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1 Lateral Specialization in the Surgically Separated Hemispheres

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ABSTRACT New evidence concerning cerebral dominance, left-right specialization of verbal vs. perceptual functions, and the localization of consciousness in the human brain comes from follow-up studies on people who have undergone cerebral commissurotomy for severe intractable epilepsy. In commissurotomy patients, it is possible to measure and compare the positive performance of each hemisphere of the same individual functioning independently on the same test task, and the two hemispheres can be pitted against each other for response dominance. Fine differences can be measured under these conditions and qualitative distinctions discerned that are much more difficult or even impossible in comparisons involving different persons. Results indicate two distinct modes of central processing in the disconnected left and right hemispheres.

Introduction

UNLIKE THE brains of most mammalian species, the human brain already at birth possesses an intrinsic left-right differentiation that appears to be predetermined to a considerable extent by inheritance, and for which various genetic models have been suggested. The latest of these proposed by Levy and Nagylaki (1972) involves two genes with four alleles. One gene determines which hemisphere will be language dominant, with the allele for the right hemisphere being recessive, and a second gene determines whether hand control will be contralateral or ipsilateral to the language hemisphere, with ipsilateral control being recessive. This gives a total of nine possible different allelic combinations or genotypes for handedness in man, with the weaker mixed combinations presumed to be more easily reversible by training.

Handedness in animals, or paw preference, has been shown not to be genetically determined in rats (Peterson, 1934) and mice (Collins, 1969), and such determination in the higher subhuman primates is still uncertain. Recently Collins (1970) in a widely cited article, poetically entitled, "The sound of one paw clapping," has concluded from an analysis of published human data that in man, also, the evidence does not support a genetic basis for handedness. This conclusion is contested by Nagylaki and Levy (1973), who claim that "the sound of one paw clapping" is not sound and is based on a misinterpretation of the sibling-sibling relationship. They reaffirm their two gene-four allele model as the best fit for the evidence now available.

Most of our information regarding the nature and functional role of hemispheric specialization comes historically from the kinds of functional impairments produced by asymmetric brain damage (Zangwill, 1964; Mountcastle, 1962; Milner, 1971). In the last eleven years, this evidence has been strengthened and extended by observations on patients with midline cerebral commissurotomy. This is an operation that eliminates direct cross-communication between the hemispheres but leaves both hemispheres otherwise intact and functioning independently. In persons having had this operation, each hemisphere can be tested separately for its positive as well as its negative competence, and direct comparisons can be made for the independent performance of the left and right hemisphere in the same individual.

The following comes mainly from studies by a long line of colleagues and me on a group of such patients operated upon for treatment of severe, intractable epilepsy. These are all patients of P. J. Vogel, Chief of Neurosurgery at the White Memorial Medical Center, and J. E. Bogen, Ross-Loos Medical Group, in Los Angeles. The patient group is small, because this is a kind of surgery that is undertaken only as a last resort measure in an effort to control advancing life-threatening epilepsy where it cannot be contained by medication nor by simpler unilateral ablations.

In a total of only 16 persons operated upon to date, the majority have complications including preoperative asymmetric brain damage that makes them unsuitable for many studies of hemispheric specialization, depending on the specific problem. Furthermore, a new form of the operation that involves only a partial commissurotomy, i.e., section of the anterior two-thirds of the corpus callosum along with the anterior commissure (Gordon et al., 1971), promises to render the complete disconnection unnecessary in most future cases.

The surgery with which we are here concerned includes

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complete section of the large corpus callosum in its entirety plus, also, the smaller anterior commissure (Bogen et al., 1965). The thin hippocampal commissure subjacent to the callosum is not separately visualized but is presumed to be sectioned along with the corpus callosum. The massa intermedia, which is variable in man, is also sectioned when it is found. Only the subordinate right hemisphere is exposed and slightly retracted. All the cross-connections are sectioned completely in a single-stage operation, and it is this mainly that distinguishes the operation as reintroduced by Vogel in 1961 from that used earlier in the late 1930s by Van Wagenen (Akelaitis, 1943), in which the deconnections were either only partial or performed in stages, or both.

As the brain is basically bisymmetric in its structural plan, each disconnected hemisphere retains a full set of cerebral centers and interconnections for all the different kinds of cerebral function, excepting, of course, those that involve cross-connections between the hemispheres (Figure 1). Some of the more obvious problems created by the elimination of cross connections are indicated in Figure 2. Note that the optic image of the outside world on its way into the brain is divided down the middle into right and left halves, which then are projected separately into the disconnected left and right hemispheres, respectively. The same applies to the cerebral representation for the right and left hands and legs. This includes both the sensory and the primary motor control centers for the limbs. Note especially that the surgery separates the entire right hemisphere, and all that goes on in that hemisphere, from the speech and main language centers located in the left hemisphere.

Considering the enormous size of the sectioned neocortical systems, estimated to contain over 200 million fibers cross-connecting nearly all regions of the cerebral cortex, with some decussations to subcortical centers, it is generally agreed that one of the more remarkable effects of this kind of operation is the seeming lack of effect insofar as ordinary daily behavior goes. A person two years recovered from the operation and otherwise without complications might easily go through a routine medical check-up without revealing that anything was particularly wrong to someone not acquainted with his surgical history. Speech, verbal intelligence, calculation, established motor coordination, verbal reasoning and recall, personality, and temperament are all preserved to a surprising degree in the absence of hemispheric interconnection.

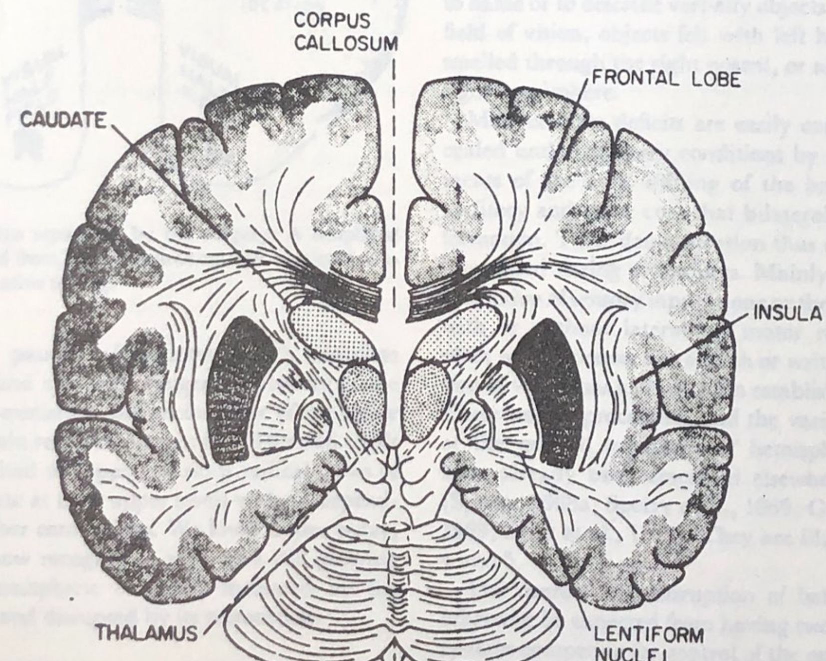


Figure 1 Anatomical effect produced by midline section of the forebrain commissures shown schematically.

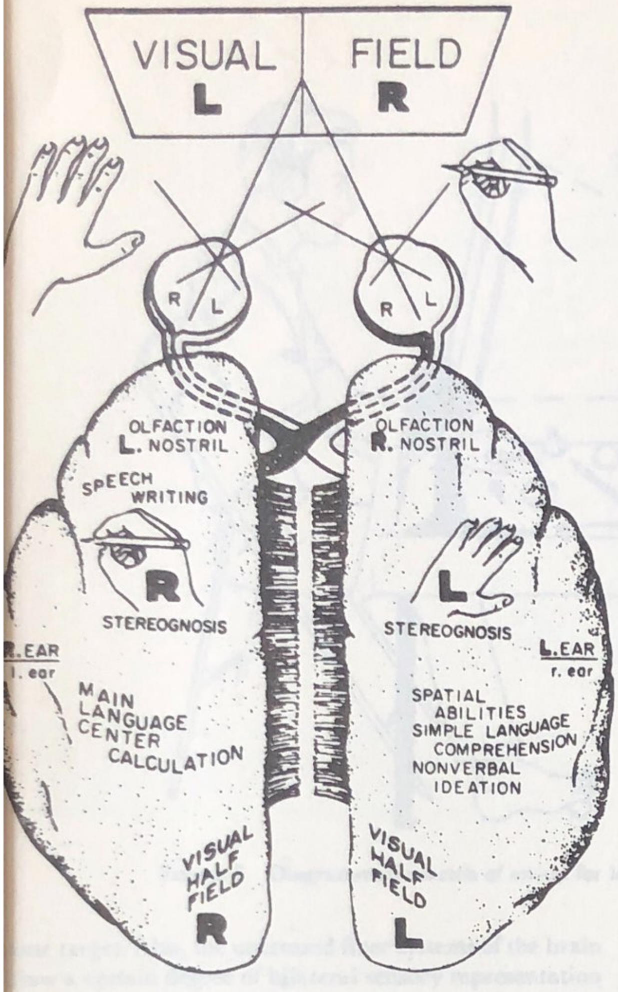


FIGURE 2 Functions separated by the surgery: A simplified summary combined from known neuroanatomy, cortical lesion data, and postoperative testing.

The amazing paucity of symptoms with complete surgical section and also with congenital absence of the great cerebral commissure had become one of the major challenges for brain research back in the 1940s and 1950s and was being cited to support various radical views of how brains operate at their upper levels without depending on specific fiber connections. We know better today, of course, and now recognize a wide and still growing array of interhemispheric functions mediated by the corpus callosum and disrupted by its transection.

Brain bisection and conscious awareness

Despite the apparent normality of these people under ordinary conditions and in contradiction to the prevailing neurological doctrine of the 1950s we can now demonstrate with appropriate tests a whole array of distinct impairments (Sperry et al., 1969) that are most simply summarized by saying that the left and right hemispheres, following their disconnection, function independently in most conscious mental activities. Each hemisphere, that is, has its own private sensations, perceptions, thoughts, and ideas all of which are cut off from the corresponding experiences in the opposite hemisphere. Each left and right hemisphere has its own private chain of memories and learning experiences that are inaccessible to recall by the other hemisphere. In many respects each disconnected hemisphere appears to have a separate "mind of its own."

This presence of two rather separate streams of conscious awareness is manifested in many ways in different kinds of testing situations. For example, following surgery, these people are unable to recognize or remember a visual stimulus item that they have just looked at if it is presented across the vertical midline in the opposite half visual field; that is, the normal perceptual transfer that one expects to find between the left and right halves of the field of vision is lacking. Similarly, objects identified by touch with one hand cannot be found or recognized with the other hand. Odors identified through one nostril are not recognized through the other nostril (Gordon and Sperry, 1969). Following surgery, these people are unable to name or to describe verbally objects seen in the left half field of vision, objects felt with left hand or foot, odors smelled through the right nostril, or sounds heard by the right hemisphere.

Most of these deficits are easily compensated or concealed under ordinary conditions by exploratory movements of the eyes, shifting of the hands, and through auditory and other cues that bilateralize the sensory information. Their demonstration thus requires controlled lateralized testing procedures. Mainly, these involve the restriction of sensory input to one or the other hemisphere, with or without lateralized motor readout, combined often with processes like speech or writing, the lateralization of which has already been established (see Figure 3). These testing procedures and the various manifestations of the general syndrome of hemisphere deconnection have already been described elsewhere in some detail (Sperry, 1968a; Sperry et al., 1969; Gordon and Sperry, 1969; Levy et al., 1972). They are illustrated in Figures 4 and 5.

The conflict and disruption of behavior that might otherwise be expected from having two separate cerebral systems competing for control of the one body is counteracted by a variety of unifying mechanisms. For example, the two retinal half-fields of the eyeball move as one, and eye movements are conjugate, so that when one hemisphere directs the gaze to a given target the other hemisphere is automatically locked in at all times on the

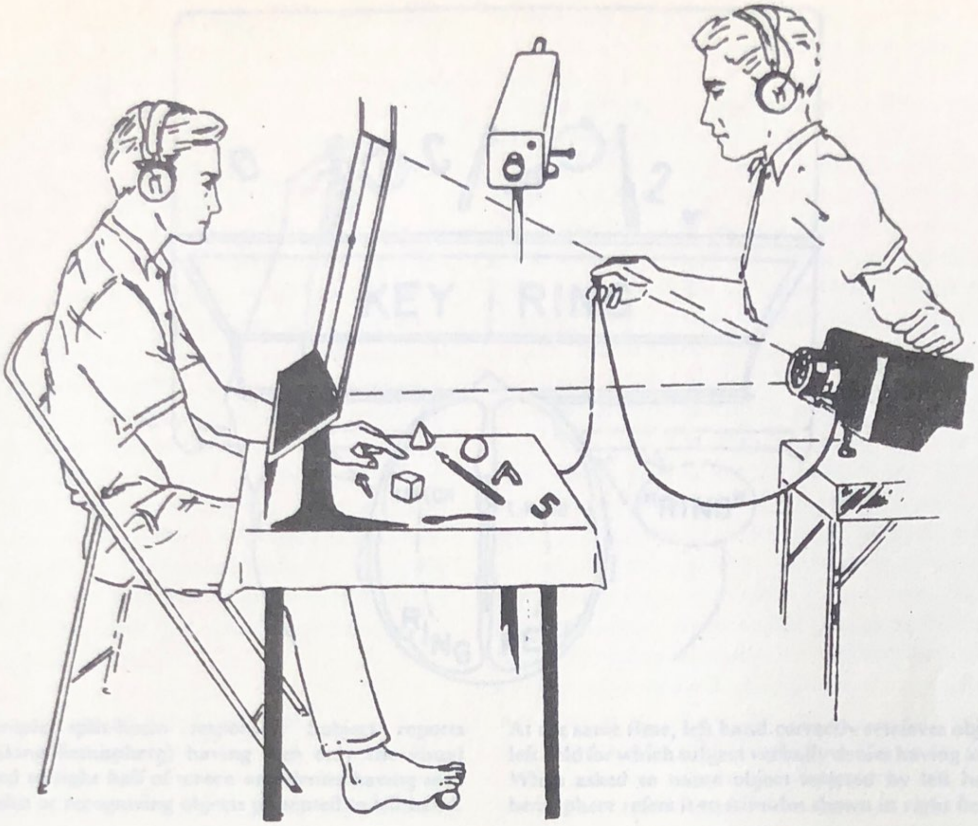


FIGURE 3 **Diagrammatic sketch of set-up for lateralized testing after hemisphere deconnection.**

ame target. Also, the uncrossed fiber systems of the brain llow a certain degree of bilateral sensory representation nd motor control within each hemisphere that helps reatly to keep behavior unified.

Emotional effects triggered through one hemisphere as y lateral presentation of an offensive odor, embarrassing hoto, etc., tend to spread easily into the opposite hemisphere, presumably through intact brainstem routes and hrough feedback from peripheral changes. Vascular reactions like blushing and alterations in blood pressure, acial expressions, giggling, frowning, exclamations, and he like all help to bilateralize an emotion and to counteract attempts to establish concurrent conflicting emotional ets on left and right sides. Whether a central emotional tate could survive in one hemisphere in the presence of conflicting emotional expression imposed peripherally rom a different emotional state in the other hemisphere has yet to be determined. The possibility that mild emotional experiences may be confined temporarily to one hemisphere is by no means ruled out, but this is difficult to demonstrate (Gordon and Sperry, 1969; Gazzaniga, 1970) and would seem to be more the exception than the rule. Emotional processes thus appear to exert a general unifying influence, and this applies also when affect is involved as reinforcement in learning. Reinforcement along with other feedback effects must be laterally controlled and strong emotional responses avoided.

Mechanisms of orientation and attention likewise tend to bring hemispheric activity into a unified focus. Active task performance on the part of one disconnected hemisphere will ordinarily interfere in varying degree with simultaneous performance on a different task by the opposite hemisphere. Such interference is, of course greatly reduced over that obtained with the commissures intact, and can be largely nullified with practice under the right conditions (Gazzaniga, 1970). Interference between the disconnected hemispheres is reduced when a common motor posture is utilized for both left and right tasks, or when both tasks involve the same general mental set. Separate parallel performance on different tasks, though possible under special facilitating conditions, seems not to be the general rule. The fact that attention in many tests seems to become focused in one separate hemisphere and simultaneously become repressed in the other would appear to reflect lateral differentiation in the

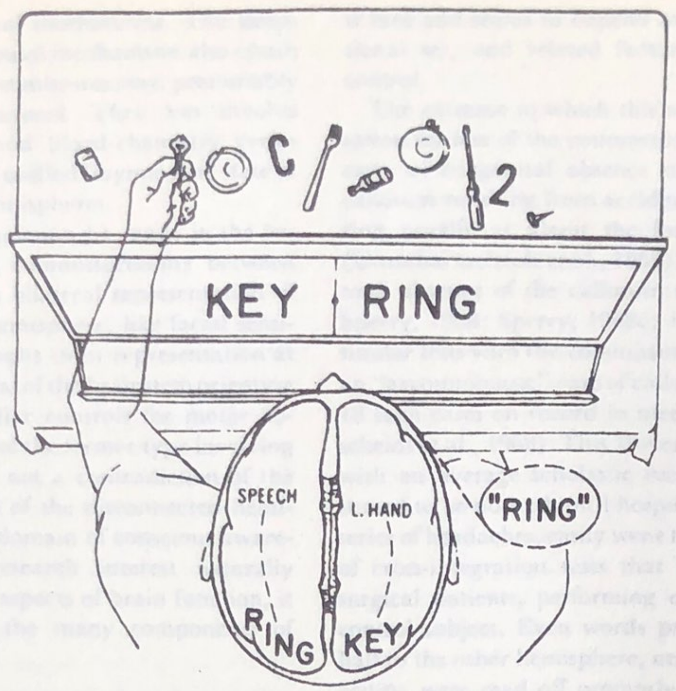


FIGURE 4 Sample split-brain responses: Subject reports (through speaking hemisphere) having seen only the visual stimulus flashed to right half of screen and denies having seen left-field stimulus or recognizing objects presented to left hand. At the same time, left hand correctly retrieves objects named in left field for which subject verbally denies having any knowledge. When asked to name object selected by left hand, speaking hemisphere refers it to stimulus shown in right field.

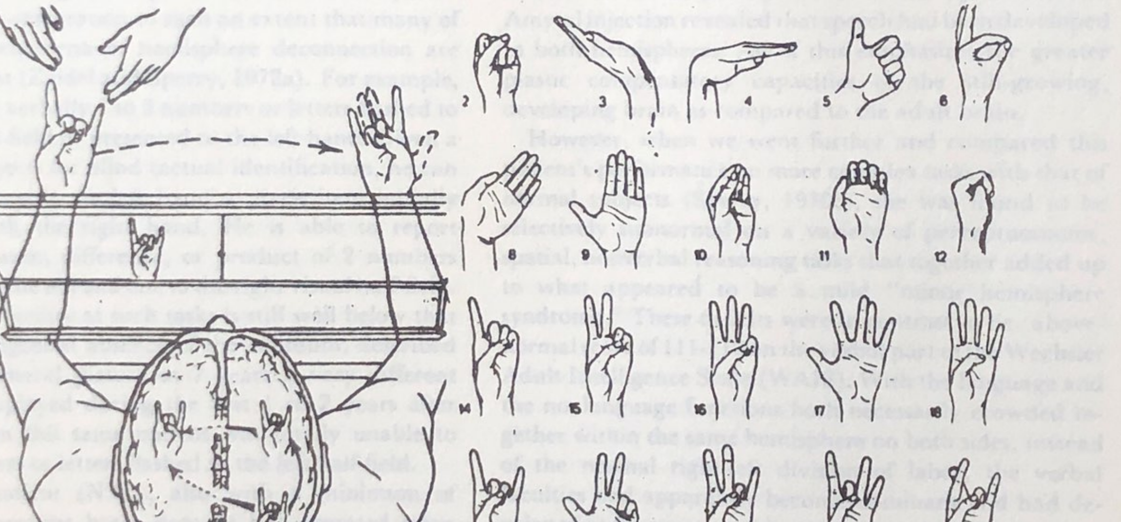


FIGURE 5 Additional tests used by author to detect lack of interhemispheric integration following commissurotomy. Subject attempts to replicate complex hand and finger postures flashed to left and right visual half-fields or imposed directly on one hand by examiner. Intrahemispheric combinations are performed successfully but crossed combinations fail.

alamo-brainstem attentional mechanisms. The sleep-
ıke cycle and associated arousal mechanisms also retain
ong bilateral unity after commissurotomy, presumably
ntered in midbrain structures. They too involve
etabolic, blood-pressure, and blood-chemistry cycles
at together help reinforce a unified bisymmetric state of
sal arousal level in both hemispheres.

It is important that a distinction be made in the be-
vioral unity that survives commissurotomy between
at which is attributable to bilateral representation of
e given function in each hemisphere, like facial sensi-
lity, and the unity that results from representation at
wer undivided levels, like that of the brainstem orienting
echanisms and the cerebellar controls for motor co-
dination. Functional unity of the former type involving
mispheric reduplication is not a contradiction of the
neral conclusion that each of the disconnected hemi-
heres has its own separate domain of conscious aware-
ss. With most of our research interest naturally
ncentrated on the divided aspects of brain function, it
easy to underemphasize the many components of
havior that remain unified.

ompensatory readjustment and agenesis

stoperative use of the above unifying mechanisms and
sociated cross-cuing strategies can be significantly
engthened by practice. We find evidence of this par-
ularly in the youngest patient operated upon at age 13.
7 years after surgery this patient (L.B.) shows improve-
ents in cross-integration to such an extent that many of
e basic phenomena of hemisphere deconnection are
rdly evident (Zaidel and Sperry, 1972a). For example,
can report verbally 1 to 3 numbers or letters flashed to
e left visual field or presented to the left hand. Given a
ries of 8 objects for blind tactual identification, he can
oss-retrieve with the left hand a given item initially
entified with the right hand. He is able to report
rbally the sum, difference, or product of 2 numbers
shed one to the left and one to the right visual half-field.
though his facility at such tasks is still well below that
en with congenital absence of the callosum, described
low, the general picture at 7 years is very different
om that displayed during the first 1 to 2 years after
rgery, when this same patient was totally unable to
port numbers or letters flashed to the left half-field.

Another patient (N.G.), also with a minimum of
own preoperative brain damage but operated upon
uch later in life (at age 30), shows much less improve-
ent after 8 years. She occasionally is able to report single
rge numbers and geometric shapes from the left half-
eld of vision and to align bars across the visual midline,
hich she could not do previously, but such performance is rare and seems to depend on transient shifts in attentional set, and related factors not consistently under control.

The extreme to which this sort of functional compensation for loss of the commissures can go is illustrated in cases of congenital absence or agenesis of the corpus callosum resulting from accidents of development occurring usually at about the fourth month of gestation (Unterharnscheidt et al., 1968). A person with congenital total absence of the callosum was studied by Saul and Sperry, 1968; Sperry, 1968c; 1970c), and compared on similar tests with the commissurotomy patients. This was an "asymptomatic" case of callosal agenesis, one of about 18 such cases on record in medical history (Unterharnscheidt et al., 1968). This 19-year-old college sophomore, with an average scholastic record and previously presumed to be normal until hospitalized and X-rayed for a series of headaches, easily went through the entire battery of cross-integration tests that we had devised for the surgical patients, performing essentially like a normal control subject. Even words projected half to one and half to the other hemisphere, near the threshold of visual acuity, were read off promptly with no difficulty. This was true even where the pronunciation depended on cross-integration between the two halves of the word.

The anterior commissure appeared to be present in the X-rays and somewhat enlarged, and presumably the functions of the uncrossed or bilateral fiber systems of the brain had been enriched by use. Further, lateral anesthetization of one hemisphere at a time by intracarotid Amytal injection revealed that speech had been developed in both hemispheres. All of this emphasizes the greater plastic compensatory capacities of the still-growing, developing brain as compared to the adult brain.

However, when we went further and compared this patient's performance on more complex tasks with that of normal subjects (Sperry, 1970c), she was found to be selectively subnormal on a variety of perceptuomotor, spatial, nonverbal reasoning tasks that together added up to what appeared to be a mild "minor hemisphere syndrome." These deficits were in contrast to her above-normal score of 111-112 on the verbal part of the Wechsler Adult Intelligence Scale (WAIS). With the language and the nonlanguage functions both necessarily crowded together within the same hemisphere on both sides, instead of the normal right-left division of labor, the verbal faculties had apparently become dominant and had developed at the expense of the nonverbal. As will be evident below, this tendency for language to develop at the expense of the competing nonverbal functions is more the rule than the exception. Even though the spatial-perceptual-performance functions appear to have primacy in terms of evolution and also seem to get a head start over nguage during development, there seems to be someing about the growth and maturational processes in the iman brain that tends to favor the elaboration of laniage. All of which brings us now more directly to the iestion of the nature of the functional differences tween the left and right hemispheres.

lemispheric dominance and differentiation

he commissurotomy patient, as mentioned, offers ecial advantages for the study of hemispheric specializaon in that it is possible to measure and to compare the isitive performance of each hemisphere functioning dependently. Direct comparisons can be made for perrmance on the same task in the same individual where e life history and other background factors are all uated, and the two hemispheres can be pitted against ch other for response dominance. Fine differences can measured under these conditions and qualitative stinctions discerned that are much more difficult or en impossible in comparisons involving different perns. Earlier caution and conservative uncertainties rerding the extent and the importance of hemispheric ecialization still being voiced in the early 1960s Mountcastle, 1962) tend to dissolve in the face of direct oss-comparisons of this kind. It is most compelling to e the same individual performing the same test task in ery different ways, and with different strategies, deending on whether he is using his left or his right emisphere.

Repeated examination during the past 10 years has onsistently confirmed the strong lateralization and ominance for speech, writing, and calculation in the isconnected left hemisphere in these right-handed atients. The minor, right hemisphere, by contrast, is nable to respond in speech or writing in the great ajority of test situations. Nor can it typically perform alculations except for simple additions up to sums less han 20. The language-dominant hemisphere is also the nore aggressive, executive, leading hemisphere in the ontrol of the motor system. After the surgery, these atients seem to run primarily on the left hemisphere. This is the hemisphere that we mainly see in action and he one with which we regularly communicate. It is the ighly developed and dominant capacities of the left emisphere apparently that are largely responsible for he earlier impressions that cerebral functions persevere vith little impairment in the absence of the corpus allosum.

The mute, minor hemisphere, by contrast, seems to be arried along much as a passive, silent passenger who eaves the driving of behavior mainly to the left hemiphere. Accordingly, the nature and quality of the inner mental world of the silent right hemisphere remains relatively inaccessible to investigation, requiring special testing measures with nonverbal forms of expression. Although some authorities have been reluctant to credit the disconnected minor hemisphere even with being conscious, it is our own interpretation based on a large number and variety of nonverbal tests, that the minor hemisphere is indeed a conscious system in its own right, perceiving, thinking, remembering, reasoning, willing, and emoting, all at a characteristically human level, and that both the left and the right hemisphere may be conscious simultaneously in different, even in mutually conflicting, mental experiences that run along in parallel.

Though predominantly mute and generally inferior in all performances involving language or linguistic or mathematical reasoning, the minor hemisphere is nevertheless clearly the superior cerebral member for certain types of tasks. If we remember that in the great majority of tests it is the disconnected left hemisphere that is superior and dominant, we can review quickly now some of the kinds of exceptional activities in which it is the minor hemisphere that excels. First, of course, as one would predict, these are all nonlinguistic, nonmathematical functions. Largely they involve the apprehension and processing of spatial patterns, relations, and transformations. They seem to be holistic and unitary rather than analytic and fragmentary, and orientational more than focal, and to involve concrete perceptual insight rather than abstract, symbolic, sequential reasoning. However, it yet remains for someone to translate in a meaningful way the essential right-left characteristics in terms of the brain process, and accordingly we still do well to refer to the actual test activities.

The superior minor hemisphere

It was shown very early in the study of these patients by Bogen and Gazzaniga (1965; Bogen, 1969; Gazzaniga, 1965) that the right hemisphere is superior to the left in the construction of block designs, and also in copying and drawing test figures like a Necker cube, a house, a Greek cross, etc. This is consonant with prior evidence for visuospatial constructional apraxia following right hemisphere lesions (Arrigoni and DeRenzi, 1964; Hécaen, 1962; Piercy et al., 1960; Zangwill, 1964). These differential hemispheric capacities were shown by Levy (1969a) to involve more than just praxic ability. She developed a test for these patients involving intermodal spatial transformations in which praxic or motor requirements were kept extremely simple, namely, manual pointing, but which required complex perceptual and cognitive central processes. Three-dimensional blocks of various shapes were placed in the subject's right or left hand to be perceived blindly by touch and then matched to two-dimensional patterns, perceived in free vision, of what the blocks would look like if made of cardboard and unfolded.

In addition to a striking quantitative superiority of the minor hemisphere, Levy also found qualitative differences, the performance with the left hand being rapid, silent, and direct, whereas that with the right hand was more hesitant and accompanied by a running verbal commentary that was difficult to inhibit. The final response of the right hand was apparently dependent on a sequence of verbal reasoning. It was concluded that the disconnected left hemisphere was applying a verbal analytic mode of thinking in contrast to the right hemisphere that had reasoned by direct perceptual, synthetic, or Gestalt, processing. With further analysis of which items were most easy and which most difficult for each hemisphere, she inferred that the left and right modes of central processing would mutually interfere within the same hemisphere and that this would give a rationale for the evolution of cerebral dominance.

The left-hand performance of patient L.B., who scored highest on this cross-modal test, was found to be better than 31% of college sophomores when the test was later standardized at the University of Southern California. However, on a similar visual test for spatial relations presented in free vision with unrestricted hand use, this same patient failed completely, rating lower than 99% of the population of his age and education. This striking contradiction seems best explained as another example of the suppression and interference caused by left hemisphere activity upon the expression of abilities centered in the right hemisphere.

Similar qualitative differences in the problem-solving strategies of the separate hemispheres were later observed on a modification of the Raven's Progressive Matrices Test administered separately to the left and right hemispheres by Zaidel and myself (1973). The choice array of figures containing the correct answer was presented in the form of raised patterns for tactual discrimination by left and right hands separately. It was necessary to reduce the standard six-item choice array to three items under these conditions as in the above-mentioned test used by Levy. The commissurotomy patients became too confused when obliged to keep track of more than three items in blind touch. Apparently, they have a reduced mental grasp for holding in mind a series of newly identified tactual stimuli. Although the colored stage of the Raven's test in particular appears to require mainly spatial insight, the left hemisphere (right-hand performance) was nevertheless found to be able to attain a score only slightly below that of the right hemisphere by using a slower process of verbal reasoning. Thus both hemispheres could find the correct answers but by employing different strategies. We concluded that the scores for the Progressive Matrices Test do not in themselves eminently distinguish left and right hemispheric capabilities.

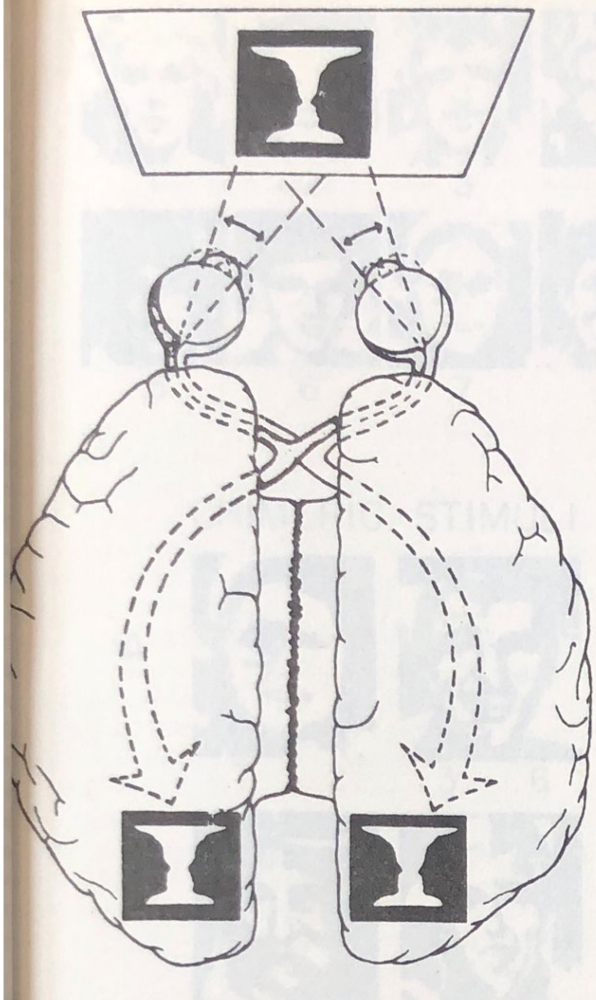
The special spatial aptitude of the disconnected minor hemisphere is not confined to the visual modality. This was shown in tests by Milner and Taylor (this volume) that were based entirely on tactual discrimination and memory for nonsense shapes made of bent wire. In tests involving the perception of part-whole relations worked up by Nebes (1971), a strong superiority of the right hemisphere was also evident in a task presented entirely through touch. The task involved the matching of a given sample circle-segment or arc to the correct one of an array of three whole circles of different sizes. Both sample and array were presented by touch with vision excluded. The test was also given cross-modally, going from vision to touch, or from touch to vision, with similar results in all three modes of presentation. Scores for normal control subjects using both hemispheres and without medication or a history of epilepsy (and with considerably higher IQs than these patients) averaged only 10 to 15% better than those for the disconnected minor hemisphere.

In another test used by Nebes (1971), the subjects examined a fractured or exploded figure in free vision and then searched blindly by touch behind a screen for the correct, intact pattern to match, from among an array of three raised figures, using one or the other hand. Again the left-hand right-hemisphere system came out far ahead. The scores for the left hemisphere in this and the preceding task were hardly above chance; apparently this kind of task was almost too difficult for the disconnected left hemisphere.

In a modification of the Kasanin-Haufmann Concept Formation Test used by Kumar (1971), the subjects had to sort 16 blocks into four categories using blind tactual identification. It was required that the subject discover by trial and error which of several possible criteria, like shape or size or weight or height, etc., was the correct one for the classification. The minor hemisphere scored almost twice as well as the major in terms of time and correct choices, whereas in a similar test involving 16 familiar objects easily named, the score standings were reversed.

Duplicate and competitive right-left processing

Figure 6 illustrates how normal scanning movements of the eyes from right to left edge of an object being examined, would give two sensory representations or percepts of the object, one in each hemisphere (Sperry, 1970a). The constancy of the visual field in the presence of eye movements must be taken into account, and inversions of the visual pathways assumed. We have long



IGURE 6 Diagram showing how exploratory eye movements ve two full percepts of an examined object, one in each hemi- here. Position constancy in the presence of eye movement must taken into account and image inversion in the optic pathways sumed.

ondered about the functional utility of this kind of ght-left redundancy in the normal brain, but if the two emispheres process sensory information in distinctly fferent ways as we now think, then perhaps this left- ght doubling makes sense.

In recent studies (Levy et al., 1972), the two sensory nages perceived in right and left hemispheres are ranged to be different and conflicting. A series of visual imuli are split down the middle and then recombined nd joined at the midline to make composite right-left nimeras (see Figure 7). These chimeric figures are then ashed to the subject while the gaze is centered, as dicated in the figure. The missing half of each image nds to be filled in by each hemisphere according to a general rule for perceptual completion (Trevarthen and Kinsbourne, 1973). Since each hemisphere is cut off from the conscious experience of the other, the split-brain subjects remain blandly unaware of even gross discordance between the left and right halves of these composite stimuli.

The result is that the two hemispheres are induced to see two different things occupying the same position in space at the same time, something that the normal brain of course rejects. With rival, competing perceptual processes thus set up on left and right sides, it becomes possible to determine which hemisphere is the more proficient in dominating the response. The response may be verbal or manual, like pointing to a matching item among a choice of alternative possibilities. This same principle has been used with nondescript and geometric figures, faces, objects, perception of movement, words, clock faces, serial patterns, colors, and combinations of these, under different testing conditions, that is, with different mental and motor sets, and with verbal as well as manual readout.

In general, the results with composite input conform with earlier findings in that if linguistic processing is involved, the subject's response is dominated by the disconnected left hemisphere selecting in favor of the right half of the composite stimulus. On the other hand, with nonlinguistic, manual readout either side may dominate. With the perception of faces and of complex or nondescript patterns, and with any direct visual-visual matching of shape or pattern, the right hemisphere is dominant. This applies even for words, provided that no interpretation of word meaning is involved. When a conceptual translation or verbal reply is required, the dominance promptly shifts to the opposite left hemisphere. Nondescript shapes proved to be extremely difficult for the left hemisphere, even without concurrent right hemispheric stimulation.

An unexpected minor-hemisphere dominance for letter and word percepts has been found with bilateral competitive input in the tactual mode (Preilowski and Sperry, 1972). The task involved tactual discrimination and retention of competing pairs of three and four letter nouns and verbs presented simultaneously to the left and right hands one letter at a time. The response consisted of pointing to a choice array of words presented in free vision. A change to purely verbal response brought a prompt shift of dominance to the left hemisphere.

The chimeric results also demonstrated that the disconnected minor hemisphere is capable of capturing and controlling the motor system under conditions where the two hemispheres are in equal and free competition, that is, where the sensory input is equated and the subject is quite free to use either left or right hand. Although this had been seen sporadically in occasional tests before

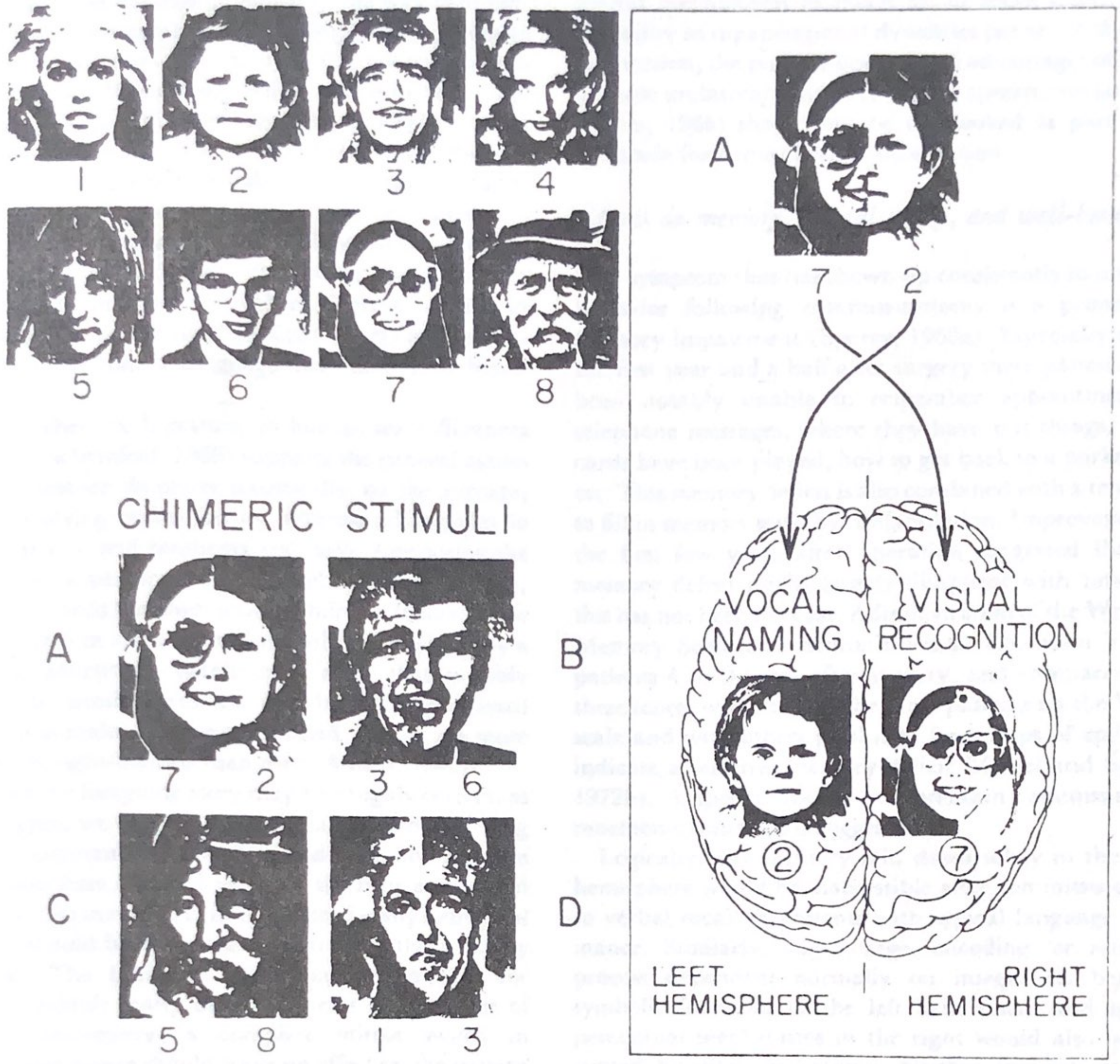


FIGURE 7 Composite face stimuli for testing hemispheric specialization for facial recognition. From Levy et al. (1972). See explanation in text.

under special conditions, we had not previously obtained the phenomenon so consistently or convincingly. The same was found in the above-mentioned study with competitive bilateral tactual stimulation. These observations favor the view that in the normal brain volitional movements may be directly controlled from either hemisphere depending on which is superior and dominant for a given activity. The chimeric findings also reaffirm the impression that the disconnected left and right hemispheres apprehend and process things in different ways. In dealing with faces, for example, the right hemisphere seems to respond to the whole face directly as a perceptual unit, whereas the left seems to focus on salient features and details to which verbal labels are easily attached and then used for discrimination and recall.

Verbal vs. nonverbal in dominance relations

If a special mutual antagonism exists between the mode of cognitive processing used for language and that used for spatial perceptual function, as postulated by Levy, this ought to show up statistically, she predicted, as a perceptual deficit among left-handed persons, because sinistrals are known to be more bilateralized for language ompetence than dextrals as shown in the way such perons recover from cerebral injury. Supporting evidence as been found (reviewed in Levy, 1973) not only among inistrals in their IQ subtest profiles but also in perceptual ests with persons with right-hemisphere speech resulting rom early injuries to the left hemisphere, and in the case f callosal agenesis described above. The inverted handvriting seen in many left-handers and very rarely in lextrals is tentatively attributed by Levy to the developnent in left-handers of ipsilateral motor control from a eft language-dominant hemisphere. Normal writing in eft-handers is accordingly thought to reflect contraateral control from a language-dominant right hemiphere.

A comprehensive literature on human sex differences Garai and Scheinfeld, 1968) supports the generalization hat adult women do better statistically, on the average, n tasks involving verbal facility, whereas adult males do etter in spatial and mathematical tasks. Appraising the vidence in the perspective of hemispheric specialization, evy (1973) finds the lower spatial ability in females to be imilar to that in sinistrals and describes it as probably a ex-linked genetically determined factor that possibly esults from hemispheres less well laterally specialized han those of males. On the other hand, women are more onsistently right-handed than men (Annett, 1970).

Though the foregoing story may be roughly correct, as ar as it goes, we can expect the total picture regarding erebral dominance, sinistrality, and sexuality to be less imple than here outlined when all the facts are in, and articularly so in regard to implications for any individual rain. It should be remembered that all of this is highly tatistical. The brains of individual left-handers, for xample, exhibit many different forms and degrees of ight-left asymmetry; a complete mirror switch in erebral dominance should leave no effect on the pattern f abilities. With variations of this kind innately preletermined to a considerable extent, it may be seen that lifferential balancing of these left and right hemispheric bilities could provide quite a spectrum of individual variation in the structure of human intellect (Sperry, 1971).

Regardless of the indications for an intrahemispheric ntagonism between the verbal and spatial modes of hinking, the two modes apparently integrate quite armoniously under normal conditions, i.e., in the preence of the corpus callosum. This harmony could be chieved conceivably through a distinct right-left, back nd forth, on and off switching between the two hemipheres, but there are reasons to favor the view (Sperry, 1973) that a smooth integration of the two into a unified process is the more general rule. If so, this would suggest hat the interference obtained intrahemispherically may be a result of competition for the same cellular systems and circuit mechanisms as much as, or more than, incompatibility in organizational dynamics per se. In this same connection, the possible operational advantages of having a single unilateral control center for speech and language (Jones, 1966) should not be overlooked as part of the rationale for hemispheric specialization.

Effects on memory, mental grasp, and well-being

One symptom that has shown up consistently in ordinary behavior following commissurotomy is a pronounced memory impairment (Sperry, 1968a). Especially during the first year and a half after surgery these patients have been notably unable to remember appointments or telephone messages, where they have put things, which cards have been played, how to get back to a parked car, etc. This memory deficit is also combined with a tendency to fill in memory gaps by confabulation. Improvement in the first few years after operation suggested that the memory defect might largely disappear with time, but this has not been the case. Administration of the Wechsler Memory Scale and Benton's Visual Retention Test in patients 4 to 9 years after surgery, and comparisons of these scores with those of the same patients on the WAIS scale and with others published for groups of epileptics indicate a selective memory deficit (Zaidel and Sperry, 1972b). A specific role of the forebrain commissures in mnemonic functions is suggested.

Logically, any memory laid down solely in the right hemisphere would be inaccessible after commissurotomy to verbal recall in patients with typical language dominance. Similarly, any storage, encoding, or retrieval process dependent normally on integration between symbolic functions in the left hemisphere and spatioperceptual mechanisms in the right would also be disrupted by commissurotomy. Neither the patients nor their families on being questioned have noticed or complained about any general loss after the surgery of longterm memory. In some instances, however, subnormal retention for events during the several years preceding the operation is suspected. The absence of any conspicuous loss in old memory could mean that firmly established, frequently used memories become in time sufficiently verbalized in the left hemisphere to make the loss of the right hemispheric component pass unnoticed.

Under testing conditions favoring performance with the right hemisphere, it appears that the minor hemisphere can readily learn and remember such things as spatial relationships and related sorting and assembly tasks. Similarly simple verbal memory seems to be well preserved in the left hemisphere. Thus, processing and laying down of memory within each hemisphere may be little affected as such, implying the general impairment to be a reflection primarily of transactional aspects of interhemispheric integration. The memory impairment as displayed in ordinary unrestricted conditions is tied in part to the problem of the extent to which memory lodged in the minor hemisphere is unable to gain expression in ordinary behavior because of the prevailing left-hemisphere dominance, something about which our information remains scanty. It is interesting that the patients with only partial commissurotomy (as described in the next section) score almost as low on specific memory tests as do those with complete callosal section and during the first 3 to 4 years at least show comparable mnemonic impairments in general behavior.

Studies of bimanual motor coordination (Preilowski, 1972) show the commissurotomy patients to be severely impaired in performing new movements that require interdependent regulation of speed and timing between right and left hands. This is in contrast to habitual long-established bimanual coordinations, like tying neckties or shoelaces, which have been found to survive the surgery with little or no detectable deficit. The contrast between new and old motor coordinations suggests that prolonged use brings a change in the higher control mechanisms such as a shift to lower undivided centers like the cerebellum, or a shift to a cerebral mechanism that governs both contralateral and ipsilateral hands from the same hemisphere.

A postoperative loss in general unrestricted performance of what might be called "mental grasp" is indicated in the patients' consistently low scores after operation on the digit-symbol and arithmetic subtests of the Wechsler Adult Intelligence Scale and on the Verbal and Abstract Reasoning parts of the Differential Aptitude Test. It was evident also in various lateralized tests as for example in the subjects' inability to keep track of more than three patterns perceived sequentially by touch in the Progressive Matrices Test and in Nebes' Circle-Arc Test, and may have been a factor in low performance on the Milner-Taylor (1972) Bent Wire Test. In regard to subnormal scores on any minor hemisphere task, however, one must also rule out interference effects from the dominant hemisphere. This latter and the consequent inability of the minor hemisphere to gain unhampered motor expression under ordinary conditions seem to be responsible in large part for the minor hemisphere syndrome that is typical of the commissurotomy patient.

In addition to measurable data from specific tests, one gets also a general impression from working with these patients over long periods that their overall mental potential is affected by the commissurotomy. Perseverance in tasks that are mentally taxing remains low in most of the patients, as does also the ability to grasp broad, long-term, or distant implications of a situation. With the exception of the youngest patient, their conversation tends to be restricted mainly to what is immediate and simple. Undue repetition of the same information or anecdote is common. There are indications of a tendency to fantasize, and a mild logorrhea seems to be present in some cases. Most of these symptoms, however, have not yet been subjected to specific study, and also most of the patients have substantial extracommissural damage contributing to such effects.

Although the bisected brain may perform certain simple double tasks better than the normal intact brain, under very selected conditions (Gazzaniga, 1970), implications that brain bisection produces an advantageous increase over the normal channel capacity of the brain have not been regarded seriously by most investigators who have worked with these subjects. The great bulk of the evidence continues to support our general impression (Sperry, 1970a) that two hemispheres united are much to be preferred over two hemispheres divided.

It has been noted from the start that the commissurotomy patients, following recovery from the surgery, are inclined to experience an improved sense of well-being and generally do not display particular anxiety about their symptoms even when the testing conditions evoke and force attention to conflicting experiences in left and right hemispheres. Part of this can be attributed to the reduction in medication and in the incidence of seizures, and also to the apparent obliviousness on the part of each hemisphere to the presence and experiences of the other (Sperry, 1968a, b). The following factor may also be involved: Local electrical lesions of the genu of the corpus callosum that interrupt the transcallosal cingulostriate pathways have been used to treat chronic psychiatric symptoms of tension and anxiety and are reported to result in a feeling of well-being and relaxation (Laitinen, 1972). Such lesions would of course be included as part of the fiber transection in the surgery in all of these patients.

Commissurotomy with partial sparing of callosum

In an effort to avoid the more pronounced symptoms now known to result from hemisphere deconnection while at the same time hoping to preserve the therapeutic effect on seizure control, Vogel has sectioned in the last three patients operated only the anterior commissure and front two-thirds of the corpus callosum, sparing the posterior callosum. Study of two of these latter partial commissurotomy patients (Gordon et al., 1971) has shown them to be remarkably free of the basic disconnection symptoms described above that involve cross-integration between the hands, visual half-fields, and the language centers.

One is impressed that a little callosum, at least at its posterior end, goes a long way functionally.

Presumably many functions yet to be delineated are mediated through the sectioned anterior half of the callosum for which proper tests have not yet been found. The partial commissurotomy subjects score almost as poorly as those with complete deconnection on standard memory tests including the Wechsler Memory Scale and the Benton Revised Visual Retention Tests (Zaidel and Sperry, 1972b). Also, in comparison with normal subjects they show definite impairment in the learning of bimanual motor coordinations (Figure 8) that require mutually dependent timing of movements of the two hands (Preilowski, 1972). The initial bimanual motor performance is much better than in the patients with complete callosal section, and early stages of motor learning were found to not be markedly retarded so long as the movement was relatively slow and subject to visual guidance. However, more advanced stages of motor learning that appeared with practice in the normal controls failed to occur in the partial commissurotomy patients. These involved further smoothing and speeding of the hand coordinations and seemed to depend on an advancement from visual to kinesthetic control and a closer integration between the hemispheric control centers for right and left hands.

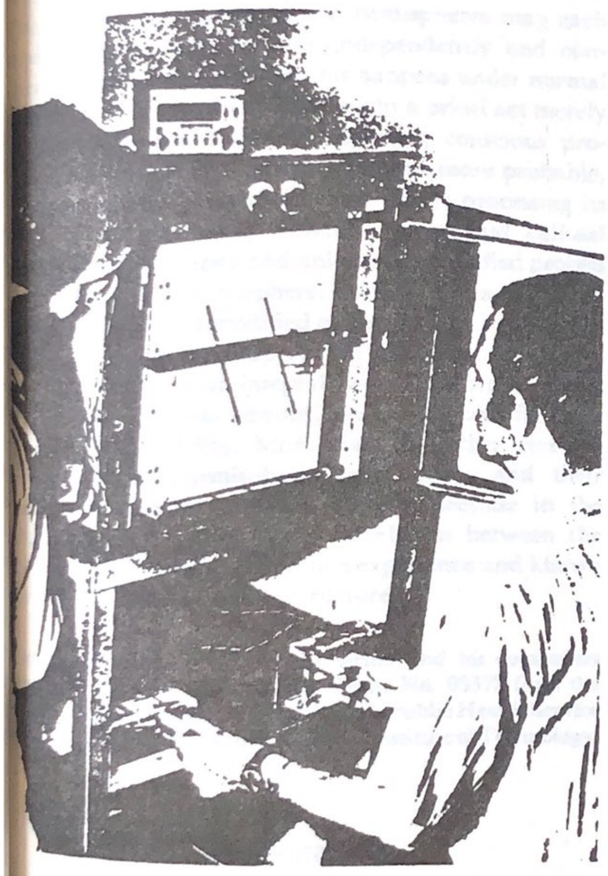


FIGURE 8 Bimanual motor task of Preilowski (1972) impaired in subjects with partial commissurotomy. Cranking speed for left and right handles is mutually interdependent.

Replication and interaction at conscious levels

The general observation that hemisphere deconnection creates two distinct left and right realms of conscious experience leaves unexplained many details regarding the extent and nature of this separation. Bilateral sensory representation like that for the face and for other axial structures, along with crude sensibility even in the extremities, makes for a large common denominator of identical experience in right and left hemispheres (Sperry, 1968a). There also is strong bilateral projection in the auditory pathways and in the proprioceptive system for movement and position sense (McKloskey, 1973). Even in the visual system bilateral projections have recently been described that involve pathways through the superior colliculus, pulvinar, and inferior temporal area (see Graybiel, this volume). The latter would in effect bring the ipsilateral half-field of vision into each hemisphere along with the main contralateral representation transmitted through the geniculostriate system. The more robust geniculate half-field is favored by attentional and other factors that seem to suppress actively the second system most of the time. Under the right conditions, however, it seems the subordinate half-field may be perceived and integrated with the main contralateral activity (Trevarthen, 1970).

Attentional reversals are seen on exceptional occasions that bring the subordinate half-field of vision or the subordinate hand into focus, while at the same time suppressing the usually dominant contralateral system to the point where the subject can talk about objects in the left visual half-field of vision but not in the right (Trevarthen and Sperry, 1973) or can perform linguistic operations like spelling with the left hand but not with the right (Preilowski and Sperry, 1972). To what extent these may involve shifts of attention between hemispheres as well as between subsystems within the same hemispheres is not clear. With reference to the latter, it would appear that the ipsilateral and contralateral systems within the same hemisphere tend to be used quite separately in these kinds of situations with active attention to one switching off the other.

The large common overlap of identical experience within the hemispheres that results from bilateral sensory projection and other factors described above represents a complicating and misleading element in descriptions of conscious mental or functional unity in the bisected brain. Though the experience within each hemisphere is presumed to be cut off from its identical counterpart in the other, the demonstration of this duplication must rest always on extrapolation from experiences that are not identical but in some way differ in the two hemispheres. Further, with respect to those facets of conscious experience that remain unified, it is not now possible to determine how much of such conscious unity is a result of the foregoing bilateral representation within each hemisphere and how much alternatively may come from representation at lower undivided neural levels like the brain stem and cerebellum.

The fact that surgical section of the forebrain commissures produces such a profound left-right separation in conscious awareness would seem to indicate that conscious experience is not centered in the mesencephalon, cerebellum, or other lower structures. It tells us further that the mediating cerebral mechanisms are in principle restricted and localizable and may in time be identified. The fact that the two separated hemispheres may each mediate conscious experience independently and concurrently does not mean that this happens under normal conditions. The intact callosum might a priori act merely to harmonize and complete duplicate conscious processes, one in each hemisphere. It seems more probable, however, especially with each hemisphere processing its input in fundamentally different ways, that callosal excitation serves to span and unite a single unified process with parts in each hemisphere. Out of these and related concerns has come a modified concept of the mind-brain relation in which the properties of subjective experience are conceived to be an integral part of the brain process and to play a causal control role in cerebral function (Sperry, 1969, 1970b). More than any other cerebral system, the interhemispheric commissures and their cortical associations continue to offer promise in the search for an eventual direct correlation between the phenomena of complex subjective experience and known variables in specified neural structures.

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