The Split brain

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1. Terminology

The term split-brain has several meanings. Applied to the human, it denotes complete sectioning of the corpus callosum, an operation which is usually performed for medically intractable, multifocal epilepsy (Reeves and Roberts, 1995). In the experimental animal, such as the cat or monkey, it usually implies both callosal section *and* a split optic chiasm; this makes it possible to restrict visual information to one hemisphere merely by covering one eye. In the human with intact chiasm, restriction of visual input to one hemisphere requires restriction of the visual stimuli to one or the other visual hemifield. Our split-brain patients had complete cerebral commissurotomy (including anterior commissure, dorsal and ventral hippocampal commissures, and, in some cases, the massa intermedia). But it is now common to use the term split-brain to refer to cases of complete callosotomy alone, since they manifest most of the same signs and symptoms.

The term partial split has come into common usage because some seizure disorders respond well to section of only the anterior two-thirds of the callosum. Moreover, partial sections have sometimes been used for surgical approaches: examples are genu section for anterior communicating aneurysm clipping, trunk sections for access to the third ventricle, and splenial section for approaching the pineal region. Tumors (usually gliomas) can occur anywhere in the callosum, the best studied being tumors of the genu or of the splenium. Multiple sclerosis can cause callosal disconnection signs. Toxic and/or infectious lesions of the callosum occasionally occur. And from time to time an anterior cerebral artery aneurysm rupture results in hemorrhagic dissection of the callosum. These naturally occurring lesions usually result in eventually subsiding fractions of the complete callosotomy syndrome. Familiarity with the complete syndrome makes it easier to identify the partial varieties. Congenital absence of the corpus callosum (callosal agenesis) has been intensively studied; it is for the most part *not* accompanied by disconnection signs, a surprising fact believed to reflect early plasticity and reorganization of subcallosal channels.

2. Disconnection syndromes

Following interruption of large tracts of cerebral nerve fibers there occur sets of deficits called "disconnection syndromes". The clearest example is the syndrome following complete cerebral commissurotomy. This results in loss of normal communication between the two cerebral hemispheres, i.e, a split brain. This article focuses on surgical disconnection to alleviate intractable multifocal epilepsy. It updates our recent entry for the *Blackwell Dictionary of Neuropsychology* (Beaumont et al, 1996).

Following complete callosal section, it is customary to distinguish an acute syndrome, lasting weeks to a few months after operation, from a chronic syndrome. The chronic syndrome typically persists in a stable condition for many years, although with some progressive compensation as time goes by.

3. Complete disconnection

When the corpus callosum of a right-handed, left-hemisphere dominant patient is sectioned, there often follow mild akinesia, imperviousness and mutism as well as competitive movements between the two hands. There are left-hand apraxia to verbal command, left-arm hypotonia, well coordinated but repetitive reaching, groping or grasping with the left hand, and bilateral Babinski responses. Symptoms vary across patients and reflect edema from retraction (of one hemisphere to allow surgical approach) as well as diaschistic shock to both hemispheres due to the radical disconnection. It is suggested by some that complete callosotomy (section of the corpus callosum alone) in cases where speech and manual dominance are in opposite hemispheres may result in prolonged loss of spontaneous speech. Commonly, in the early postoperative period there are episodes of intermanual conflict, in which the hands act at cross-purposes. Patients sometimes complain that their left hand behaves in a "foreign" or "alien" manner, and they often express surprise at apparently purposeful left-hand actions (Bogen, 1993).

Largely absent from the acute disconnection syndrome are florid symptoms associated with unilateral lesions, including aphasia, agnosia, prosopagnosia and denial of disease as may occur with hemineglect.

4. Chronic disconnection

Synopsis of the Chronic Human Split-Brain Syndrome. When patients who have had a complete callosotomy have recovered from the acute operative effects and reach a fairly stable state, they manifest a variety of phenomena which can be grouped under four headings: (1) *Social ordinariness*. One of the most remarkable results is that in ordinary social situations the patients are indistinguishable from normal, except for certain memory problems. Special testing methods, usually involving the lateralization of input, are needed to expose their deficits (2) *Lack of interhemispheric transfer*. A wide variety of situations (to be described below) have been contrived to show that the human subjects are in this respect the same as split-brain cats and monkeys. A typical example is the inability to retrieve with one hand an object palpated with the other (3) *Hemispheric specialization effects*. The hemispheric specialization typical of human subjects results in phenomena not seen in split-brain animals. A typical example is the inability of right-handers to name or describe an object in the left hand, even when it is being appropriately manipulated (4) *Compensatory phenomena*. Split-brain subjects progressively acquire a variety of strategies for circumventing their interhemispheric transfer deficits. A common example is for the patient to speak out loud the name of an object palpated in the right hand; because the right hemisphere can recognize many individual words, the object can then be retrieved with the left hand.

Details of chronic disconnection. Within a few months after the operation, patients appear normal on routine neurologic examination as well as in social situations. Long-term personal interaction with the patients does reveal a few persisting problems. Most noticeably, the patients have a moderate memory deficit, demonstrating lower memory than intelligence quotients, particular difficulty with uncommon paired word associates, story passages and topographical memory, and selective difficulty in acquisition of new information. It is believed that these deficits are mainly due to callosal rather than fornix damage (D.W.Zaidel, 1990). Also, the patients tend to demonstrate some pragmatic deficits in conversation, inappropriate or exaggerated politeness, and a slight tendency to confabulate. They show alexithymia, i.e, impoverished verbal description of emotional personal experiences (TenHouten et al, 1986[1]). The patients fail to sustain reading of extended texts and rarely read for enjoyment.

In contrast to social ordinariness, lateralized testing in which the stimuli and/or responses are restricted to one hemisphere reveals a dramatic lack of communication between the two disconnected hemispheres, each of which appears to have its own perceptual, learning and memory systems. Thus, a typical right-handed commissurotomy patient with left hemisphere (LH) speech cannot name stimuli in the left sensory field, whether the left visual hemifield (LVF) or the left hand (Lh), and such a patient cannot make reliable same-different judgments about stimuli in opposite sensory fields, usually the two visual hemifields or the two hands.

When different but acoustically similar auditory stimuli are presented simultaneously to the two ears (dichotic listening), patients cannot name the left ear stimuli, which normally reach the LH via the isthmus of the corpus callosum (Sidtis, 1988; Zaidel et al, 1990). This is due to suppression of the ipsilateral auditory pathway. Suppression can be maximized by precise acoustic overlap of the dichotic signals and is then resistant to manipulation of attention or experience. There is a corresponding suppression of the right ear for nonverbal identification of auditory stimuli specialized in the RH, such as in complex pitch discrimination. There is no interhemispheric transfer for touch, pressure, and proprioception. Hand postures impressed on one (unseen) hand by the examiner cannot be mimicked in the opposite hand and a brief flash of a hand form to one visual hemifield cannot be copied by the contralateral hand (Sperry, 1968). There is a substantial loss of intermanual point localization, that is, loss of the ability to identify exact points stimulated on the other side of the body, especially distal parts such as the fingertips. In all these cases intrahemispheric comparisons are intact.

One would expect bimanual coordination to suffer following commissurotomy. However, motor skills learned prior to surgery such as swimming, biking, piano playing, cooking, tying shoe laces, bead stringing, and similar skills all appear intact. New bimanual tasks involving mirror image movements consisting of fine finger movements or parallel hand movements are normally executed. However, bimanual interdependent control, such as required in an Etch-a-Sketch-type task, is severely impaired (D.W. Zaidel and Sperry, 1977[1]). Even patients with partial commissurotomy (intact splenium with divided anterior commissure) are severely limited in such bimanual coordination (Preilowski[2]). Further, the chronic disconnection syndrome shows persisting mild-to-moderate left-hand apraxia to verbal command in spite of good imitation and adequate auditory language comprehension in the disconnected RH (D.W. Zaidel and Sperry, 1977[1]). Finally, following complete commissurotomy the patient is unable to name but can signal with the left hand odors presented to the right nostril (Gordon and Sperry, 1969[1]).

5. Interhemispheric transfer

With time, patients acquire a variety of extracallosal transfer mechanisms. These include cross-cueing (Bogen, 1990), ipsilateral sensory/motor projections, especially on the left side, and a number of routes for subcallosal communication. Transfer of high level semantic information can occur (Cronin-Golomb, 1986[1]; Myers and Sperry, 1985[1]); however, its extent is as yet uncertain. For example, Sergent found that complete commissurotomy patients in the Los Angeles series could assess the alignment of arrows in the two VFs, the parity of a bilateral dot pattern, the larger of two digits in opposite fields, or the lexicality of a word straddling the midline. Corballis (1995) could not replicate this on the same patients and Gazzaniga and his associates failed to find similar transfer in callosotomy patients from the Dartmouth series. More recently, callosotomy patient JW from the Dartmouth series was tested for interhemispheric integration of orientation, form, luminance and position of low spatial frequency (i.e, highly discriminable) information in the region between 2–6° off fixation. He failed on same/different judgments for orientation, form and luminance and performed barely above chance on relative position (Tramo et al, 1995).

Some results remain paradoxical. For example, it is known that patient LB in the Los Angeles series can often name LVF stimuli although he has never been able to compare stimuli across the midline (Johnson). Comparable tests on patient NG showed that she could not name LVF stimuli but she could compare (meaningful or nonsense) shapes across the midline (E. Zaidel, 1994 J. Clarke and E.Zaidel[3]). LB's verbalization of LVF stimuli could reflect subcallosal semantic transfer from the disconnected RH to the LH, and NG's cross comparison is likely to reflect limited sensory ipsilateral projection via the superior-collicular system. In any case, this double dissociation between perceptual integration and verbal awareness can serve as an anatomical model of a double dissociation between implicit and explicit knowledge.

6. Implicit transfer

We say that implicit interhemispheric transfer (priming) occurs in the split-brain if both naming of LVF stimuli and cross-matching fail, but there is nonetheless some influence of an unattended stimulus in one VF on a decision about an attended target in the other. No account of interhemispheric priming in the split brain literature to date is fully satisfactory, although each demonstrates some significant interhemispheric effects (E.Zaidel, 1994). This includes spatial attentional priming (Holzman et al, 1981[3]; Passarotti et al.[3]), negative priming in lexical categorizations or digit parity decisions (Lambert, 1993[3]), lexicality priming in lateralized lexical decision (Iacoboni et al.[3]) and bilateral Stroop (Weekes and Zaidel[3]). When they do occur, some, but not all, interhemispheric priming effects are attributable to a unified stage of response programming, late in the development of motor plans. For example, lateralized lexical decision by patient LB shows lexicality priming of word or nonword targets in one VF by word or nonword distractors in the other. But the facilitation and interference components of the lexicality priming effect appear to reflect distinct stages of processing and presumably different subcallosal channels, the former during lexical access, the latter during response programming.

What accounts for the normally unified everyday behavior of the patients (Sperry, 1968). First, there are bihemispherically appreciated visual and manual explorations of space, including conjugate eye movements. For example, Hughes et al (1992, cited in Tramo et al, 1995), provided evidence for bidirectional gaze control in each hemisphere of patient JW. Second, there is some bilateral representation of sensory information. Third, there is ongoing hormonal communication via blood and cerebrospinal fluid. Fourth, and most important, there are a variety of connecting subcallosal pathways in the cerebellum, midbrain, pons and both hypo- and subthalamus.

7. Partial disconnection

Anatomical, physiological and behavioral observations in clinical and normal populations converge on the view that the corpus callosum contains function-specific channels that interconnect cortical regions in the two cerebral hemispheres. The anteroposterior arrangement of these channels generally respects the anteroposterior arrangement of corresponding cortical regions. As a result, different partial sections produce different elements of the complete disconnection syndrome.

The evidence from partial commissurotomy for regional functional specialization in the corpus callosum is limited by the small number of cases, extracallosal pathology, lack of pre- and post-operative comparisons, and apparent individual differences in callosal organization. Complete division of the splenium, including the tip, is necessary and sufficient for visual disconnection (Maspes[1]). Two dramatic naturally occurring syndromes usually associated with posterior callosal disconnection are pure alexia and optic aphasia where visual and sometimes semantic disconnection are invoked in addition to right homonymous hemianopia to help explain selective failure of reading or naming of visual stimuli, respectively. If only the tip of the splenium is spared, there is good visual transfer but persisting unilateral left anomia, unilateral left apraxia, deficits in both tactile and kinesthetic transfer and a large right ear advantage in dichotic listening (Risse et al.[1]).

Surgical section of the anterior two thirds of the corpus callosum, sparing the splenium, can result in little or no disconnection symptoms. There may be some relatively subtle deficits in bimanual coordination and in tactile or motor transfer, and memory for new events is also impaired. Nonepileptic patients with surgical removal of parts of the trunk of the corpus callosum sometimes have more or less subtle tactile or motor disconnection symptoms. Division of the isthmus usually but not always results in auditory disconnection. One possible cause of differences across patients is extent of extracallosal damage, which may interrupt some callosal conduction or disable a region that usually suppresses inhibition of transfer through some callosal channels. Another is individual differences in organization of the callosum.

Anterior callosal section sparing the splenium can exhibit both short and long term compensatory reorganization. On the one hand, measures of callosal relay using simple reaction time to lateralized light flashes (the Poffenberger paradigm) show a shift from motor to visual relay within a week postsurgically. This suggests a shift to a previously active but subdominant channel (Iacoboni and Zaidel[2]). On the other hand, the same surgery (section of the isthmus is presumably critical) resulted in a presumed progressive shift of an auditory relay channel (of the left ear signal from the RH to the LH) in dichotic listening to nonsense consonant-vowell syllables from the sectioned isthmus to the intact anterior splenium over a period of three years. Moreover, the reorganized channel is attention-specific: The shift occurred for divided attention but not for focused attention, the latter continuing to show a massive right ear advantage characteristic of auditory disconnection (Weekes, Fried and Zaidel[2]).

8. Hemispheric specialization and independence

The full disconnection syndrome has supported the doctrine of complementary hemispheric specialization: LH specialization for language and analytic processing, RH specialization for visuo-spatial and gestalt processing. But more importantly, it has advanced the concept of hemispheric independence: that each hemisphere can constitute a separate cognitive system operating independently of and in parallel with the other (Fig. 1) (Bogen, 1990; Sperry, 1974).

A view of the cerebrum from above, indicating hemispheric dominance for various tests based on evidence from cases of lateralized lesions and from split-brain patients.

8.1 Attention

There is some controversy on whether the disconnected RH is more vigilant than the disconnected LH (Dimond, 1979[1]) or not (Ellenberg and Sperry[2]). Experiments on covert orienting of spatial attention using the Posner paradigm confirm the existence of two different attentional systems in the two hemispheres (E.Zaidel, 1994). Both disconnected hemispheres show benefits from valid cues but the RH is more likely to show costs from invalid cues (Passarotti, Rayman, and Zaidel[3]). There are also suggestions that the attentional system in the LH is more object-based and that in the RH it is more location-based (J. Driver, personal communication). A visual search task has suggested independent allocation of attention in the two disconnected hemispheres (Luck et al, 1989[1]) and some disconnected RHs may be selectively able to benefit from guided visual search (restricting attention to a subset of stimuli defined by a relevant feature, Kingstone).

Covert orienting of spatial attention. There is as yet no detailed computational model that explains intra- and interhemispheric priming effects observed during covert orienting of spatial attention in both the normal and split brains. But the data are consistent with a model which assumes that (1) the RH has an attentional map that includes both VFs; (2) the LH has an attentional map that includes only the RVF; (3) the LH controls attention for RVF targets and the RH controls attention for LVF targets; (4) the two attentional systems do not necessarily communicate with each other even when visual information can transfer across the hemispheres through the corpus callosum; (5) the RH exhibits greater costs from invalid cues than the LH; and (6) the attentional system in the RH, i.e, the one controlling responses to LVF targets, with a representation of both fields has access to RVF information with both callosally and extracallosally mediated components, both facilitatory and inhibitory (E.Zaidel, 1994).

Redundancy gain. The ability of target detection to benefit from multiple copies of the target is called a "redundancy gain" and it may reflect parallel processing with unlimited resources leading to a horse race, or it may reflect earlier neural summation resulting in a larger gain. Do the disconnected hemispheres show a differential capacity for parallel processing, i.e, a different redundancy gain? Patient LB performed simple reaction time to lateralized light flashes with blocked targets and redundant copies within the target VF. He showed a redundancy gain in both VFs but a greater gain (neural summation) in the RH. However, neither LB nor NG showed redundancy gain in either hemisphere in a (horizontal/vertical) line identification task. Callosotomy patient JW from the Dartmouth series surprisingly showed a large redundancy gain in simple reaction time with *bilateral* presentation (one stimulus copy in each field) (Reuter-Lorenz et al.[2]). Commissurotomy patient LB from the California series exhibited a similar large and paradoxical gain with bilateral presentation in a simple reaction time task (Iacoboni and Zaidel[2]) as well as in a tachistoscopic visual search task (Pollman and Zaidel[2]), but the gain was sensitive to specific conditions of interhemispheric interaction. Thus, the split brain can exhibit a supra-additive interhemispheric interaction that surpasses the interhemispheric effect in the normal brain.

Perception and space. The disconnected RH was found superior to the disconnected LH on modified versions of spatial relations tests (J. Levy, 1974[1]; S. Kumar[2]), on part-whole and gestalt completion tests (Nebes, 1974[1]), on the use of perspective cues (Cronin-Golomb, 1986c[1]), and on tests of geometric invariance (Franco and Sperry, 1977[1]). The disconnected RH was also found superior for complex pitch discrimination (Sidtis, 1988) and for harmonic progression (Tramo and Bharucha, 1991[1]). The disconnected LH was superior in figure-ground disembedding (E. Zaidel2). The components of mental imagery are differentially specialized: the RH was found superior for mental rotation (Corballis and Sergent, 1988[1]), the LH superior for image generation (Farah[2]). But there are no hemispheric differences for image scaling and scanning (Matteson[2]), and both hemispheres are capable of performing all these component operations. Other tests, such as the Mooney Faces or face recognition tests failed to show the expected RH superiority (E. Zaidel[2]). Experiments on hierarchic perception showed only an occasional RH specialization for global decisions and LH specialization for local decisions (Robertson et al, 1993[3]; Zaidel, 1994). The consistency effect (interference of inconsistent global stimuli with local decisions) can occur in either disconnected hemisphere (Weekes, Carusi and Zaidel[3]).

Nonverbal Piagetian tests for spatial development (Stereognosis, Localization of Topographical Positions) at the pre-operational and concrete operational stages showed mixed hemispheric superiorities across tests and patients and did not succeed in characterizing each hemisphere as performing at some consistent developmental stage (Zaidel, 1978).

The disconnected RH has a rich pictorial semantics. It recognizes objects, scenes, landmarks and personally relevant people and events (e.g, Sperry, Zaidel and Zaidel, 1979[3]). But in contrast to the disconnected LH, it shows a selective advantage for stereotypical exemplars of natural categories and for conventionally organized scenes (D.W. Zaidel, 1994).

8.2. Memory

The disconnected RH was superior to the LH in memory of tactile nonsense shapes either when the responses were signaled by touch (Milner and Taylor, 1972[1]) or by drawing (Kumar, 1977[1]), and the disconnected LH was superior for tactile or visual memory for ordered sequences of figures, both common objects and nonsense shapes (D.W. Zaidel, 1990). The multiple choice version of Benton's Visual Retention Test showed an RH advantage at short (15 s) delays but no hemisphere difference at 60-s delays (Zaidel, 1978). More recently, concept decision tests of long term semantic memory with pictorial exemplars showed an advantage for atypical exemplars in the LH and for typical exemplars in the RH (D.W. Zaidel, 1994). Further, the disconnected RH had a greater deficit than the LH in recognition memory for scenes that violated logical, physical and social conventions, suggesting that the RH has a greater role in error monitoring and the LH is more flexible in processing novelty (D.W. Zaidel, 1994; but cf. Goldberg and Costa[2]). Subsequently, Metcalf et al.[2] showed that the RH of JW was better able than the left to reject new events similar to originally presented material of several types, arguing for a hemispheric difference that makes it possible to distinguish veridical perceived information (the RH) from inferred information (the LH). Ramachandran[2] similarly speculates that the LH maintains a stable world view by being impervious to inconsistencies, whereas the RH can play the "devil's advocate" and challenge the existing world view.

In most tests, memory in either disconnected hemisphere of patients in the California series is generally lower than normal, though better than in patients with amnesia, suggesting that the forebrain commissures are important for the formation of some kinds of memory. Data from the Dartmouth series is used to argue that posterior callosal sections which include the hippocampal commissures cause a mild memory deficit (in standardized free field testing) which involves recognition but not recall (Tramo et al, 1995).

9. Language

The disconnected LH (in right handers) has a generally normal clinical language profile. Its subtle psychometric deficit may be attributed to lack of normal RH contribution. In the Los Angeles series the disconnected RH has little or no speech, little writing, a substantial visual vocabulary, and a larger and surprisingly rich auditory vocabulary. Visual word recognition in the RH proceeds ideographically, without grapheme-phoneme translation. Both disconnected hemispheres show sensitivity to word frequency, concreteness, emotionality, and length. The disconnected RH has a rich if diffusely organized lexical semantic system but a poor phonology and an impoverished syntax (see entry by E. Zaidel on Language in the disconnected right hemisphere), although it may be capable of some grammaticality judgments (Baynes and Gazzaniga, 1988, cited in Tramo et al, 1995). It has a very limited short term verbal memory capacity of 2±1 items. The RH understands the meaning of verbs but has difficulty initiating action to printed or pictured commands. It has special paralinguistic competence in appreciating the communicative significance of prosody, facial expression and bodily postures (Benowitz[2]). The mental age profile of RH language abilities is very irregular, showing no correspondence to any single stage in first language acquisition.

Baynes et al. noted that callosotomy patient JW from the Dartmouth series has shown a progressively increasing capacity to name LVF stimuli and argue that this reflects the postsurgical development of RH speech. But the data are indecisive. Recent experiments with patient LB from the California series, who shows a similar pattern of occasional prompt naming of LVF stimuli, suggest sporadic control of fluent speech.

10. Reasoning

The disconnected RH was superior on a tactile version of a concept formation test (Kumar[2]) and it can process abstract concepts (Cronin-Golomb, 1986[1]). The RH was superior on both a tactile and a visual version of the Raven Colored Progressive Matrices, which requires the coordination of abstract rules (D.W. Zaidel and Sperry, 1973[1]; Zaidel, Zaidel and Sperry, 1981[1]). The LH was superior on the more difficult Raven Standard Progressive Matrices. A form board version of the test which permits a trial and error strategy showed that only the LH benefited from error correction.

11. Learning

This important area has been neglected and deserves further study. The disconnected RH can be superior in tactile concept classification tests by sensory cue (size, shape, roughness; Kumar[1]). The LH was superior on reversal learning of letter sequences (Lee-Teng[2]). The RH may be competent to detect certain linguistic errors, such as spelling violations in words, but it fails to take advantage of external error correction (E. Zaidel[2]). Training with feedback improves lateralized lexical decision in both hemispheres but especially in the LH (E. Zaidel[2]). Rotation of mental images shows an initial RH superiority but greater learning from experience in the LH (Corballis and Sergent, 1988[1]). It is likely that the two hemispheres use different learning strategies. RH performance is more variable from session to session than the LH (E. Zaidel, 1979, cited in Zaidel et al, 1990). The RH has not been shown to possess one-trial learning nor to benefit from feedback during trial and error but has responded better with redundant, complete and concrete models (E. Zaidel, 1987, cited in Zaidel et al, 1990).

12. Control

In general, not only partially but also fully split-brain patients behave in a coordinated, purposeful and consistent manner, belying the independent, parallel, usually different and occasionally conflicting processing of the same information from the environment by the two disconnected hemispheres. Free field performance often resembles that of the superior hemisphere (horse race), especially when the task is linguistic and performed better in the disconnected LH. Occasionally the LH dominates free field responses even when it is inferior to the RH. On rare occasions the RH dominates in spite of being inferior, particularly when the task has prominent visuospatial components. Thus, hemispheric dominance in responding is not always the same as the superior unilateral competence (Levy and Trevarthen, 1976).

When the two hemispheres receive competing stimuli at the same time, the response mode tends to determine which hemisphere controls behavior: Lh responses reflect RH decisions and Rh responses reflect LH decisions, even when these decisions are in mutual conflict. A variant of this technique presents brief chimeras consisting of competing half stimuli around fixation, divided along the vertical meridian (Levy and Trevarthen[2]). In this case, both the nature of the task and the response mode interact to select a behaviorally dominant hemisphere.

Bimanual responses facilitate interhemispheric cooperation for compatible stimuli in the two VFs even in the split brain. It seems that motor responses tend to be unified so that in the chronic condition the two hands do not respond in conflict with each other even when the two hemispheres make conflicting decisions.

The disconnected LH can be said to be generally dominant for several reasons. First, it is more likely than the RH to assume control over behavior in unlateralized situations. Second, it has better ipsilateral visual and tactile-kinesthetic sensory-motor control than the RH. Third, LH performance is more stable and less sensitive to small task differences. Fourth, although each disconnected hemisphere is hemianopic with respect to ipsilateral half space and does not deny ipsilateral perceptual experience, the disconnected LH does routinely express disbelief of correct RH responses to left sensory field stimuli.

13. Consciousness

Long-term observations showed that each disconnected hemisphere possesses not only a separate sensory-motor interface with the environment, its own perceptual, mnestic, cognitive and linguistic repertoires, but also a distinct personality, as well as characteristic preferences and dislikes (D.W. Zaidel, 1994). Thus, the two hemispheres have similar, but not identical, concepts of self, past and future, family, social culture and history (Sperry, Zaidel and Zaidel, 1979[3]). After some testing experience with the patients, examiners spontaneously refer to the two hemispheres as if they were distinct people, e.g, "the LH was upset at the RH responses today". While such references may be regarded as shorthand for patterns of behavior with specific lateralized stimuli and responses, they nonetheless express a strong phenomenological sense of two coexisting streams of consciousness. Both hemispheres can probably be simultaneously and independently conscious; both can simultaneously possess conflicting wills so that the split-brain can exhibit two distinct, and possibly incompatible, loci of moral responsibility (Iacoboniet al, 1996 ; but see MacKay and MacKay, 1982[1]).

Recognizing that the disconnected RH is conscious provides additional evidence that language is not necessary for human consciousness. More important, using the split brain as a model for the normal mind, a normal individual's consciousness can then be viewed as the net result of an interaction among at least two distinct states of consciousness. The question then arises why the normal person with an intact brain experiences consciousness as unified rather than dual. Sperry reasoned that normal consciousness is a higher emergent entity that transcends the separate awareness in the connected left and right hemispheres, supersedes them in controlling thought and action, and integrates their activity. Alternatively, Bogen (1990) and many of us argue that normal consciousness is also dual, with partially separate parallel processing in the two hemispheres which sometimes does result in subjective feelings of conflict. Moreover, some normal subjects behave like split-brain patients during lateralized tests, thus demonstrating spontaneous or dynamic functional disconnection (Landis, Iacoboni).

It is noteworthy that the two chronically disconnected hemispheres generally do not engage in overt conflict. This is partly explained by characteristic RH passivity, LH dominance, and a unified system of motor control, as well as shared subcortical structures as discussed under "interhemispheric transfer" above. Intermanual conflict has usually been observed in the acute stage following surgical disconnection and in partial disconnection due to natural lesions, as in cases of the alien hand syndrome. However, even in the chronic stage we often encounter LH disbelief of intentional RH output.

14. Generalizability

The Los Angeles series of commissurotomy patients is unique because (1) the patients were relatively high functioning (2) They suffered from relatively minor extracallosal damage rather than from massive early lesions causing hemispheric functional reorganization (3) These patients have diverse neurological histories yet show similar functional hemispheric profiles (4) In general, the predominant hemisphericity of extracallosal damage in these patients does not correlate with behavioral laterality effects. Thus, it is unlikely that the disconnection syndrome observed in these patients represents an abnormal state of cerebral dominance.

The chronically disconnected LH does not show neglect of the left half of space or prosopagnosia and the disconnected RH is neither word deaf nor word blind. The linguistic profiles of the disconnected RH do resemble those of patients with dominant hemispherectomy for late lesions, as well as the pattern observed in large heterogeneous aphasic populations. Indeed, the language profile observed in the disconnected RH has facilitated the reinterpretation of some paradoxical syndromes, such as covert reading in pure alexia, semantic errors in deep dyslexia or misnaming with good miming in optic aphasia, as reflecting the contributions of the intact RH.

Thus, the disconnected hemispheres are generally free of the dramatic deficits that sometimes follow focal hemispheric damage. It seems likely that focal lesions involve both diaschisis and pathological inhibition of residual competence in the healthy hemisphere. As a result, the disconnected hemispheres often suggest greater hemispheric capabilities than inferred from lesion studies. At the same time, even when the hemispheres of normal subjects demonstrate independent strategies or apparently different representations, their competence and range of abilities is greater than seen in the disconnected hemispheres. It is likely that the normal hemispheres can borrow resources from each other and affect each other by more or less subtle automatic priming/interference effects. Even the split brain permits some interhemispheric exchange through multiple subcortical pathways so that the competence of the disconnected hemispheres in turn may overestimate the overall competence of residual hemispheres following hemispherectomy for lesions of late onset. Some normal cognitive effects, such as the consistency effect in hierarchic perception (global interference with local decisions), the Stroop effect, discourse processing, or verbal access to emotions may be inherently interhemispheric, and hence reduced in the split-brain.

The split-brain remains a model system for behavioral laterality effects in the normal brain. It operationalizes the concept of "degree of hemispheric specialization" by demonstrating independent processing of the same task in each hemisphere and interpreting the expressions "hemisphere X performed better than hemisphere Y on test A by amount d", or "hemisphere X performed task A better than task B by amount d". Further, the split-brain has motivated the useful distinction for behavioral laterality effects in normal subjects between "callosal relay" tasks that are exclusively specialized in one hemisphere, "direct access" tasks that can be processed independently in each hemisphere, and "interhemispheric" tasks that routinely require hemispheric integration. Most important, the disconnection syndrome motivates recent inquiries into "degrees of hemispheric independence" in the normal brain (E.Zaidel, 1994).

15. See also

Language in the disconnected right hemisphere
Corpus callosum
Hemispheric specialization
Handedness
Consciousness: neural basis of conscious experience
Control systems

16. Further reading

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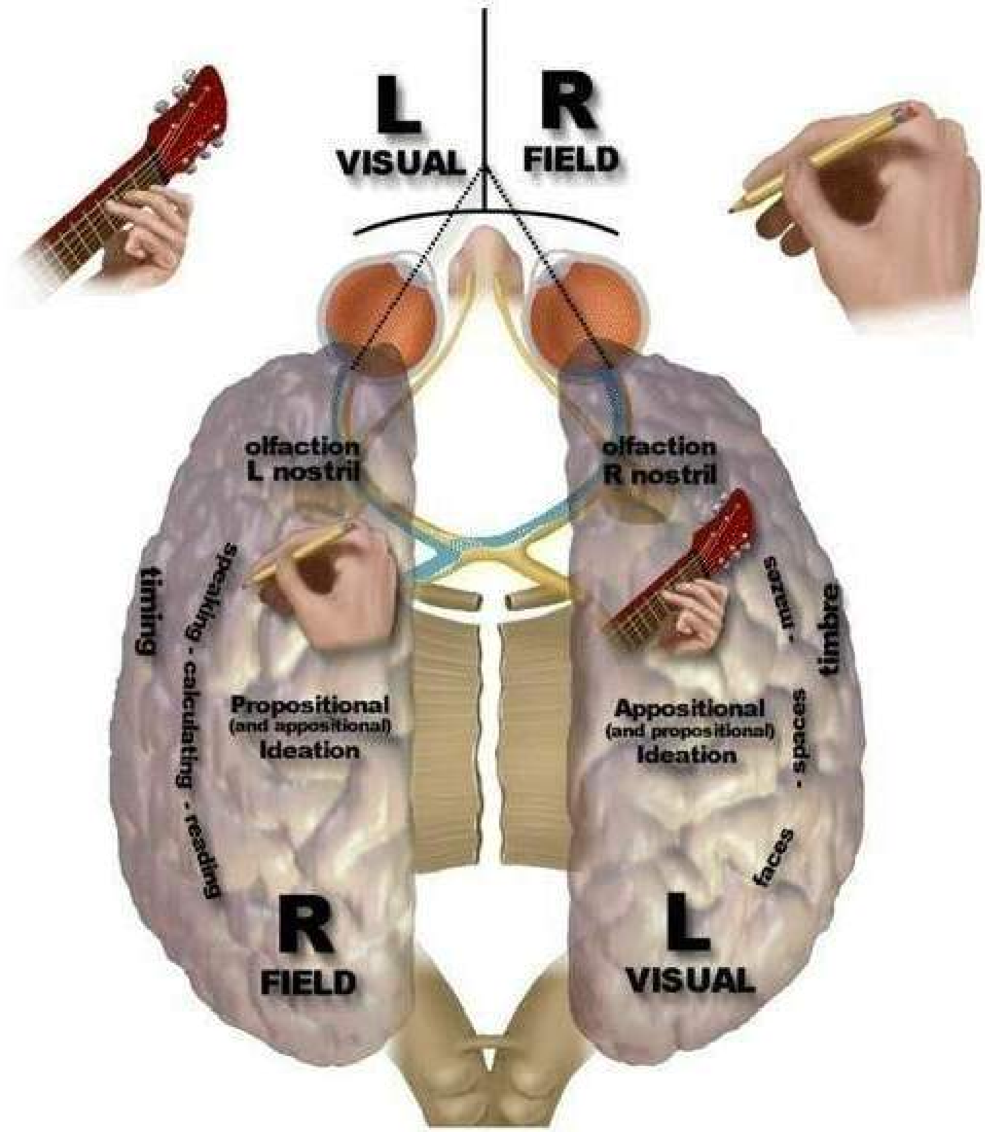

Figure 1. A view of the cerebrum from above, indicating hemispheric dominance for various tests based on evidence from cases of lateralized lesions and from split-brain patients.

[1]Cited in Bogen, 1993.

[2]Names in parentheses without dates identify prominent contributors to the relevant findings in order to facilitate literature searches.

[3]Cited in E. Zaidel, 1994.