Changing Views of the Corpus Callosum

- - - - - - - on the functions of the c.c.

RW Sperry

Division of Biology
Calif. Inst. of Tech
Pasadena
Calif.

The literature on the corpus callosum prior to the middle 1930's contained contradictions and inconsistencies that added up to a major puzzle. (summarized in Kraemer,) In particular, the reported absence of any definite functional impairments in a number of cases of complete agenesis and surgical section that had been recorded and general doubt as to whether any of the functions implicated in other studies of these could be reliably ascribed to the callosum, all of which was most difficult to reconcile with the huge size and strategic position of the corpus callosum great cerebral commissure.

The most extensive study of the effects of surgical section in the human brain was that of Van Wagenen, Akelaitis, and A. J. Smith

in the late '30s
involving a series of some
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~~in which with~~ in which complete and
partial sections of the corpus
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also notable

The brain by virtue of its development and evolution is naturally divided into fairly distinct ~~and separate~~ right and left halves. Particular the higher cerebral levels the r & l hemispheres are

Dr. Sperry - rough draft

Introduction: the Riddle of the Corpus Callosum

RECENT DEVELOPMENTS IN STUDIES OF BRAIN BISECTION

~~A good way to ease into this material is to turn back some~~ About 25 years ago ~~now to~~ in upstate New York ~~where~~ some two dozen ~~persons afflicted with epilepsy~~ epileptic patients underwent surgery of the brain that consisted essentially of disconnecting the right from the left hemisphere, ~~but~~ by cutting the corpus callosum, and in a few cases also the anterior commissure. ~~the~~ It was hope ~~being~~ that this might help prevent the spread of siezures from one to the other side of the body and might also ~~help~~ enable these epileptics ~~perhaps~~ to retain consciousness during their attacks, at least in one hemisphere. ~~The first slide will serve merely to refresh your memories regarding the~~ As is evident in Figure 1 the corpus callosum general size and relations of the corpus callosum ~~in the human brain.~~ It is the largest by far of all the fiber tracts in the brain; ~~practically all parts of the cerebral cortices being~~ Nearly all cortical regions of the two hemispheres are cross-connected through this largest of the commissures.

Never before nor since has section of the callosum been carried out on so massive a scale in human ~~subjects~~ patients. This series of cases is also notable for the rather extensive battery of neurological and psychological tests that was applied before as well as after the surgery ~~, in some cases,~~ in the hope of pinpointing some of the functions mediated by the corpus callosum. Already at this time the callosum had become something of a puzzle, and was well on its way to gaining the reputation of being the "largest, most useless" structure in the brain. The results, insofar as controlling the epilepsy were concerned, were only mildly successful, not enough so, apparently, to warrant continuation of this major surgery for this purpose. The results with respect to detecting functional deficits attributable to the corpus callosum were practically zero. The end effect of the series of reports to come out of these studies was only to further accentuate the already present discrepancy between the large size and apparent importance of the "great cerebral commissure" and the lack of any definite functional deficit following its complete surgical section. Experimental section of corpus callosum in monkeys also failed to produce detectable behavioral impairment.

The situation in 1940 was summed up by Warren McCulloch in his now well known statement, "The only demonstrated function for the corpus callosum seems to be that it aids in the transmission of epileptic siezures from one to the other side of the body." and he still asserts that this statement was not made lightly. During the next ten years there was little change, and as recently as 1951, K.S. Lashley, probably the world's most eminent neuropsychologist, was still referring to his own little joke about the corpus callosum, namely that as far as he could judge from the literature, at this time, it would seem to him that the functions of the callosum must be mostly mechanical, its main purpose being, that is, to keep the hemispheres from sagging.

Although these findings, or rather the lack thereof, on the callosum came to be cited with some satisfaction by certain deviant schools of brain theory, for most of us working on the brain, however, they represented for many years one of the more puzzling enigmas of brain function. This, then, is the general background that prompted us to look into the problem experimentally, beginning back about 1950. We still, at the present time, are heavily involved in various ramifications and developments that have come out of it.

Today, as many of you know, the old riddle of the corpus callosum is no longer what it used to be, in that it has been possible, in a series of animal experiments in recent years, to demonstrate definite and important functions for this structure. The animal studies from the beginning have confirmed the older observations to the extent that complete section of the callosum produces surprisingly little, or no disturbance, insofar as generalized behavior is concerned. In a sense it is still correct to say that the most remarkable effect of cutting the corpus callosum is the lack of effect. Even when additional cerebral commissures are sectioned along with the callosum, including all the cross connections that above the tegmentum, that is all those labeled in the next slide. Cats and monkeys recovering from the surgery, display amazingly little in the way of evident behavioral defects under most ordinary conditions.

Only when one begins testing specifically for right-left cross integration in cerebral function, cerebral functions that either naturally or as a result of training are strongly lateralized, does the loss of the cerebral commissures seem to make a real difference.

To review briefly first the animal findings bearing on the functions of the callosum. One of the earliest and more consistently demonstrated functions relates to the interhemispheric transfer of learning and memory effects. In short, if you train a cat or monkey to perform a tactile or motor problem using only one hand or forepaw exclusively, then after it has fully learned, test the ability of the animal to perform the same problem with the opposite hand or paw, you find that the training transfers at a high level if in the normal animal with callosum intact, but fails to transfer in the callosum-sectioned animal. When the callosum-sectioned animal is switched to the second paw it has to relearn all over again.

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Functions of the corpus callosum demonstrated in these animal experiments in animal experiments to date: ~~To review briefly first the animal findings bearing on the functions of the callosum.~~ One of the earliest and more consistently demonstrated functions of the callosum relates to the interhemispheric transfer of learning and memory effects. In short, if you train a cat or monkey to perform a tactile or motor problem using only one hand or forepaw exclusively, then after it has fully learned, test the ability of the animal to perform the same problem with the opposite hand or paw, you find that the training transfers at a high level ~~if~~ in the normal animal with callosum intact, but fails to transfer in the callosum-sectioned animal. When the callosum-sectioned animal is switched to the second paw it generally has to relearn the problem all over again.

The same kind of thing is true of the learning and retention of visual discriminations when the visual inflow is restricted to one hemisphere by ~~monocular~~ training through one eye after ~~and~~ section of the crossed optic fibers in the chiasm. (As diagrammed in the next figure, chiasm section leaves the animal with practically a full visual field, but ~~[illegible]~~ stereoscopic overlap is eliminated, and of course each eye is left connected only to the homolateral side of the brain.)

Under these conditions, visual discriminations learned by cats and monkeys through one eye could not be remembered through the other eye in the absence of the corpus callosum. On the other hand, this interocular transfer of cortical learning presented no problem if the callosum were intact, or, ~~-~~ in fact, if just the posterior third ~~quarter~~ of the callosum, which connecting ~~connects~~ the visual areas ~~of the cortex~~ were preserved.

By further analysis it has been shown that the callosum may function in two rather different ways, in affecting such intermanual and interocular transfer. First, it may be used during the ~~n~~ initial learning for the laying down of a second or duplicate memory system in the opposite hemisphere. This is demonstrated by training with the callosum intact and then ablating the cortex of the trained hemisphere, in which case, the second eye or hand can still perform the problem by ~~through~~ using the second memory system in the opposite hemisphere. Alternatively the memory with callosum intact may be laid down only in the directly trained hemisphere during initial learning. In this ~~which~~ case, when the animal is forced to work through the untrained hemisphere the ~~corpus~~ callosum may be used to tap ~~[illegible]~~ the memory file of the educated trained hemisphere. ~~This kind of thing~~ We ~~presume~~ presume this must ~~to~~ occur in the human brain on a major scale where language is all laid down in the one dominant, or major, hemisphere.

The effect is demonstrated in animals by training one hemisphere with the callosum intact and showing ~~the~~ that the second eye or hand can perform the problem also, but only so long as the callosum is intact. After its section the animal performs only through the initially trained hemisphere.

Various methods have been used in these studies to restrict vision to one eye: The animal may be trained to wear an eyepatch as shown in the next figure, or one may sew the eyelids together, and later ~~then~~ release them, or the animal may be trained ~~forced~~ to work through peepholes accessible only to one or the other eye, or the animal may be trained to wear goggles as shown in the next figure, or, instead of goggles one may use corneal contact lenses. In these lenses, goggles, peepholes and the like, it is possible to incorporate light filters, polarizing or ~~inter~~ interference filters that are mutually exclusive for the two eyes. Then, by manipulating the ambient lighting or the light for the projection of the stimulus figures, one can, with a flick of a switch or push of a button, bring in one hemisphere or the other at will. The testing apparatus which we are currently using for monkeys, and by which we can control the use of the eyes or the hands, or hard to attain, all possible eye-hand combinations is shown in the next figure.

By the use of training and testing methods of this sort it has now been possible to show that the callosum ~~also is important~~ in the monkey at least is important for the right-left cross integration involved in a variety of other cerebral activities; for example, the voluntary visual control or monitoring of hand movements across the vertical mid-plane of the focussed visual field. Though possible in the absence of the callosum, it is markedly aided by its presence. Recall that the right hand, and the right half of the visual field are projected together into one hemisphere, and the left hand and the left half of the visual field in to the opposite hemisphere. Visual-motor coordination that for the hand governed from the side still receiving vision.

draws on the visual center of one cortex, the motor center of the opposite hemisphere is much stronger, quicker and precise when the callosum is present.

If learning is lateralized to one hemisphere by training through one eye or one hand, the motor expression of such a lateralized performance effected via the limb governed from the opposite hemisphere is significantly facilitated by the callosum, and definitely impaired by its section.

Experiments that are still in progress show that the cross-comparison and discrimination of objects or stimuli presented in the separate halves of the visual field goes readily in the presence of the callosum, but only with great difficulty and at a simple level in its absence. For example, a chiasm-sectioned monkey can be trained to select the larger of any two circles taken from a series of five different sizes, so that he can do it easily with either eye alone, or with both open. If then one separates the inputs by means of the light-filtering system so that one circle is projected to one hemisphere and the other to the other, the performance breaks down and is relearned only with great difficulty. The same is true in matching-from-sample problems where the correct one of two patterns placed side by side is determined by a sample placed immediately above. The performance goes well in a chiasm-sectioned monkey so long as the entire problem can be seen through one eye, but when the sample is deliberately projected to one hemisphere and the two patterns to be discriminated to the other hemisphere, then the problem breaks down. Similar results have been obtained for conditional visual problems. If the chiasm-sectioned monkey is working at a task that involves intensive use of one hand, paired with the visual half-field of the same hemisphere, its capacity to perceive and to harmonize sensory information entering the opposite hemisphere is greatly reduced by commissurotomy. These and related observations indicate that the callosum also is used to bilateralize and to unify attention and perceptual awareness.

It follows logically from some of the foregoing that the learning process is speeded by the presence and retarded by the absence of the callosum in any situation where the sensory cues involved are projected partly to one hemisphere and partly to the other, and perhaps also where the motor control must come partly from one and partly from the other hemisphere.

Finally, the post-surgical convulsions that we see during the first three weeks or so after surgery in a minority of our commissurotomized monkeys, show a tendency to remain lateralized, which supports the conclusion that the callosum does aid in the transmission of epileptic siezures.

During the past ten months we have had an opportunity to check for some of these functions in a human patient with recent complete section of the corpus callosum plus the anterior commissure plus the hippocampal commissure -- thanks to Drs. Vogel and Bogen of the Loma Linda Neurosurgical unit in Los Angeles. The surgery was undertaken as a known risk by all concerned, on a nothing-left-to-lose last resort kind of basis for a man that for ten years had suffered from severe intractable major convulsions, on an average of one to two per week, that culminated in status epilepticus every two or three months. It is too early, of course, to predict the results three years from now, but the surgery was performed last February and this person has not had a major siezure since. There have been a few, but no more than a half-dozen or so minor episodes confined to one side and mostly without loss of consciousness. These are considered inconsequential compared to the kind of siezures he was having previously, and his sedative drug dosage has been reduced now to one-third what it was prior to surgery. In short, omit everyone concerned is tremendously pleased with the outcome therapeutically to this date, and the results suggest at least some reopening of our minds to this kind of surgery for such cases.

Most of the functional testing that I'll describe has been carried out (the psychobiology lab at Caltech and in the patient's home) in weekly sessions at ~~the laboratory~~ by Mike Gazzaniga with Dr. Bogen in collaboration, and myself serving ~~only~~ mostly in an advisory ~~or~~ and consultant capacity.

Disconnection of the hemispheres in this person has not produced ~~a gross disruption of generalized behavior, nor~~ any overall personality or intellectual deterioration, nor ~~has he complained of splitting headache.~~ gross disturbances in general behavior. In a casual meeting ~~with this person~~ over a cup of coffee and a cigarette and a conversation ~~regarding~~ on the Telstar or the ~~Cuban~~ Medicare situation (he's a man of 48 or so and above average intelligence), one might ~~not~~ easily fail to note any particular functional impairments. However, with specific tests for right-left cross integration in the same spheres of activity in which the split-brain animals have been found defective, one can show that this patient behaves indeed as if he had a right half brain and a left half brain, and the two ~~brains~~ had been separated. Nearly all the callosal functions demonstrated in the animal studies, plus perhaps a couple of new ones have now been documented in this person.

In addition to section of the corpus callosum, the anterior commissure and the ~~soltorium (sp.?), the plan was to cut also~~ psalterium during the operation the massa intermedia ~~but at the time of operation~~ it was judged that this ~~structure~~ was already ~~absent~~ separated which is not uncommon of course in the human brain. ~~So~~ The only structures left for cross integration in this person are those below the dotted line in the next figure. It should be remembered that the optic chiasm was not cut here as ~~it was~~ in most of the animal ~~experiments~~ work, so the testing of vision is not an eye-to-eye

~~proposition~~ problem, but rather a matter of testing the ~~a~~ left half visual field ~~to~~ against the right half-field. ~~matter.~~ This is done by having the person fixate on a point and presenting the material ~~then~~ to the left or to the right of the point, usually with an exposure of 1/10 to 1/100 sec to prevent his use of eye movements to get the material into a different part of the retina. ~~using a tachistoscope. This is an apparatus with a mechanical shutter in it that permits quick flash presentation of material at a 1/10xxxx1/100 tenth, a hundredth and so on per second, much like the shutter of a camera.~~ It is also worth mentioning here ~~before going further~~ that whereas in the animals work we have to go to a great deal of training and ~~memxand~~ trouble to lateralize learning, ~~and~~ memory and other functions to one hemisphere, in the human brain the lateralization of learning and memory is already there in ~~the~~ highly developed form just waiting to be tested in that everything associated with language is laid down in the one major hemisphere.

In line with this, one soon finds in applying tests involving language that this mans acts as if he had one literate hemisphere connected to the right side of the body and the right half of the visual field, and another ~~very~~ illiterate hemisphere connected to the left side of the body and the left half of the visual field. Performances involving the one are for the most part roughly normal; ~~whereas~~ those ~~xxxx~~ involving the other are ~~extremely~~ definitely retarded. For example, he is unable to read any material ~~presented~~ that falls in the left half of the visual field; he is unable to write anything meaningful with his left hand or left foot even crudely. He is unable to execute verbal commands with the left hand or leg; this last difficulty is not ~~as~~ so severe as it was initially after surgery and is beginning to clear gradually but it is still pronounced. He is unable to give a verbal description of objects presented in the left half of the visual field, or of objects placed in the left hand ~~with~~ when he is wearing a blindfold. ~~on~~. Also, if he is blindfolded he is unable to ~~tell you~~ say where he has been touched or tapped on the left side of the body, on the left leg or left arm. He is unable to tell the position of the left elbow, the wrist or ~~xixxxx~~ fingers, whether they are flexed or straight, rotated ~~xx~~ and so on. He

The moment the glasses or cigarette touch his face he knows what these objects are in his speech hemisphere but until then he is completely unable to tell what the objects are in his left hand

is unable to describe movements or acts carried out by the left hand, in the absence of vision, and sometimes also even in the presence of vision which I'll go into more later on.

There were no problems of this kind before surgery. Furthermore, with non-verbal tests one can show that he still sees and feels and has good motor function on the left side, or in other words, in the minor right hemisphere. For example, in blindfold tests, if one places a cigarette in his left hand he will move it around, and rather quickly place it between his fingers and raise it to his lips in the proper position. If one puts his eye glasses in the left hand, these too will be manipulated and soon are brought up properly by one temple to the eyes. A toy pistol is moved around in the hand and then is raised, aimed and the trigger cocked in a typical pistol fashion. A ring is moved, rubbed, pressed and twisted and finally run down over the ring finger into correct position.

These and similar differential, refined, and selectively appropriate, manipulatory movements show that the sensory and the motor pathways and the cortical centers of the left hand are still in good functional condition. It's only that when he has to reply via the language hemisphere that you find that this major hemisphere no longer is in contact with or knows or remembers anything of the experiences and activities of the other, the minor, hemisphere connected to the left side.

This lack of interhemispheric contact applies also of course in the opposite direction, but it is not so easy to find out what the illiterate hemisphere knows, sees or feels, since it lacks language. One has to resort to non-language, more behavioristic types of testing.

In such tests also the mental duplicity produced by the surgery in this individual is clearly evident, for example, in tests of cutaneous localization in which the subject tries to point with his finger to a spot on the body surface which the experimenter has just touched with the tip of a pencil or a small stylus, On the right side he may know with his major hemisphere what spot was touched, but he still is unable to control the left hand sufficiently with that hemisphere to bring it to the correct point.

With the left hand he is able to ~~locates~~ locate readily all points on the left half of the body, and with the right hand similarly all points on the right half of the body ~~, but he fails when~~ However the cross-localization of points across the midline is impossible with either hand. ~~is required across the midline.~~ ~~The axxxxxxxxxxxxx~~ On the left side localization then breaks down ~~completely~~ and he usually often can't tell whether it's his left leg or ~~his~~ the arm that has been touched, or even whether he's been touched at all. ~~He~~ The ~~exception here is the~~ head and ~~neck where~~ face represent an exception to the foregoing. Here, he ~~he~~ has no trouble localizing with either hand on both sides. This fits with the anatomical and physiological evidence that the ascending pathways of the cranial ~~trigeminal~~ nerves involved project from each side ~~are projected bilaterally~~ into both hemispheres.

Similar localization tests involving vision can be carried out by having ~~In the visual testing of retinolocal sign, where~~ the subject ~~sits~~ sit in front of a screen and point with his hand and arm at a spot of light flashed ~~projected briefly~~ on the screen in front of him. Given ~~with~~ free use of either hand ~~he~~ he uses the right hand always to point to the light spot when it falls in the right half of the visual field, and the left hand is used for all points in the left half of the visual field. If he's forced to use one hand, then he nearly always misses the light when it falls in the opposite ~~wrong~~ half of the visual field, not only the position of the light, but he is ~~he is~~ often unaware that the light ~~it has~~ appeared at all.

In another test the subject is seated ~~If he is sitting~~ at a table and ~~you tap~~ Unbeknownst to him ... out of sight under the table his foot is tapped one to four times and he is instructed ~~ask him~~ to tap with the hand the corresponding number of times on the table this goes fine from the right foot to the right hand, and then from the left foot to the left hand, but he is unable to do it across from the left foot to the right hand or vice versa.

~~If you test the~~ Joint and ~~in~~ position sense can be tested by putting, for example, the end of a pencil in one hand and having him hold it at different angles and positions with the one hand ~~and different degrees of rotation, then ask him to~~ while reaching across ~~and pick~~ for the other end of the pencil with the opposite hand. ~~you find~~ He's quite unable to do this, so it's not just that the right hand (in this man) knoweth not what the left hand doeth, but his one hand doesn't [illegible] even know where his other hand is.

With simple jigsaw puzzle tests consisting only of two large pieces that fit together he can be taught to put them together with the left hand or with the right hand, but if you then put one piece in each hand he's unable to work the two together. With further trials on this, however, he ~~simply~~ found that if he simply kept one piece still and worked around attending to one hand only, he was able eventually to get the two to fit. It would appear from this and other observatinns that he is unable to attend in the two hemispheres at the same time.

The learning and memory of simple tactile discriminatinns, such as which of two containers has a sip of milkshake in it, the rough or the smooth, the large or the small, the warm or the cool, and so on, ~~when learned~~ with one hand ~~the learning fixed~~ failed to transfer to the other hand. Of course this takes only a few trials in the case of the ~~human brain. Gazzaniga~~ described persistent preferences of the left illiterate hand, that is it will persistently pick smooth, rather than the rough, and then after a while it may shift around and pick the rough instead of the smooth, regardless of which one is correct, and one wonders what's going on in this other brain, this other mind, what it's thinking to make it select this or that at different times.

Usually the left hand cooperates with the right in general motor activity, but not always. Occasionally the left hand will go off ~~into~~ independent, even antagonistic movements of its own. We ~~don't~~ see this ~~except~~ rarely in the laboratory. ~~The~~ accounts of it ~~[illegible]~~ from home, ~~but in many cases they have~~ occurred on a scale sufficient to be bothersome ~~and such that he will complain of them, so we don't question their existence~~. For example, he will pick up the evening newspaper with the right hand, ~~start walking off with it~~, transfer it to the left, which ~~the left going by some furniture~~ promptly puts it down again and He has to turn around, pick it up again with the right hand. ~~and go on~~. Or, he has some ~~s got a~~ fresh laundry ~~some~~ in each hand, walking back through the house to ~~pxxx~~ put it away, where the left hand ~~out of the left half of his field he sees a waste basket, as he goes by~~ he dumps to load ~~the fresh laundry~~ into a ~~the~~ waste basket, along the way and he then has to come back later and gather ~~pick~~ it up again. Or, he's tying the belt of his robe, the left hand works along with the right fine and he gets the belt tied, and then he goes off about his business to other things with the main hemisphere, but the left hand doesn't seem to know when to quit and it proceeds to methodically carry through and untie the belt again. He has to go back and tie it over again. Occasionally in dressing, usually his left hand will work along with the right, but at times the left seems toforget whether he's pulling his trousers ~~up~~ on or taking them off, and we find him pulling them up with the right hand and trying to take them off with the left, and vice versa. In the early month after surgery he and his wife used to refer to his sinister left hand, she would be attending to him and her attentions were welcomed on the one side, but his left hand would start getting very aggressive and pushing her away with apparent displeasure that didn't seem to be felt at all in his major hemisphere. Such indications, however, of the separation of emotion on the two sides are relatively rare. Sometimes he deliberately puts ~~He's acquired the habit of putting~~ his left hand into his pocket in order to keep it out of mischief. It has a tendency to grab doorknobs, or hold the door frame, the door-jamb, as he is trying to get through, and hold him up. I doubt if this patient himself would want to trust his left hand with a loaded pistol. I asked Gazzaniga about this last night or the day before and he said, "Boy, he wouldn't want to be in the same room." Fortunately the question has not yet arisen as to who or what is liable for criminal acts committed by the left hand, which as you can see at times tends to be a rather irresponsible part of the whole.

We've also seen this kind of thing: he's working a visual discrimination problem with the left hand that involves picking up ~~xxxxxf~~ the correct one of ~~two~~ several cards~~, the card with the correct pattern on it~~ marked with different patterns. ~~He goes along, and eventually rather quickly~~ By trial and error he soon learns which is the correct ~~of the two cards, and after~~ rewarded card. After a successful run of five or so and he has put down the last card, ~~you s top him and ask him~~ he is interrupted and asked which one is the correctcard, or which is the card that he just ~~picked up~~ put down. He ~~may~~ react with a startled, blank and slightly guilty expression as though caught by surprise, and he's unable to ~~answer~~ say, i.e., he doesn't know (with the speech hemisphere) which card ~~was~~ is correct, ~~which one he picked up, althoughhe was right there with both eyes open watching the whole procedure.~~ It's as if in working with the left hand he had been working ~~xx~~ only with the minor, the illiterate hemisphere, ~~and~~ while the major hemisphere meantime, though watching, just wasn't seeing or perceiving what was going on. ~~there, wasn't with it--it was blanked out, or inhibited.~~ ¶ Similar episodes suggest an unnatural separation and lateralization of the brain processes of perceptual ~~xxxxxxxx~~ awareness ~~and a draining off xx of the perceptual tension and awareness processes~~ as if the processes of attention and perception were concentrated to one hemisphere, leaving the other ~~one~~ blanked out. ~~or inhibited.~~ This ~~is the case,~~ would seem to apply especially ~~in~~ to one-handed activities or activities involving language. This latter, and a number of the functions of the callosum seem to become ~~more~~ increasingly important as one ascends the phylogenetic scale from cats to man. ~~We~~ Phenomena that we see ~~them~~ in the monkey ~~they~~ are more pronounced in this human ~~case~~ subject, and ~~xxxxxxxx~~ were not seen at all in the earlier cat experiments.

An extreme example of the above phenomenon occurred on one occasion at which he reports scalding his left hand rather badly while he was shaving with the right hand, and of course attending very carefully to what the hand was

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doing, and using probably the corresponding half of the visual field primarily. When he's working with his left hand, however, it readily discriminates warm from cool, and it is very quickly drawn back from a heated surface. This raises the possibility that the left side may be protected from pain, perhaps intractable pain, by switching in attention to the other hemisphere.

It's probably worth re-emphasizing at this point that excepting for the independent movements of the left hand just mentioned, the great bulk of the impairments described do not show up in the daily living activities of One has to blindfold him, or one has to use a tachistoscopic projection of the visual material, and so on. With respect to those impairments that are bothersome, we suspect that many of them may be subject to an improved control as we learn more about the properties of the split brain, and are able to teach him how to switch in one or the other hemisphere and so on.

The observations in this patient appear in our own minds at least to have pretty well removed the discrepancy that has existed between the human and the animal data regarding section of the callosum. From the combined evidence that is now available, it would seem that one can begin to put together a working picture of the great cerebral commissure that is much less mystifying and more reassuring, that the fiber connections of the brain, even at the highest level, do have real and understandable functions. There remain, of course, many interesting unknowns regarding the callosum and its function awaiting more detailed analysis. Meantime, however, the interests of our laboratory group for some years have been centered less on the callosum and its functions per se, than on the kinds of things that one can do experimentally in its absence, that is the kinds of things that one can do by using the split-brain or the bisected brain as an experimental preparation for approaching problems of cerebral organization in general. In the time that is left I shall try to give a few quick glimpses of some of the kinds of things that we have been using the split-brain preparation for experimentally. When one starts to consider ~~using~~ the split brain as a tool or method, then the problems involved begin to spread all over the neurological map, and ~~of course~~ the discussion becomes even less coherent. And let me emphasize at this point that the work that I've been discussing so far, as well as the following, has been very much a group effort, and has been carried out in large part by graduate students and research fellow associates.

It is clear from ~~what I have been saying~~ the foregoing that the anatomical splitting of the brain results in a considerable doubling of its ~~s~~ mental and psychic properties. ~~In the long view,~~ The bisected brain, that is, ~~it~~ has two ~~memory chains, it perceives on one side, and what it perceives on one side cannot be detected, is out of touch with what is going on on the other side, and so on.~~ separate sensing, perceiving & learning systems each with its own memory chain and each largely inaccessible to the other except by indirect means. It's also clear that there is a lot of alternation and switching back and forth from one to the other of these doubled gnostic spheres and control systems. It is still not clear whether it is physiologically possible to have within the single cranial vault two separate spheres of consciousness, doing different things, having different experiences simultaneously. There is, however, ~~this~~ suggestive evidence ~~that indicates~~ indicating that this may be ~~the case~~ possible from some experiments carried out in recent years by Trevarthen. The experimental apparatus is diagrammed in the next ~~slide~~ figure. Essentially the monkey is working an automat for his meal. If he pushes the correct one of the two small plaques in front of him he is rewarded by a peanut, a dehydrated banana pill, or some other primate tidbit. A top view of the set up (and how it works) is diagrammed in the next slide. Two sets of patterns from two projectors are shown on top of each other on the plastic screen. The naked eye sees the combined doubled figures, however, ~~but because~~ the patterns are projected with polarized light, and ~~putting~~ another polarizing filter in front of ~~the~~ each eye ~~at the vertical or horizontal orientation~~ occludes the image from one or the other projector. The right-left position of the filters ~~varying on a suitable random schedule.~~ in front of the projectors is changed on a prearranged pseudorandom schedule.

The monkey reaches out and pushes one or another of the screens and discovers on a trial-and-error basis that only one of the patterns is consistently rewarded and the other mildly punished regardless of its right-left position. Thus, one eye and hemisphere discover that the circle is to be pushed and the cross avoided, while the other eye and hemisphere watching the very same process, see that the cross should be pushed and the circle avoided. Learning is allowed to proceed with both eyes working until the learning curve reaches the 90-percent level. The eyes are then tested individually to find out if the learning has occurred in one or in both half-brains.

The tendency is for one hemisphere to lead in the learning with the other knowing its problem only partially or not at all. However, in a minority of cases it has been found that each hemisphere has fully learned its own problem. This suggests that the two separated hemispheres may be able to ~~work simultaneously in parallel to~~ perceive, learn, and remember in parallel while performing two mutually contradictory tasks. It would seem to follow that these split-brain monkeys are able to see two different things at the same place in space at the same time.

The possibility that they were alternating rapidly from one to the other hemisphere instead of working both simultaneously has yet to be checked. We find in this connection that when the stimuli are exposed at 1/10 of a second to one or the other eye on a pseudo-random schedule that neither eye is caught napping. This shows, at least, that both hemispheres can be simultaneously ready to perceive.

The feasibility of dividing the brain anatomically into two separated half-brains each with practically a full set of cerebral controls and each capable of carrying on most of the higher functions of the brain, has opened many new possibilities for experimental analysis of cerebral function. Many of these have already been spelled out in recent reviews. To avoid repetition material already familiar to a sizeable minority present, ~~I shall try in the following to run quickly over some of the developments that~~ the ffg is confined largely to some of the more recent developments.

One frequently wonders how far down it would be feasible to split the brain without producing severe incapacitation. As yet we have not tested the extreme limits. The deepest bisections to date were used by Dr. Voneida in studies, aimed at dissecting out the cerebral centers and pathways of the cat brain involved in the formation of a conditioned response. The brain was completely divided in a single operation down ~~through~~ part the midbrain ~~through~~ the rostral third or half of the pons as indicated in the figure. Although the animals required special care and hand feeding for about 10 days, they subsequently achieved excellent recovery until at 12 months the only characteristic by which they were readily distinguished was a mild ataxia attributable to interruption of the main fiber connections from the cerebellum. For unexplained reasons this deep bisection left the animals blind for about 6 weeks after which they recovered fairly good vision. The functional capacities of these deeply divided brains with respect to perception, learning, memory, and other cerebral activities has yet to be tested.

In monkeys we routinely divide the brain in a single operation down through the quadrigeminal plate of the midbrain and through the rostral tip of the tegmentum. ~~leaving [illegible]~~

Th ~~[illegible]~~ for brainstem integration

Bisection of the cerebellum can be added to the above in a separate operation, leaving for cross-integration only the upper lower portion of the brain stem illustrated in the figure.

Deep bisection of this kind has been used in a project involving adaptation to optic prisms that deflect the whole visual field sideways some 15° (Fig. X) When the prisms are first worn the monkey is off target by 15° when he reaches for small objects such as a peanut, grape, or raisin. As seen in the figure, the hand movement is hidden from sight except for its end-result to prevent ~~correction~~ visual correction en route. In time the monkey adapts to the prism effect and his reaching movements are thereafter accurately on target.

If this adaptation is achieved through the use of one hand only, it fails to transfer to the opposite hand in either normal or split-brain monkeys or in normal human subjects; the process has to be repeated with the other hand, indicating a rather localized one-sided adjustment in the motor sphere. If the prism adaptation occurs through the use of 1 eye in the split brain monkey will transfer to the other eye also fail? The somewhat surprising answer is 'no' according to Hamilton and Bossom, it transfers 100%. Furthermore this is true when the midbrain commissures are also sectioned and even when bisection of cerebellum is added. Where the visual inflow from either side engages the lateralized motor adjustment is a still a problem under these conditions.

Further surgical analysis is aimed at learning more about the brain centers and pathways involved.

one now tests for transfer from one to the other hand, this intermanual transfer fails completely. In fact, for reasons not entirely understood, the intermanual transfer of this type of visuomotor adjustment fails to transfer even in the normal monkey or human subject. Further surgical analysis is aimed at learning more about the brain centers and pathways involved.

One of the principal advantages inherent in the split brain approach is the more extensive cerebral surgery that it makes possible. The cat or monkey can get along quite well after complete removal of an entire hemisphere. Therefore if one disconnects the two hemispheres, preserving one of them for the animal, there is no limit functionally to the extent of the surgery that can be carried out on the other side for the investigation of any specific functions experimentally restricted to that side.

Figure X illustrates the various cerebral structures that it has been possible to remove in combination without destroying the ability to use the hemispheres to perceive, learn, and remember tactile discriminations. The immediate aim is to determine the minimum critical essentials in cerebral machinery required for perceptual or discriminative learning.

insert ⊗ here

In this and related studies and also in the somewhat similar approach to conditioned reflex learning we have been impressed by the fundamental (and relatively unexpected) role played by the sensori-motor somatic area of the cerebral cortex, an area that had been pretty well written off in earlier attempts to localize the engrams of learning. It seems to be critically involved even in vision. The devious cerebral routes by which the split brain cat with different patterns of cerebral lesions can still perform a conditioned foreleg withdrawal to a flashing light stimulus supports the view that conditioning does not involve the formation of new nerve connections between the stimulus and response centers of the brain. Deflection of the stimulus into new response channels is attributed instead to the selective opening of the response pathways by the arousal of transient patterns of cerebral facilitation.

Survival of learning and memory

The removal of the hippocampus in the foregoing is of special interest. Bilateral loss of this structure in man has been found to eliminate all recent memory, though long-fixed memories of earlier life remain. Such persons are unable to recall from one hour to the next what they've been doing, can't find their way home if they have moved to a new address since the brain damage and will page through the pictures of a magazine over and over again without recognizing they've ever seen them before. 'Any new learning is of course, pretty well excluded.

Similar effects have not been seen in animals and it appears that experimental studies of the hippocampus must be directed at the precursor function out of which its role in man has evolved. Removal of the hippocampus from one hemisphere of the split brain cat leaves the animal capable of ordinary learning with either hemisphere but reversal learning failed on the side of the hippocampal-ectomy — unless reversal learning had already been practiced by that hemisphere prior to removal of the hippocampus.

The next figure refers to another project concerned with the use of auditory cues in the volitional control of limb movement. The cat reaches out with one paw and tests with light pressure one or both of two pedals. Light pressure of the paw on the pedal activates a small loudspeaker to the left or the right of the animal. If the loudspeaker tone comes from the animal's left, further pushing of the pedal releases a food reward; if the speaker comes from the right, only an unpleasant bright flash of light results from pushing the pedal. The right-left connections with the speakers is varied at random and the animal learns to test the pedals for the direction of the tone and to push accordingly. The hearing centers of the cerebral cortex are then removed from one hemisphere and the centers for motor control are removed from the other and the various commissural cross connections are then cut in an effort to discover the essential cerebral circuitry by which the above performance is achieved.

We have the impression that these and the other split-brain projects we've undertaken to date only begin to scratch the surface of the many possibilities for cerebral analysis that have been opened by the development of this midline surgery and related techniques. One gets the feeling in applying split-brain surgery ~~and~~ in its various ~~[illegible]~~ forms ~~[illegible]~~ that it is now possible to really take the brain apart in a way that 10 years ago seemed prohibitive. Even the innermost secrets of brain function seem much more accessible.