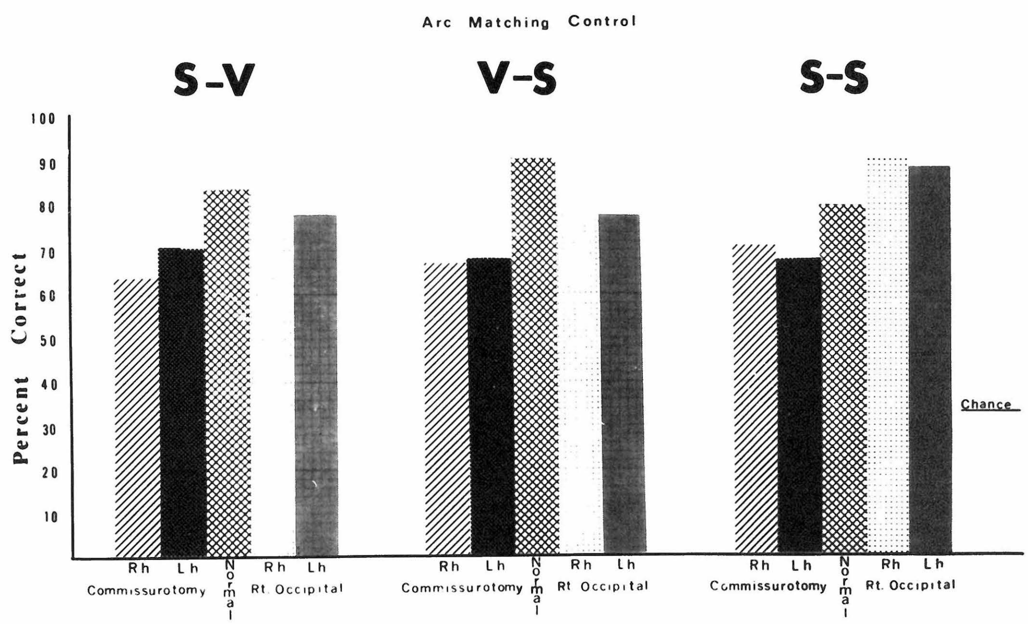


Figure 13. Comparison of Brain Operated and Normal Subjects on the Two Controls for the Three Forms of the Test.

the two control tests (Figure 13) both hands were within 15 points of the unoperated individuals. Thus, in comparison to the control subjects, the left hand of commissurotomy patients was equally proficient at both the experimental and and control tasks, while the right approached normalcy only with the control procedures.

As with the commissurotomy cases, both hands of the right occipital lesion patient were subnormal on the experimental tasks, although here the right hand was the least effected, actually having a normal score on the S-V form (Figure 12). With the other two procedures, however, his right hand was inferior not only to the normals, but also to the left hand of the split brain subjects. By contrast, the control tests (Figure 13) proved very simple for H.D., with both hands scoring at, or above the normal level. This led to truly huge discrepencies between his left hand's performance on the experimental and control tasks.

d) Comparison of Right Handed and Left Handed Normal Subjects. Individual results on the experimental part of the S-V form are displayed in Figure 14. Both right and left handed subjects are ordered according to their left hand scores.

The graph shows that, as a group, right handers did considerably better than did non right handers. While 14 was the lowest score attained by any right hander, left

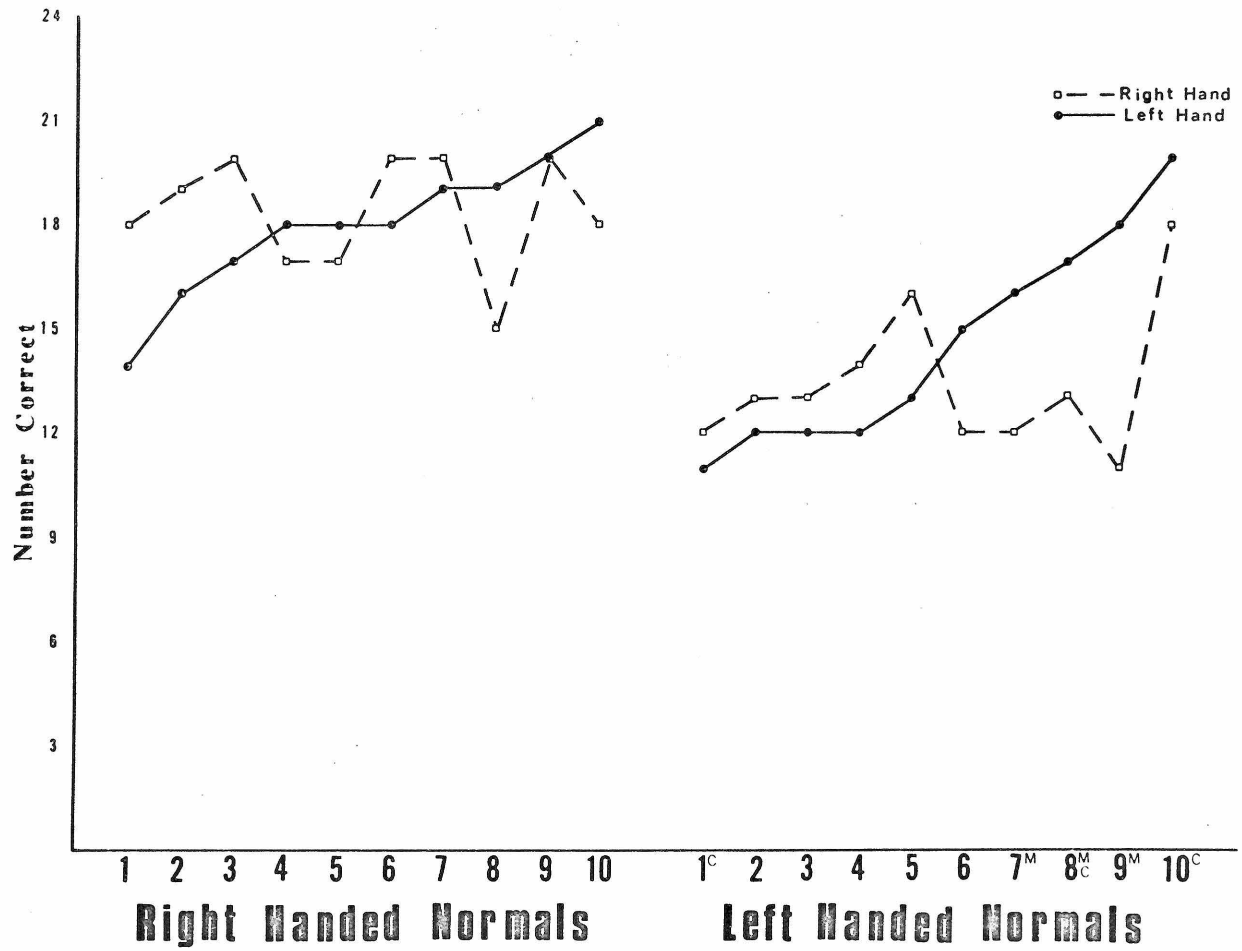


Figure 14. Comparison of Ten Right Handed and Ten Left Handed Normal Subjects on the Experimental Part of the S - V Form of the Test. C = a person converted to right handedness; M = someone of mixed handedness.

handers equalled or fell below this twelve times. Only one of the ten sinistrals scored above 14 with both hands, while only one dextral failed to do so. Analysis of the data according to the completeness of the arc, or the size of the circle failed to reveal any other striking differences between the two groups.

A statistical treatment of the results showed the mean score for the right hand of dextrals to be 18.4, for sinistrals 13.5, yielding a $\underline{t}$ of 4.19 ($p < .001$, two tailed $\underline{t}$ test for uncorrelated means). The means for the left hands of the two groups were 18 and 14.3 ($t = 3.1$, $p < .01$). When the scores for the two hands of each individual were combined, the mean for right handers was 36.4 of a possible 48, for left handers 27.8 ($t = 5.37$, $p < .001$). It is highly probable, therefore, that the capacity for somesthetic-visual matching of arcs to complete circles is not uniformly distributed throughout the human population, but rather is correlated in some way with handedness.

4. Discussion

From their scores on the experimental part of the three test forms it is obvious that in matching arcs to the appropriate size of circle commissurotomy patients were far more accurate with their left hand than with their right. Since previous work on these patients (30,31) has shown somesthetic information from each hand to be perceived solely by the contralateral hemisphere, this left hand advantage translates into a right hemisphere superiority. By contrast, the major hemisphere's capacity for these tasks is revealed to be very low, leading to chance performance by the right hand. This, however, does not eliminate the possibility that in the intact brain the left hemisphere collaborates with the right in solution of this type of problem. Indeed, the fact that the minor hemisphere's scores were lower than those of control subjects would suggest an appreciable contribution by the major hemisphere in normal individuals. It should, however, be noted that the control subjects for this experiment were of average or above average intelligence, and thus their pre-eminence may result from factors other than participation by their major hemisphere. It is conceivable that a control group composed of unoperated epileptics matched in intelligence to the commissurotomy patients would have lower average scores, thus implying that, even in the undivided brain, the major hemisphere does not play a significant role in the execution of this task.

With regard to interaction between the two hemispheres on this problem, the case of L.B. is very instructive. This young boy was the only commissurotomy patient whose right and left hands did not differ in their ability to carry out the experimental procedures; this was surprising in view of the strong lateralization of perceptual function he had exhibited in a previous experiment (83). However, although this earlier test did entail a tactile examination of the stimuli, the proprioceptive component involved was quite small, whereas with the arcs and circles it is the main sensory cue. This difference in the relevant somesthetic properties is probably crucial, as there is evidence from two sources suggesting that each of L.B.'s hemispheres receives proprioceptive information from both hands. The strongest proof comes from the cross retrieval control of the present experiment, in which L.B., alone of all the commissurotomy patients, could cross match the test stimuli between his two hands. Corroborating this finding is an earlier report (7) which also concluded that this subject's major hemisphere was aware of left hand proprioceptive events. This leads to an interesting situation in which both of L.B.'s hemispheres have access to the sensory information necessary to make a choice, and although the minor hemisphere is better suited for the task, without a callosum it may be unable to inhibit the major hemisphere from attempting to solve the problem in its own way. The left hemisphere could, thus, very well be the source of L.B.'s frequent use of conceptual stratagems such as measuring the chord of the arc. Since these tactics were notably unsuccessful, the responses by the major hemisphere would tend to lower the subject's scores with both hands to a level below that attained by the right hemisphere of the other patients, a result already noted.

The data obtained from H.D., the right hemisphere lesion case, were of special interest, as prior to surgery his jobs as a machinist and draftsman had involved detailed work with proportions and precise measurements. During the present test H.D. repeatedly claimed that, with his experience and skills, he ought to have a perfect score. In actual fact, on the control tests, matching sizes of circle or degree of curvature, he was generally more proficient than even the normal subjects. When, however, required to choose the circle size from which a given segment had come, his performance was greatly impaired, especially with the hand contralateral to the injured hemisphere. Only on the S-V form of the test did the subject's right hand approach normalcy, and this was due to the comparatively low scores of the control subjects with this procedure, rather than to any increase in H.D.'s accuracy over that with the other two forms.

The poor performance of neurologically intact left-handed individuals on the experimental part of the S-V form was surprising, especially in view of their otherwise high intelligence. Many of these sinstrals when first informed of the requirements of the test were very pessimistic as to how well they would do. Whether this negative attitude resulted from previous difficulty with a similar problem, or from a general frustration with manual activities in a right handed world, was not clear from their comments. One interesting fact which emerged from analysis of the data was that, although in their scores the sinistrals resembled brain damaged subjects, in the pattern of their errors they were closer to right handed normals, as they made no more mistakes on the smaller arcs than on the larger ones. This is in sharp contrast to the right and, to some extent, the left hands of commissurotomy patients. Any explanation, therefore, of the left hander's poor performance in terms of hemispheric specialization must account for this differing pattern of success.

Before drawing any conclusions as to the meaning of the present results with regard to the lateralization of function in the human brain, the exact operation being tested must be determined.

The most obvious source for the observed differences between the right and left hands of commissurotomy patients would be a disparity in their somesthetic sensitivity. Such a right hand deficit should, however, be as evident on the control tests as on the experimental. This is especially well illustrated by the V-S procedure where the somesthetic stimuli for both the first control and the experimental tasks were identical, and yet the right hand's performance fell below that of the left only when the visual stimuli were arcs rather than complete circles. The data, thus, do not support any explanation of the results in terms of a simple sensory factor, but rather a higher level process is indicated.

One perceptual quality which has previously been claimed to differentiate the hemispheres is that of difficulty, the right hemisphere supposedly being specialized for the handling of visually complex and perceptually difficult tasks. In the present test, however, the arcs and circles were certainly not complex, and as for difficulty, although the left hand of commissurotomy patients found the arc matching control and experimental trials equally demanding, the right hand failed to measure up to the left only on the experimental tasks.

A common perceptual deficit after cortical injury is spatial disorientation, as manifested in such symptoms as a poor memory for position (88), and defective route finding (89). A similar difficulty in following visual maps has been found to be associated with an incapacity for recognizing objects by touch (asterognosis) (90). This asterognosis can exist independently of disabilities in size, weight or texture discrimination, being concurrent only with a spatial defect (91). Although in the previous two studies spatial disorientation occurred after damage to either side of the brain, a more recent report (92) has shown that, in the absence of tactile deficits, right hemisphere lesion cases more often then left failed to visually pick out a shape they had blindly traced with one finger. The authors interpreted this as a right hemispheric spatial disability impairing the patient's capacity to use the changes of direction in space made by his finger to "reconstruct" the shape.

There are, however, several reasons for doubting that this spatial factor plays a significant role in the arc-circle matching. An attempt by Harold Gordon and myself to replicate the finger tracing work revealed no difference between the hands of commissurotomy patients in their ability to select a visual representation of a multiple T maze they had tactually examined with one finger. In other tests, these same patients were shown to orient their bodies in space as well with a tactual map felt by the right hand, as with one felt by the left (93). Related evidence comes from a report (66) showing the right hemispheric loci for deficits in spatial relations and in perceptual closure to be different, the first lying along the midline of the posterior parietal region, the second at the junction of the occipital and temporal lobes. Of these patients, only those with a closure disability had a coincident difficulty in facial recognition (prosopagnosia). Since H.D. shows no obvious spatial disorientation, but does suffer from prosopagnosia, this suggests that his poor performance on the arc-circle test may be more closely related to a closure deficit than a spatial one.

The term closure as applied to such psychological tests as the Closure Speed, Gollin figures, or Mooney faces, refers to the process of recognizing as a meaningful figure, a stimulus from which a substantial portion of the contour is missing. This phenomenon very often occurs in an all or none fashion, the shape suddenly standing out from what was previously an unorganized jumble of detail. Once the form has been seen, however, its missing contours do not noticeably impair its structural unity. Performance on the above tests by persons with unilateral brain damage has shown defects in closure to be associated mainly with injury to the right hemisphere (74,75,76).

Conceptually such a closure process would seem the simplest means of solving the arc-circle test, for although the configuration of an arc is not as complicated as say that of the Mooney faces, it too requires that its contour be completed in order for it to have any meaning in the context of the test. If this is indeed the case, then the sensory modality through which the arc is presented should be of importance only insofar as it affects the ease with which the segment's dimensions can be accurately determined. In this respect vision is obviously superior to somesthesis, as the results indicate.

The other obvious method of accomplishing this task would be for the subject to directly compare his visual and somesthetic, or somesthetic and somesthetic experiences of curvature with the arcs and rings. However, if this were true then the left hemisphere of the commissurotomy patients should have equalled the right on the experimental trials as it did on the second control test, which also required curvature matching. It thus appears that neither hemisphere of the commissurotomy subjects relied on this sort of sensory equivalence matching in order to choose the proper size of circle.

As for the normals, remarks by several of the control subjects are relevant here. While feeling the arc in the S-V procedure, these individuals did not look at the choices until ready to make their selection, claiming that the sight of the full circles was distracting. They also commented on the V-S and S-S forms that they first decided which size of circle the arc was from, and then went out and searched for it tactually.

It thus seems likely that performance on the arc-circle test involves a visualization of the whole circle from a part by some process similar to that responsible for the phenomena of closure, i.e. a mental filling of the missing contours according to some innate perceptual rules. The left hemisphere's failure, therefore, demonstrates its incapacity for conceiving the whole figure implicit in the part. Why it did not fall back upon its ability to match curvatures is not clear, although the very completeness of a circle may in some way change its apparent curvature in comparison to the incomplete segment.

The main question remaining concerns the implications of the demonstrated discrepency between the performances of right handed and left handed individuals on the present test. Non right handers (left handed and ambidextrous persons) have long been known to differ from the rest of the population in more than just their hand preference, having a greater tendency toward developmental difficulties such as stuttering and dsylexia (94). Sinistrals are more likely than dextrals to suffer from aphasia after damage to either side of the brain, but they also have a greater chance of making a complete recovery from this language disturbance. Both effects are presumeably due to the language capacities of left handers being less lateralized than those of right handers (95).

In a recent theory (87) on the basis of hemispheric specialization in humans it was suggested that language and Gestalt perceptual abilities have been segregated through evolution into different hemispheres due to a basic antagonism between their methods of processing data. Left handers, with their more bilateralized speech, should, therefore, be inferior to right handers on tasks requiring minor hemisphere function. This prediction has been borne out by reports showing sinistrals to be worse than dextrals on the performance scale of the W.A.I.S. (87), as well as on tests of spatial (96) and closure (97) abilities.

The present results could also be interpreted as a strong confirmation of this theory, in that a task on which the right hemisphere of commissurotomy patients excelled, also served to distinguish right handers from left handers. However, although the arc-circle test does show the minor hemisphere of the sinistrals to be less competent than that of the dextrals, it does not prove that this is a result of interference by language processes present in the right hemisphere. Indeed, if left handers have in effect two left hemispheres, you might expect their pattern of success with the various sized segments to be similar to that of the left hemisphere of commissurotomy patients, rather than paralleling at a lower level that of right handers.

The deficits of the sinistrals could just as conceivably spring from a less developed capacity for all higher mental activities, both language and perceptual. The lack of general language disability can be attributed to the educational system which puts great stress upon verbal faculties but leaves relatively untrained the perceptual ones.

D. Figural Unification

1. Introduction

The results of the previous experiment suggest that the minor hemisphere is superior to the major in its ability to visualize the whole from a piece. In order to study this process further, a test was devised in which the overall shape of a figure had to be inferred from its disconnected parts. Here, although none of the stimulus was actually missing, its fragmented condition required a conceptualization of the total contour similar to that necessary in the arc - circle test.

In this experiment the fragmented figures were presented only visually, as tactual examination proved too difficult for most of the subjects.

2. Method

The visual stimuli consisted of twenty line drawings, each depicting a geometric shape that had been cut up, and the several pieces pulled apart. Half of the figures were taken from Pintner's General Ability test (98), while the rest were created especially for this experiment. The subject's task was to decide which of three alternatives was represented by the fragmented figure. The choices were solid forms made from 1/8" lucite sheet. Both the figures and the choices were fairly evenly divided between common (square, circle, triangle etc.) and uncommon geometric shapes. Of the two incorrect alternatives for any figure, at least one the same contour as one of the fragments, while the other was of the same general size and angularity as the correct form. The subject at no time saw these choices, but rather was restricted to feeling them with one or the other hand.

At the beginning of the experiment, each person was given several examples in which the alternatives as well as the fragmented figures were presented in free view. To insure that he understood the nature of the task, one of the figures was made of cardboard pieces which could actually be moved together to form a united shape. The individual was instructed that he would be shown a series of forms, each of which had been broken up, and the parts dispersed in such a way as to maintain their original orientation and position relative to one another. All he had to do was to mentally slide these fragments together, find the reconstructed shape among the three choices he felt behind the screen, and tap it.

The twenty figures were split into two sets of approximately equal difficulty (Figures 15 & 16). The order of presentation for all subjects was : group I - left hand, group II-right hand, rest, group I -right hand, group II - left hand. The arrangement of the three alternatives for every figure was the same for both the right and left hands. Each of the somesthetic stimuli was used only once in a set.

At the end of the session the subject was given the Hooper Visual Organization Test (99). This standardized test for organic brain damage requires verbal identification of thirty common objects portrayed in fragmented pictures (Figure 17). A score of 25 to 30 is considered normal, while 20 to 24.5 reflects a mild organic deficit, and 10 to 19.5 a moderate one.

At a later date, each individaul was tested again, with the same visual shapes as before, but this time in a non-fragmented form; the order of presentation and the alternatives were identical to the experimental session. In this control, therefore, the subject had only to find the tactual choice with the same contour as the figure he saw before him.

This study was carried out on seven commissurotomy patients (A.A., L.B., C.C. , N.G., R.M., N.W. and R.Y.), a

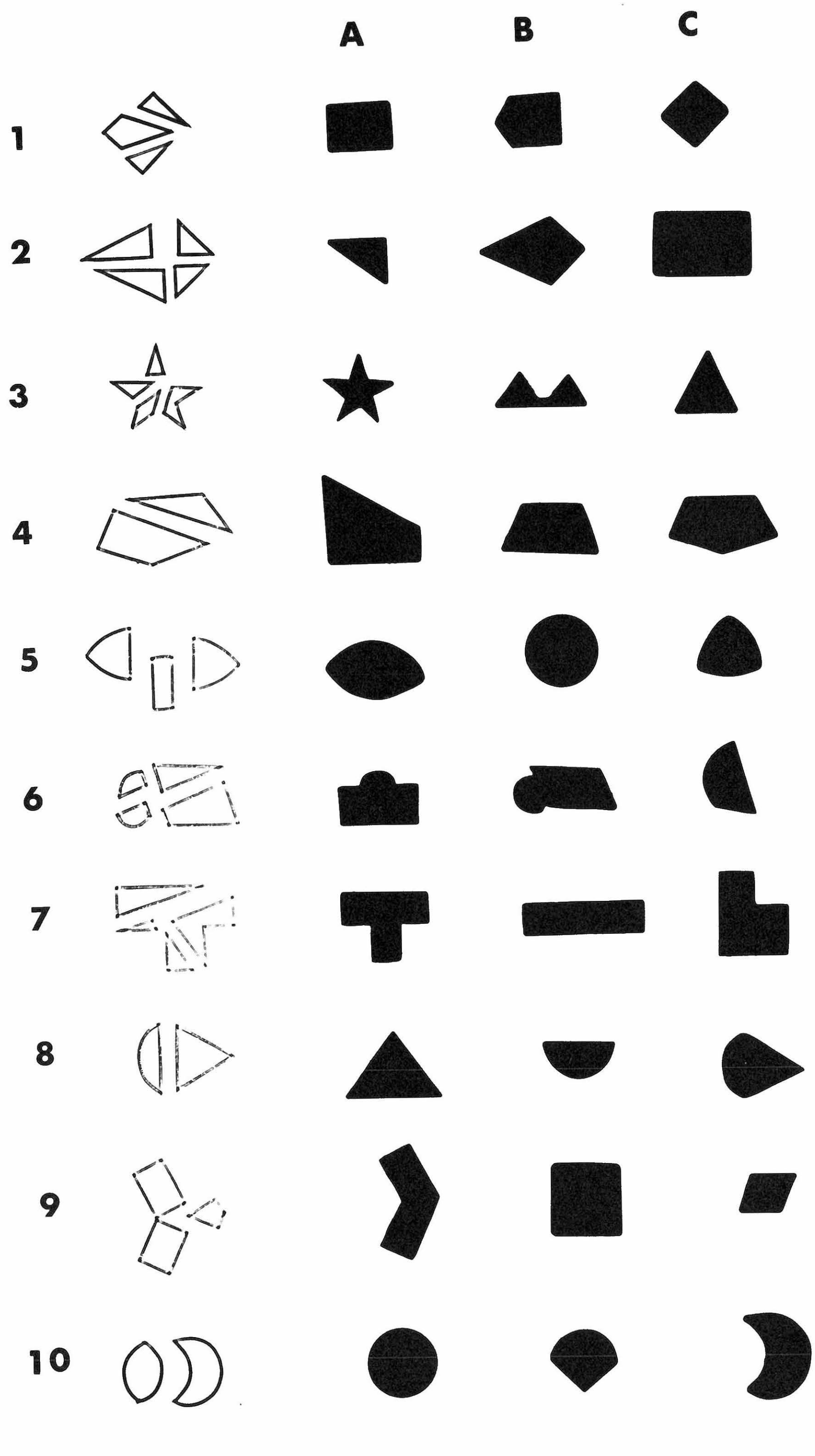


Figure 15. Stimuli for the Figural Unification Test Set 1.

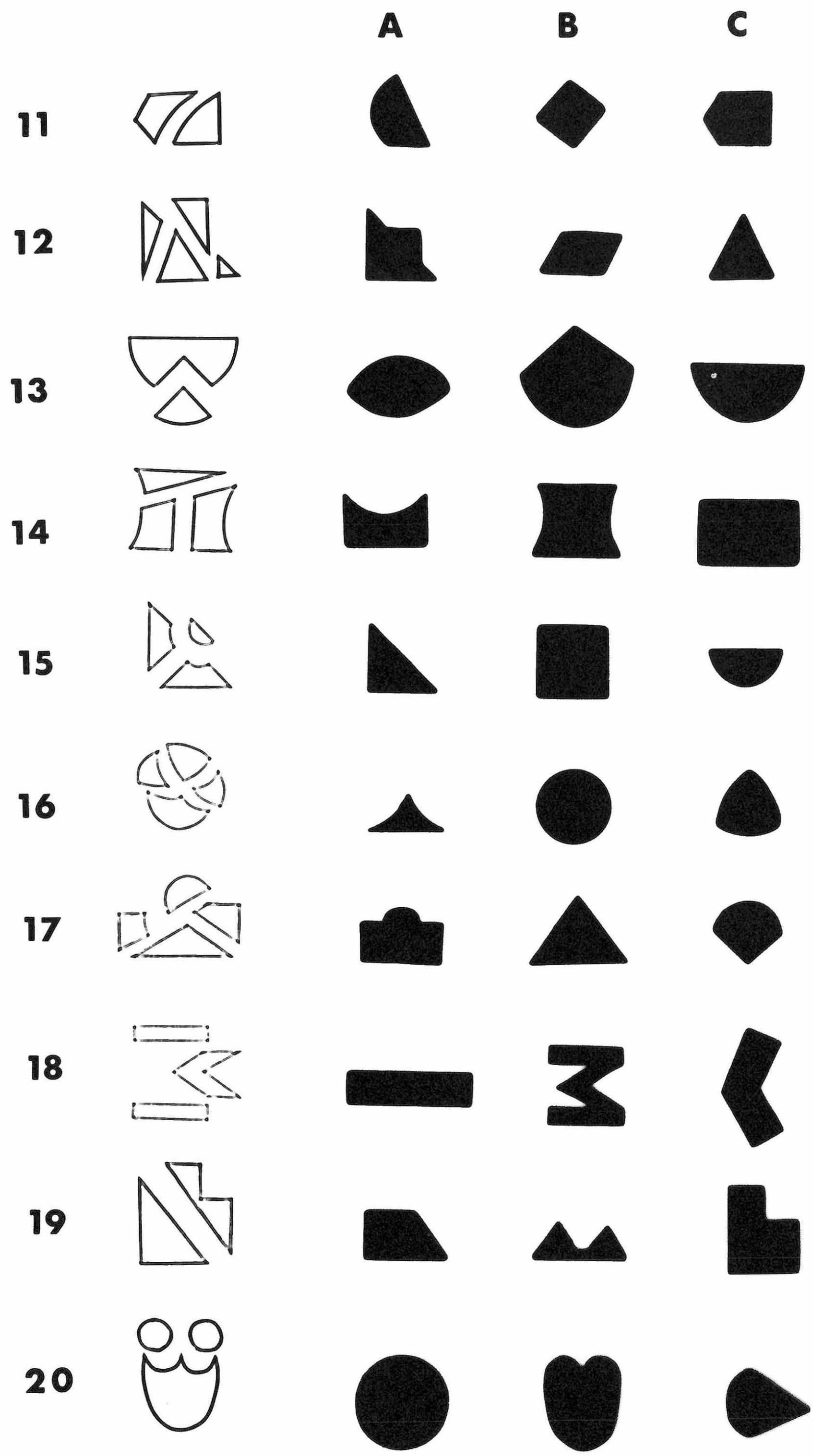


Figure 16. Stimuli for the Figural Unification Test Set 2.

Figure 17

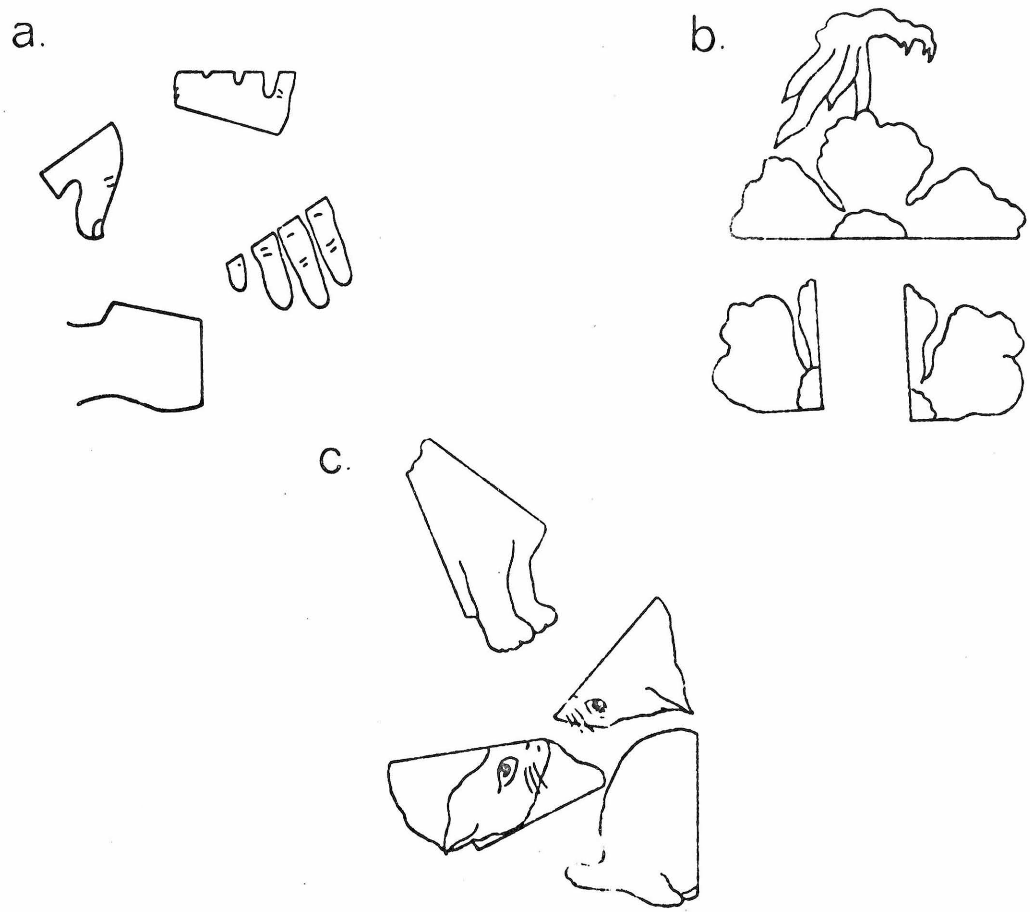


Figure 17. Examples of the Hooper Visual Organization Test -a) hand, b) flower, c) cat.

right hemisphere lesion case (H.D.), and five normals (four right handers and one left hander); except for A.A. and C.C., all of these persons had taken part in the previous experiment.

The scores from the two hands of each individual were compared in a 2 X 2 chi square contingency table using the Yates correction whenever an expected frequency fell below 11. The probability of each score, experimental or control, having arisen by chance was found by use of the binomial expansion.

3. Results

The scores for the right and left hands of all commissurotomy patients are found in Table XI and in Figure 18. From the chi squares it is evident that six of the seven patients were significantly more accurate in finding the pictured figure with their left hand than they were with their right. When using the left hand they averaged 16.9 of 20, while with the right, no one besides L.B. scored above chance, the average being only 9 correct. Just how poor their right hands actually were, can be seen by comparing them to the hands of the five normal subjects which, without exception, had perfect scores.

As in the last experiment, L.B. was the sole commissurotomy patient not to exhibit a left hand superiority. Although he did make several mistakes with the right hand, his overall performance with either hand was swift, confident and highly

Table XI

Figural Unification Results

		A.A.	L.B.	C.C.	N.G.	R.M.	N.W.	R.Y.	Total
Experimental test	Lh	17/20	20/20	14/20	15/20	18/20	17/20	16/20	117/140
	Rh	9/20*	17/20	6/20*	7/20*	9/20*	8/20*	7/20*	63/140
	x^2	5.38	1.43	4.9	4.94	7.28	6.28	6.54	37.29
	p	< .05	N.S.	<.05	<.05	<.01	<.01	< .01	<.01
Control test	Lh	19/20	20/20	17/20	19/20	20/20	20/20	20/20	135/140
	Rh	17/20	20/20	18/20	17/20	20/20	20/20	18/20	130/140
	x^2	< 1	=0	< 1	<1	=0	=0	<1	<4
	p	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Hooper test		20	29	19.5	18.5	25	17.5	14.5	Average = 20.5

* = chance score

N.S. = Not significant

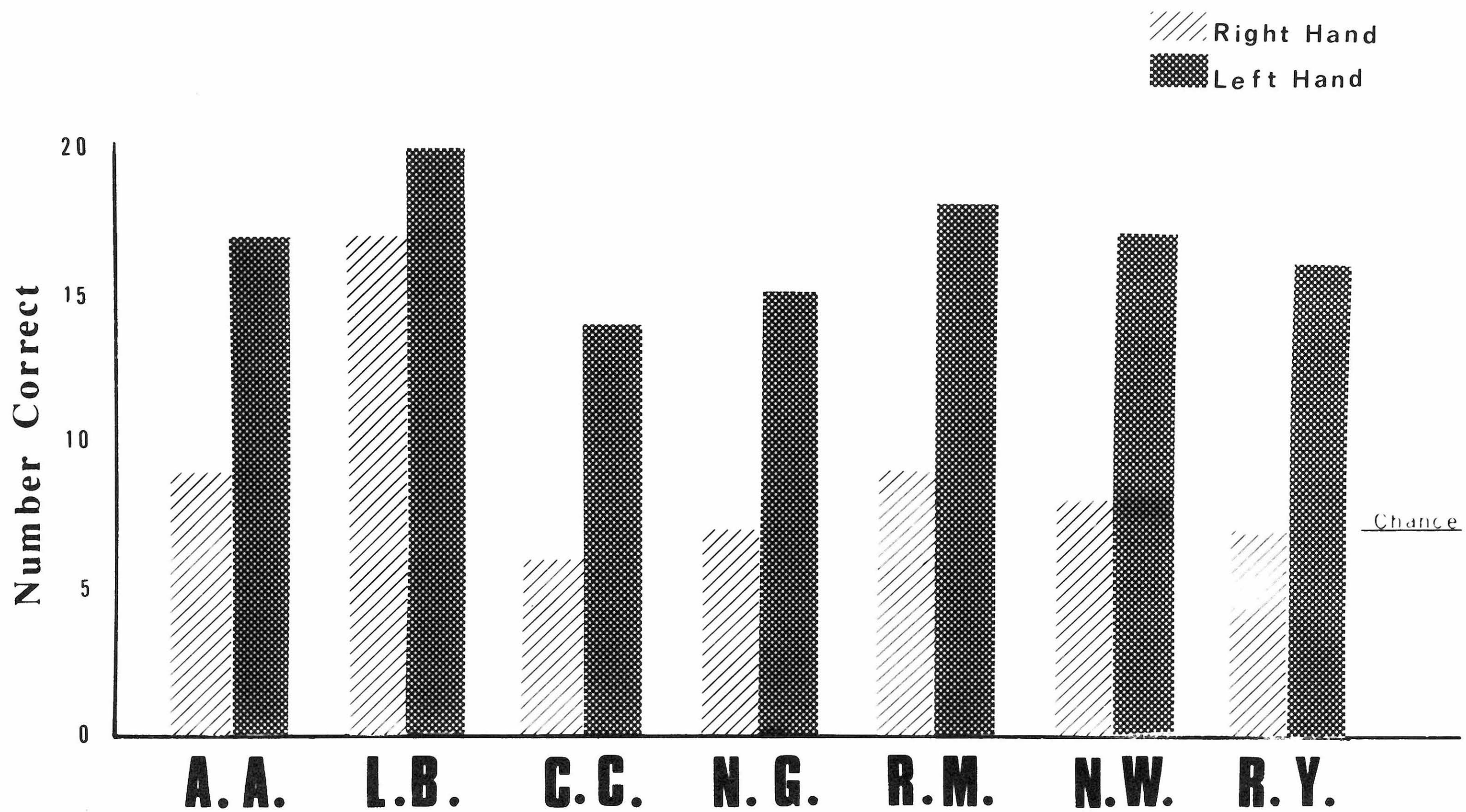


Figure 18. Scores of the Commissurotomy Patients on the Figural Unification Test.

accurate. This was true also of the right occipital case, who got 17 correct with his right hand and 16 with his left.

On the control trials where a simple visual-tactile comparison of complete shapes was required, both hands of the commissurotomy patients did extremely well, the right hand making only a few more errors than the left. Normal subjects again had perfect scores, as did H.D.

The answers given by the right and left hands of all commissurotomy patients combined are shown in Table XII. The three columns represent the three possible alternatives (see Figure 15 & 16), while the numbers signify how many times they were chosen. Since each fragmented figure was shown to a subject only once per hand, the numbers actually reveal how many persons chose that shape. The underlined scores are those for the right choice.

Looking at the distribution of the correct answers, the domination of the left hand is readily apparent. On eleven of the twenty figures it had a perfect score, that is all seven subjects choose correctly with their left hand; on four other shapes only one person made an error, thus yielding a score of six. By contrast, the most subjects correct on any one figure with their right hand was five, and this occurred only three times; on seven other stimuli three or less individuals chose correctly with that hand. While the figures causing the left hand some trouble (#4,9,16) were invariably difficult for the right, the reverse was not

Table XII.

Distribution of Answers on Figural Unification Test

	Right Hand			Left Hand		
	A	B	C	A	B	C
1.	2	1	4	0	0	7
2.	4	3	0	6	0	1
3.	0	5	2	0	7	0
4.	4	3	0	1	2	4
5.	3	3	1	6	1	0
6.	2	1	4	0	5	2
7.	5	2	0	7	0	0
8.	3	1	3	1	0	6
9.	1	1	5	3	0	4
10.	3	1	3	7	0	0
11.	2	1	4	0	0	7
12.	5	1	1	7	0	0
13.	2	1	4	0	3	4
14.	2	2	3	0	7	0
15.	3	3	1	5	0	2
16.	0	2	5	0	4	3
17.	4	0	3	6	1	0
18.	1	4	2	0	7	0
19.	2	3	2	0	0	7
20.	3	4	0	2	5	0

The underlined scores are those for the correct choices.

always true, as in numbers 10, 14, and 19, where the right hand had a score of two or three, the left a perfect seven.

Looking at the errors it is evident that while in many cases there was a tendency to choose a shape similar to one of the fragments of the figure (2a,9c, 16c and 20a), in several other instances (5b and 6c) there was just as strong a preference for a form unlike any of the pieces.

The data from the Hooper test are given in the bottom line of Table XI. While normal results were obtained from L.B. and R.M., the rest of the patients had scores indicative of mild or moderate brain pathology. The five control subjects all fell in the normal range, averaging 27.5 of 30 correct.

4. Discussion

From the present results it is clear that, while the right hemisphere of commissurotomy patients had very little difficulty discriminating which of the tactual shapes was depicted by the fragmented visual stimuli, the major hemisphere was deficient to the point of actually performing at chance. The possibility that the left hemisphere does, however, participate in the solution of this problem in normal individuals was again raised by the failure of the disconnected minor hemisphere to achieve a score equivalent to that of control subjects. As in the arc-circle test no definitive answer can be given without data from persons whose intelligence and brain disfunction are comparable to the commissurotomy cases, but whose callosum is intact.

The only patient to attain near normal scores was L.B., who performed equally well with either hand. It cannot be determined from these data whether this bimanual success was a result of his minor hemisphere controlling the choices of both hands, or of his major hemisphere successfully pursuing some perceptual strategy of its own. Since the level of ability required by this test was set for the majority of patients possessing low intelligence, it is very likely that the task was not sufficiently difficult to differentiate the perceptual capacities of L.B.'s two hemispheres. Similarly, H.D.'s fairly high scores could be attributed to his long experience with geometric problems.

In the control test the ability of commissurotomized individuals to tactually retrieve a pictured whole shape, while good, was not perfect. This small deficit in visuo-tactile matching, although slightly greater with the right hand than with the left, was certainly not sufficient to account for the experimental results. It is especially significant that on the control test A.A. made only two more errors with his right, sensorially deficient, hand than he did with his left. This demonstrates the relatively simple nature of the somesthetic discriminations required in the solution of this problem.

The Hooper Visual Organization Test was administered in conjunction with the present experiment for several reasons; first, the mental manipulation apparently required was very similar to that involved in the Figural Unification task; second, it would allow the performance of the commissurotomy patients to be compared with that of a standardized population. Since the Hooper test entails a verbal report, it was expected that split brain patients would do quite poorly, as the major hemisphere would be the source of all answers. This, in some respects, is what was found, with most of the subjects having a moderate or mild deficit. However, in view of the extreme difficulty encountered by the left hemisphere with the fragmented geometric figures, these deficits were not too severe. Comments by several of the patients as to how they handled the task suggested that the Hooper test may be solvable by a left hemisphere type of processing. These individuals claimed that, rather than mentally piece the fragments together, they paid attention to the details within each part. This sort of analysis would be impossible with the Figural Unification test as the shape of the fragments is the sole cue, and even this is useful only insofar as the subject can ignore the parts as individual entities, and concentrate instead on the larger whole they embody. In this respect, the contours of the pieces are a distraction from the simpler overall form inherent in the properly united parts, and thus are probably a source of confusion for the major hemisphere, due to its inclination for attending to details.

E. Perceptual Organization of Dot Patterns

1. Introduction

In the early part of this century a school of psychology arose, which was greatly concerned with the role played by the parts of a stimulus in the perception of the whole. Members of this "Gestalt" school noted that although the components of a perceptual array can be grouped in many different ways, certain arrangements tend to predominate due to several factors which act to organize the field (100). Among these, one of the strongest is proximity; the more closely elements are related in space, the more likely they will be seen as being associated.

If man's minor hemisphere actually is wholistic in its awareness of the sensory world, then it should be more proficient than the left in discovering the structure present in a visual display due to the proximity of its parts.

2. Methods

The visual stimuli were filled in squares composed of dots ordered in a regular pattern, such that there was a greater concentration of points along one dimension than along the other; this created an impression of lines running parallel to the axis with the greater number of dots (Figure 19). By changing the orientation of the array, the lines could be made to appear either horizontal or vertical. Two different arrays were used, varying only in the number of dots along the two axes; in the first, there were four points along one dimension and seven along the other, while in the second, it was five versus seven. The greater disparity in the first pattern allowed the orientation of the lines to be more easily detected. Twenty slides were made of each array, ten with horizontal orientation, and ten with a vertical.

The stimuli were tachistoscopically presented to the subject as he sat before a screen like the one described in the first section. When projected the individual dots were one twelfth of an inch in diameter, while the whole array measured two inches square and subtended a visual angle of approximately five degrees forty minutes. The patterns were flashed in one or the other half visual field, with the inner edge of the image always falling one and one half inches ($4^{\circ}17'$) from the central fixation point. All subjects were first tested with a stimulus duration of 1/100th of a second. Those for whom this proved too difficult (A.A. and N.G.) were retested at 1/50th of a second.

Before the actual trials began, each subject was shown examples of the two arrays in both orientations; he was asked whether the dots appeared to form lines, and if they

Figure 19

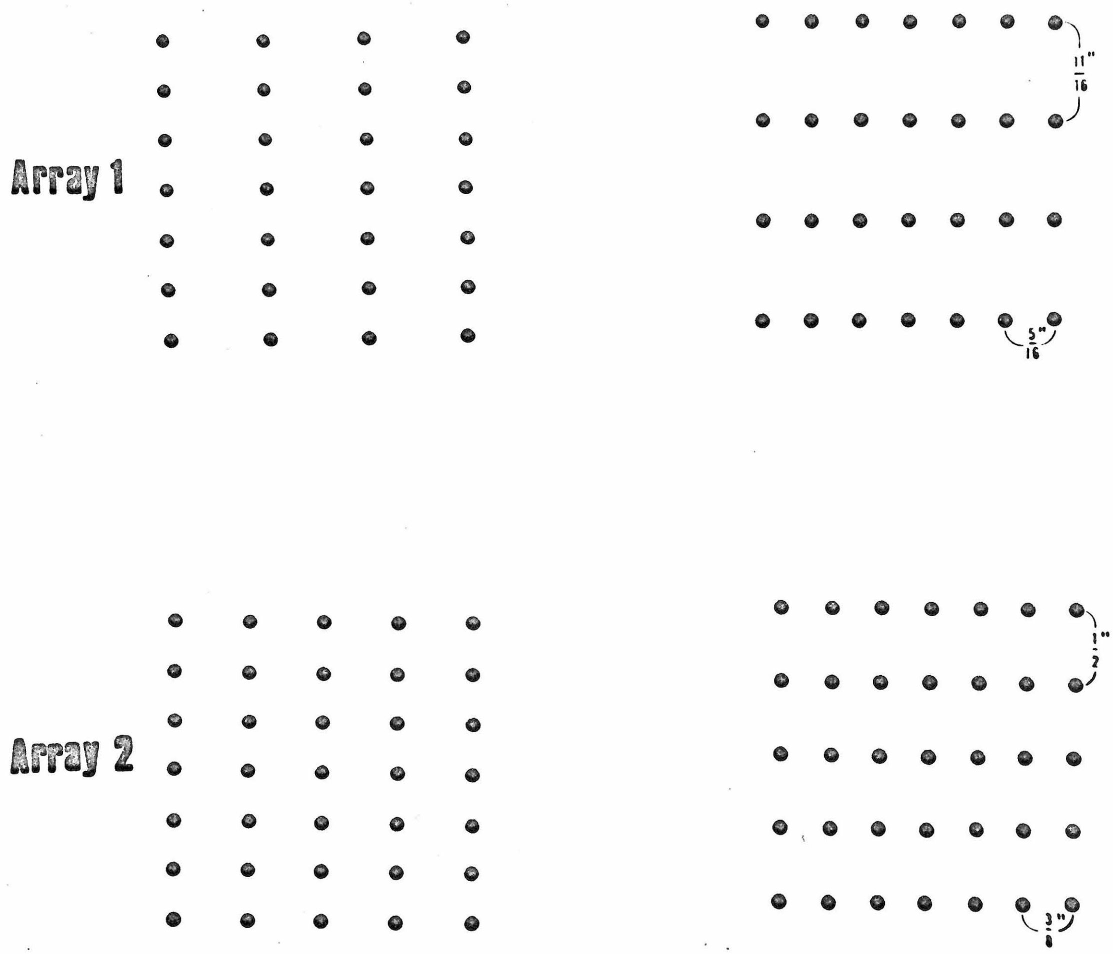


Figure 19. Stimuli for the Dot Pattern Test.

did, in what direction they were running. Everyone identified the slope of the lines without any further prompting. The individual was then instructed that when he next saw these figures he was to signal the lines' orientation by raising his forefinger if they were vertical, and not moving if they were horizontal. An attempt was made at a later session to reverse these instructions, having him raise his finger to the horizontal configurations and not to the vertical; this however, led to a great deal of confusion, and so was not pursued. Throughout the experiment the hand being tested was hidden from the subject's view behind the screen.

The data from each patient were collected over two sessions consisting of eighty trials with each hand. In both sessions first the left hand was used for forty trials, and then the right; after a rest, the right hand was again tested, followed by the left. The orientation of the lines, and the alternation between the visual fields were varied in a predetermined random fashion identical for both hands.

Of the eight persons who took part in this experiment, three were commissurotomy patients (A.A., L.B. and N.G.), while the rest were the same control subjects used in the previous studies. Two other patients, N.W. and R.Y., were dropped after preliminary testing, as they failed to score above chance with any field - hand combination, even at 1/25th of a second.

Each subject's scores were compared by means of a chi square test, with the Yates correction figured in whenever appropriate.

3. Results

The data from each individual were classified according to the visual half field in which the stimulus was presented, and the hand used to respond. The scores of the three commissurotomy patients for all four combinations of field and hand are given in Table XIII. The results of the chi square tests are shown with lines running to the two scores being compared.

The findings demonstrate that, regardless of whether the right or left hand was used to report, all three subjects were significantly more accurate with dot arrays presented in their left visual field (LVF) than they were with those in their right. The hand with which a person responded did, however, greatly influence the magnitude of this discrepency between the two half fields, for although the left field scores with both hands were very similar, use of the left hand to report right visual field (RVF) stimuli led to much lower scores than did use of the right. In one case, L.B., this handedness effect was actually large enough to be significant ($X^2 = 4.96$, $p < .05$).

In summary, when the dot patterns fell in the visual field contralateral to the minor hemisphere, the subjects' performance with either hand was extremely good; presentation

Table XIII

Results for the Three Commissurotomy Patients

	LVF Rt. Hand		RVF Rt.Hand		LVF Lt. Hand		RVF Lt. Hand
L.B.	74/80	7.06 $p < .01$	62/80	4.58 $p < .05$	72/80	17.76 $p < .01$	49/80
				21.8 $p < .01$			
N.G.	72/80	6.22 $p < .05$	60/80	12.54 $p < .01$	76/80	22.4 $p < .01$	52/80
				14.34 $p < .01$			
A.A.	67/80	5.7 $p < .05$	54/80	4.1 $p < .05$	65/80	5.36 $p < .05$	52/80
				7.32 $p < .01$			
Totals	213/240	18.98 $p < .01$	176/240	21.22 $p < .01$	210/240	45.52 $p < .01$	153/240
				43.46 $p < .01$			

of the arrays to the left hemisphere, however, diminished the patients' accuracy, expecially with a left hand report.

Table XIV shows the distribution of the correct answers among the various stimuli. Looking first at the left field scores, there is obviously little variation among the four patterns, particularly with the right hand. However, in the RVF, while performance on the vertical arrays was slightly below that in the left field, it is evident that it was the horizontal figures that produced most of the disparity in scores between the two fields. Since mistakes on the horizontal array consisted of raising the finger when no response was called for, these errors can be considered false positives, that is failures to withhold a response. The predominance of this type of error can be seen in Table XV, where with left hand reporting of stimuli in the RVF, almost twice as many errors were made on the horizontal configurations as on the vertical. This distribution is significantly different from random ($X^2 = 19$, $p < .001$).

The five normal subjects tested were given only eighty trials with each hand, as they were equally accurate in both visual fields. Overall, their performance was quite good, with one subject having a perfect score, and another making only two mistakes. The three remaining individuals totaled four, seven and thirteen errors out of one hundred and sixty trials. Most of these mistakes (three to one) were false negatives, i.e. failures to respond to a vertical array.

Table XIV

Distribution of Correct Answers

	Array 1 Vertical	Array 2 Vertical	Array 1 Horizontal	Array 2 Horizontal	Total
LVF Rt. Hand	53/60	54/60	53/60	53/60	213/240
LVF Lt. Hand	54/60	52/60	58/60	49/60	213/240
RVF Rt. Hand	50/60	44/60	44/60	38/60	176/240
RVF Lt. Hand	47/60	43/60	38/60	25/60	153/240

Distribution of Errors on the Two Orientations

	LVF Rt. Hand	LVF Lt. Hand	RVF Rt. Hand	RVF Lt. Hand	Total
Vertical	13/120	14/120	26/120	30/120	83/480
Horizontal	14/120	13/120	38/120	57/120	146/480

4. Discussion

It is evident from the data that the performance of commissurotomy patients on this task was influenced by two distinct factors: the visual half field in which the dot arrays were presented, and the hand used to signal the answer. As predicted, displays falling in the visual field contralateral to the right hemisphere were more accurately identified than were those contralateral to the left hemisphere. The minor hemisphere was thus more competent than the major in discerning the pattern inherent in the array due to the differential spacing of the dots.

The consequences of the subject using his left rather than his right hand to respond were more complex. The minor hemisphere (LVF) had no apparent difficulty replying with either hand, a surprising result in view of a previous report showing right hemisphere control over individual right hand finger movements to be very poor (101). In the present experiment, however, only one finger was being used, and it was already primed to respond, thus needing only to be triggered by the minor hemisphere. In contrast to the right, the left hemisphere had considerable difficulty with its ipsilateral hand. This occurrence after LVF presentation of a greater number of errors with the left hand than with the right, could very possibly be due to interference by the minor hemisphere, which possesses the main motor control over the left hand. If this is the case, then while the major hemisphere cannot obstruct the minor's use of the right hand, the minor hemisphere can interfere with the major's use of the left. This is the opposite situation from that found in A.A. with writing, where the left hemisphere totally blocked utilization of the right hand by the right hemisphere. In the present experiment where the stimuli are of a type more efficiently handled by the right side of the brain, the direction of this interference appears reversed. In both cases the hemisphere better qualified for the task, the major hemisphere in the case of writing, the minor in the case of preception of whole configurations, intruded into the other's performance despite its lack of the sensory data necessary to make an adaptive response.

Right hemisphere interference could also account for the predominance of false positives with the RVF - left hand combination, for if the major hemisphere, believing the stimulus to be horizontal, did not respond, the minor hemisphere might interpret this as indecisiveness, seize control, and make a positive reply. This would be comparable to A.A.'s left hemisphere usurping command of the left hand and recording an incorrect answer if, after a left field presentation, the right hemisphere was too slow in beginning to write.

In this experiment, therefore, in addition to its perceptual superiority, the right hemisphere had also a tendency to lower the major hemisphere's score even further by interfering with its use of the left hand. Thus, a true measure of each hemisphere's capacity to abstract out the whole pattern from the interrelationship of the parts can only be gained from examination of its performance with the contralateral hand.

E. General Discussion

The results of the preceding experiments demonstrate a definite disparity in the perceptual abilities of the two cerebral hemispheres. Characterization of these tests in terms of the psychological processes involved, rather than the specific properties of the stimuli, reveals all three to require a similar intellectual operation, that of synthesizing from the part or parts of a pattern a mental construct of the whole. From a comparison of the performances by the two hemispheres it is clear that, in man, this function resides mainly, if not entirely, in the right side of the brain, the major hemisphere being as fundamentally incompetent on these perceptual problems as the minor is on those involving language. While one subject, L.B., did show some signs of left hemisphere proficiency in the first two experiments, this is probably attributable to his high intelligence and possession of an ipsilateral somesthetic system, an interpretation which is supported by the results of the third experiment, where, on a fairly demanding task involving no somesthetic cues, L.B. showed as strong a lateralization of perceptual function as any of the other commissurotomy patients. Man's minor hemisphere, thus, is minor only with respect to language; in the carrying out of highly complex and sophisticated manipulations of data it is obviously as capable as the major, although in a different way.

The usefulness of these tests for research into the organization of perception in the normal brain is indicated by the differential performances of right and left handed individuals in the matching of arcs to the appropriate size of circle. Further correlation of scores on this test with measurements of general intelligence, verbal skills, spatial and closure abilities, etc. may reveal a great deal about the interrelationship of these factors, and whether, as has been suggested, some of them are antagonistic or synergistic in their action.

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APPENDIX - Effects of Interruption of Transcortical Association Tracts in the Monkey.

Introduction

There is substantial evidence, both anatomical (1,2) and physiological (3), for the existence in primates of long intrahemispheric fiber tracts forming reciprocal connections between visual association cortex and that part of the frontal lobe around the arcuate sulcus where electrical stimulation produces conjugate eye movements (4). These so-called frontal eye fields have been demonstrated to also receive input from the auditory and somatic association cortices (5,6), thus making them polysensory regions. Such a convergence of connections from the cortical representations of the various sensory modalities suggests that these fibers may compose sensory-motor loops, initiating and guiding the orientational movements of the head and eyes in response to incoming information. Other evidence indicating that this frontal area plays a vital role in the mechanisms of attention, comes from reports showing destruction of this region, both in monkey (7) and in man (8), to produce sensory neglect. The visual part of this syndrome has been termed pseudohemianopsia, for although the visual system is intact, the animal appears blind to stimuli in the half field contralateral to the lesion (9); there are also concurrent defects in auditory and tactile localization (10). All of these symptoms are generally considered to represent a disturbance in the processes of attention, since they persist long after any obvious disability in eye or head movement has vanished (9).

In order to examine the function of the long intra-hemispheric fiber tracts in the regulation of orientation and attention, monkeys, in whom these fasiculi had been unilaterally sectioned, were tested for defects in voluntary eye movements, and for visual neglect.

Method

The five animals used in this experiment were pig-tailed macaques (M. nemistrina), ranging from seven to twelve pounds in weight. Prior to any formal testing, they were checked for neurological deficits in their visual fields, eye movements or visuomotor abilities. All of the work to be reported was carried out with the animals seated in a primate chair, which, while restraining their waist and neck, left their head and hands free.

Behavioral testing consisted of several simple tasks designed to demonstrate any gross visual inattention or disturbance in eye-hand co-ordination. In order to detect unilateral neglect, the animal was presented with a board (2" x 10") containing a row of nine small candies each held in a shallow depression, one inch apart. The board was offered at the level of the monkey's stomach, with the center candy aligned with his midline. Both the order in which he took the candies, and the hand used were recorded. Another method of determining the visual field entailed one examiner holding the monkey's attention straight ahead while another, standing behind the animal, introduced a grape on the end of a thin wire into different parts of the monkey's peripheral field. A third task involved presenting by hand the two grapes, one on either side of the animal's midline, and noting the order in which he secured them. In a variation on this procedure both rewards were extended toward the monkey's midline and then suddenly separated, one to either side. In this latter case records were kept of which grape his eyes followed, and which hand he used to seize it. Another simple test for neglect was to see whether the monkey blinked when the examiner's hand suddenly approached his eyes from one or the other peripheral field.

Visuomotor abilities were examined by such tasks as having the animal retrieve a grape moving erratically on the end of a wire, or on a turntable revolving at 6 r.p.m. Specifically, the speed of his correction movements and the skillfulness of his pursuit and grasp were observed.

The interaction of the monkey's two hands in a simple co-ordinated activity was studied by means of a small box with a drawer containing a candy. Typically, the animal would pull open the drawer with one hand and take the candy with the other, using just the thumb and fore finger of both hands.

Eye movements in the form of an electro-oculogram (E.O.G.)

were recorded on a polygraph from three silver-silver chloride electrodes (In Vivo Metric "A" Pellets, 1.8 mm x 3 mm) implanted in the skull, one in the center of the frontal eye ridge, and one each in the extreme anterior lateral edges of the two orbits. The wires were run beneath the scalp to a socket cemented to the cranium. Recordings were made of the animal's spontaneous eye movements, of tracking motions, optokinetic nystagmus, and orienting responses to objects introduced into the peripheral fields.

All animals were given the complete series of behavioral tests on at least five separate occassions prior to surgery. After the operation they were checked for neurological abnormalities, and were then given the test battery four times: one week, one, two and three months postoperatively. The E.O.G. recordings were made in "Th" two weeks after surgery, while in "B.B." five months had elapsed.

Surgery for three of the monkeys ("Th" and "Tw"- left hemisphere, "Fr"-right hemisphere) consisted of a thin suction lesion through the inferior parietal lobe at the level of the postcentral dimple (Figure 20a, #1). The cut was perpendicular to the long axis of the brain and followed the lobe's white matter core down 1½ to 2 cm, cutting through the medullary substance containing the transversely running superior longitudinal and subcallosal fasiculi (Figure 20f). A fourth animal ("Sn") had his transection at the anterior end of the left parietal lobe, just posterior to the lateral

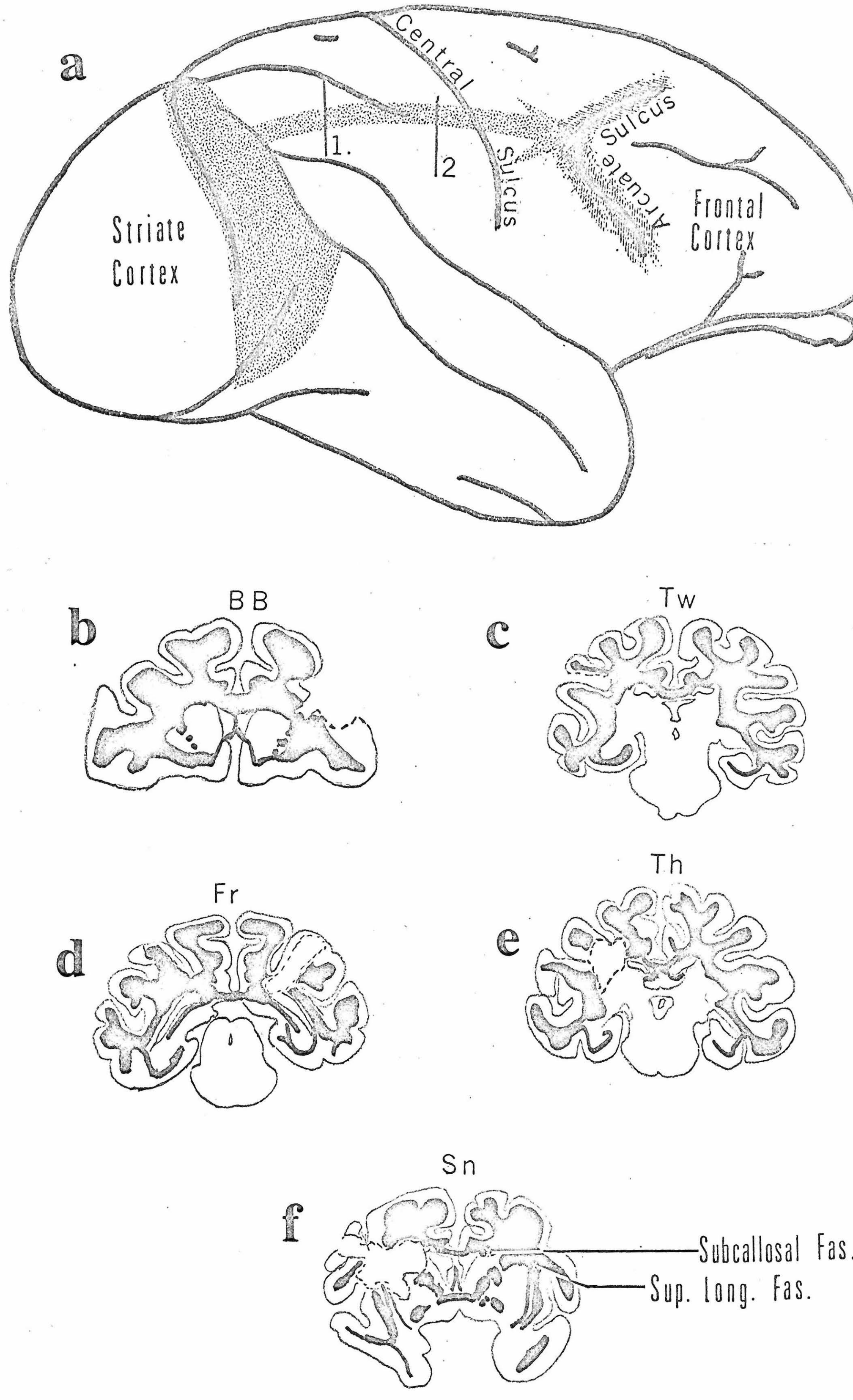
a
Central
Sulcus
Sulcus
Arcuate
Sulcus
1.
2
Striate
Cortex
Frontal
Cortex
b
BB
c
Tw
d
Fr
e
Th
f
Sn
Subcallosal Fas.
Sup. Long. Fas.

Figure 20

end of the central sulcus (Figure 20 a, #2).

In order to compare the symptoms resulting from division of the longitudinally running fiber tracts, with those following ablation of the frontal eye fields, one animal ("B.B.") underwent a complete removal of the posterior bank and floor of the angle and medial arm of the right arcuate sulcus.

After completion of the experiment, the five animals were perfused with saline followed by 10% formalin. The relevant portions of the brains were then sectioned and stained for fiber tracts with a Weil stain.

Observations

The symptoms exhibited by the monkey (B.B.) in whom the right arcuate gyrus had been ablated will be described first, in order to serve as a frame of reference for the results obtained from the animals who had undergone unilateral section of their intrahemispheric fiver tracts.

Immediately upon recovery from anesthesia, B.B. showed a deviation of her head and eyes toward the side of the lesion, coupled with ipsiversive circling. Although these abnormalities had disappeared by the end of the first week, behaviorally she still displayed a gross neglect of the left half of visual space; she did not respond to threats or rewards on this side until they came within a few degrees of her visual midline, at which time she appeared startled. With the candy board B.B. picked up exclusively those candies to the right of center, ignoring the four on the left, even when the examiner tried to draw her attention to them by pointing or tapping; only when the board was reversed, thus bringing the remaining candies into her right field, did she retrieve them. When simultaneously presented with two grapes, she took the right one and disregarded the other unless her glance happened to stray across it. When she did fixate an object, she was perfectly capable of pursuing it with her head and hand into all parts of the visual field. She used her right hand almost exclusively in these tasks, whereas prior to surgery she had preferred her left for most activities.

In later testing sessions, up to five months postoperatively, these symptoms remained fairly stable, although B.B. did learn to compensate for her neglect of the left field by making successive head movements from left to right. With the candy board this caused her center of gaze to sweep the length of the board, thus allowing her to retrieve all the candies. Similarly, when presented with two grapes, after seizing the right one, she would move her head leftwards until her glance struck the other. If, however, her attention was held straight ahead, it was obvious that she still neglected visual events in the left peripheral field.

Postoperatively the four animals who had suffered lesions to their intrahemispheric fiber tracts showed none of the disturbances in eye or head movement seen in B.B., nor did they exhibit any signs of a unilateral inattention; all four responded as well to a threat or reward in the visual field contralateral to the lesion as they did to stimuli opposite the normal hemisphere. There was, however, an obvious change in the pattern of their hand movements, in that all four animals now tended to use in visual tasks only the hand contralateral to the intact hemisphere. Thus, with the candy board, where preoperatively each hand had picked up the candies on its own side, now only the hand ipsilateral to the lesion (the left hand in "Fr", the right in "Tw", "Th" and "Sn") was active, retrieving first the candies on its side, and then working into the field usually serviced by the other hand. With presentation of two grapes, one on either side, the monkeys used only their normal hand, seizing the nearest grape first. When a grape was offered on the end of a wire in different parts of the visual field, where preoperatively the animals had taken it with either hand, they now used just the one hand.

While there were signs that in "Sn" the nonpreferred hand was partially paralyzed, the other three monkeys, in whom the transection was further posterior, seemed perfectly capable of using this hand in a natural manner, either alone, in retrieving grapes from the turntable, or in conjunction with the preferred hand, in opening a box.

In summary, although monkeys with a transverse section of their longitudinally running association tracts did show a change in hand preference similar to that seen in the frontal lesion animal, they did not exhibit any of the symptoms of unilateral visual neglect which were so prominent in B.B.

Examination of the E.O.G. records from B.B., the right frontal lesion animal, revealed that even five months after surgery, there was still a definite asymmetry in her eye movements, with most of the horizontal saccades (six to one) being toward the side of the lesion. The shapes of the saccades in the two directions were not noticeably different, except that the ones to the left tended to be smaller. Observation of the animal during the recording session disclosed that her infrequent glances toward the left were made up mainly of head movements, with her eyes not deviating much left of the midpoint in her head; it was, however, physically possible for her to turn her eyes in this direction as was demonstrated by restraining her head.

The tract sectioned monkey ("Th") did not show any obvious asymmetry in his eye movements, but rather the pattern his saccades appeared as normal as his attentional mechanisms.

Drawings of the total cross sectional area destroyed in each animal are given in Figure 20.

In "B.B." (Figure 20b) the cortex removed included all of the posterior bank of the medial arm of the right arm of the right arcuate gyrus, down to and including that on the floor of the sulcus. The white matter was relatively intact, and the internal structures of the hemisphere were untouched.

"Tw" (Figure 20c) had a thin lesion, not more than one millimeter wide, involving the ventral cortex and white matter core of the inferior parietal lobe; the area of injury did not extend outside of this gyrus, and therefore the intra-hemispheric fiber tracts were not severed.

"Fr's" lesion (Figure 20d) was approximately two millimeters wide at the base and in its course destroyed the white matter of the inferior parietal lobe and the body of the hemisphere over to the lateral ventrical, thus cutting the superior longitudinal fasiculus (SLF), but not the subcallosal fasiculus (SF).

In "Th" (Figure 20e) the region damaged was rather large and definitely included the SLF and SF; also injured was a small part of the VPL nucleus of the thalamus and the tail of the caudate.

"Sn" Had the most extensive ablation (Figure 20f), destroying the SLF, SF, and the top third of the caudate and putamen. Also injured was the top part of the internal capsule.

Discussion

The lack of any disturbance in visual orientation or attention following unilateral section of the intrahemispheric fiber tracts between the occipital cortex and frontal eye fields, supports recent work (11,12) which has rejected the traditional integrative role assigned to cortico - cortico connections, in favor of a vertical organization involving cortical and subcortical centers. It must, however, be admitted that it came as a distinctly unpleasant surprise that these tracts do not subserve the functions for which they are anatomically so well suited; this was especially true in view of a previous report of neglect after a lesion to these connections (13). In the present experiment, however, it is quite clear that these monkeys' attentional capacities were normal despite histological evidence, that in "Fr," "Sn," and "Th" the medullary substance containing the superior longitudinal and subcallosal fasiculi was thoroughly transected. A possible explanation for these negative behavioral results would be the existence of another transcortical tract performing a similar task, and indeed one other tract, the uncinate fasiculus, does project to the same region of the frontal lobe along a pathway ventral to the present lesions. However, although some fibers from a visual association area, the inferior temporal lobe, do run in this bundle, the bulk of the axons come from the auditory regions of the superior temporal lobe and from the temporal pole (2). Thus, within the sensitivity of the present tests, the cortico -cortico connections between the occipital and frontal regions do not appear necessary in order for visual input to influence behavioral processes mediated by the arcuate gyrus.

The remaining question concerns the basis of the observed change in hand preference in the tract sectioned monkeys. Here, the case of "Tw" makes any interpretation very difficult, for while the pattern of his visuo-motor activities was altered as any of the other animals, his lesion did not extend beyond the core of the inferior parietal lobe, thus leaving intact all major longitudinal fibers. As for this effect being a result of cortical damage, while there are reports (14) of shifts in hand preference following ablation of the somesthetic projection area in the superior parietal lobe, this is far posterior and superior to the present lesion, which is located in the somatic association cortex; it is also hard to conceive that a cortical ablation as small as was made in "Tw" could have such a profound effect. It is therefore impossible to draw any definite conclusions without further research in this area.

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