CHAPTER 5

Hemispheric interactions and specializations: insights from the split brain

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Introduction

In the early 1940s, Van Wagenen and Herren performed the first known split-brain operations in humans, which were intended to control seizures in patients with intractable epilepsy (Van Wagenen and Herren, 1940). The rationale for the surgery was based on speculation as to the role of the corpus callosum in the spread of epilepsy. A few years earlier, researchers had reported the spread of epileptic discharge from one hemisphere to the other in monkeys and concluded that the spread was occurring via the corpus callosum (Erikson, 1940). Others had noted that damage to the corpus callosum sometimes reduced the incidence of seizures in their patients who suffered from epilepsy (Bogen, 1995). The patients who underwent split-brain surgery in the 1940s, however, often did not experience any relief of their epilepsy and the surgeons soon stopped performing the procedure.

Twenty years later, Philip Vogel and Joseph Bogen performed a complete commissurotomy on a former patient who was experiencing severe and life-threatening seizures. These doctors, too, felt that the corpus callosum was a critical pathway for the spread of epileptic discharge from one hemisphere to the other. They speculated that the earlier surgeries performed by Van Wagenen and Herren were unsuccessful because the corpus callosum was not fully severed. In their first split-brain operation in 1962, they severed all cortical commissures, effectively separating the two cerebral hemispheres (Bogen and Vogel, 1962). The surgery was successful in controlling the patient's seizures and it was subsequently performed on a series of other patients with intractable epilepsy.

In the 1940s, a few of Van Wagenen and Herren's patients had been studied clinically to determine whether there were any cognitive or behavioral effects of the surgery. These studies failed to find any such deficits (Akelaitis, 1944). Cursory examination of Vogel and Bogen's patients might have resulted in the same conclusion, but research with split-brain rats, cats and monkeys in the intervening years had led to the development of techniques to directly assess the function of each hemisphere independently (Myers, 1956: Myers and Sperry, 1958). This began 30 years of research on split-brain humans, which has resulted in a wealth of insights into the functions of the two hemispheres and the ways in which they interact (Gazzaniga, 1998).

The split-brain syndrome

The early surgeries often involved invasion of the lateral and third ventricles in order to divide many of the forebrain commissures. This resulted in a substantial risk of infection as well as damage to surrounding structures. Following this type of surgery, patients frequently exhibited an 'acute disconnection syndrome', characterized by mutism, apathy, confusion, left limb apraxia, and partial motor
seizures (Bogen, 1993; Wilson, Reeves and Gazzaniga, 1982). It was found, however, that dividing
just the corpus callosum and hippocampal commissure was as effective in controlling seizures as section
of multiple forebrain commissures. This significantly reduced the risk of infection, and the advent
of microsurgical techniques decreased the degree of damage to surrounding structures. Later, it was
discovered that if the surgery was performed in two stages (e.g. section of anterior callosum followed
by posterior section 2 months later), the course of recovery was much smoother and the acute discon-
nection syndrome was virtually eliminated (Wilson et al., 1982). The term ‘split-brain’ is generally ap-
plied to both callosotomy and commissurotomy although there are subtle differences between the two.
Callosotomy involves separation of both the corpus callosum and the hippocampal commissure, whereas
in complete commissurotomy, the anterior commissure is also sectioned (Trumon, Baynes, Fendrich et
al., 1995).

Once callosotomy patients have recovered from any acute effects of the surgery, the most striking
impression is how ordinary they seem (Bogen, 1993; Gazzaniga, 1970). In a casual conversation, a listener
would be hard-pressed to discern any effects of complete hemispheric disconnection. A simple bedside
test, however, reveals that this impression is only an illusion. If the patient’s hands are obscured from
view and an object is placed in only one hand, the effects of hemispheric disconnection are immediately
apparent. If the object is placed in the right hand, the patient names it easily. Conversely, if it is placed
in the left hand, the patient is unable to verbally identify it. Given an array of items to choose from,
however, and the left hand is immediately able to pick out the item. This indicates that the right hemi-
sphere has knowledge about the object but is unable to verbally produce a label for it. This dichotomy is
the most striking aspect of the split-brain syndrome: the left hemisphere has access to speech and the right
hemisphere does not.

This type of bedside assessment provided the first clues that surgical section of the largest fiber
tract in the human brain did indeed have behavioral consequences. Soon other more sophisticated
techniques were developed to characterize the effects of callosotomy and probe the functions of

Fig. 1. Schematic diagram showing the crossed organization of the visual system. Axons from the nasal half of each retina project to the contralateral hemisphere, while axons from the temporal half project to the ipsilateral hemisphere. This arrangement means that visual information presented to the right of visual fixation will only be visible to the left hemisphere of a split-brain patient, and vice versa.

the two hemispheres. This type of specialized testing revealed the many subtle effects of hemispheric
separation. These techniques take advantage of the contralateral organization of the nervous system in
order to present information to each hemisphere in isolation (see Fig. 1). Some systems, such as the
auditory system, have ipsilateral as well as contralateral projections, which makes it difficult to ensure
adequate lateralization of stimuli. In the visual system, however, the projections from each hemiretina
to the occipital cortex are exclusively contralateral. Specifically, the right hemiretina of each eye projects
to the left hemisphere while the left hemiretina of each eye projects to the right hemisphere. To lateral-
ize visual stimuli, therefore, subjects fixate on a central cross-hair and stimuli are briefly flashed to
one visual field or the other. Each stimulus will then be processed exclusively by the contralateral hemi-
sphere. Although this technique ensures that each stimulus is processed exclusively by the contralateral
hemisphere, presentation times are necessarily brief, generally no more than 150 ms. More recently, a
technique has been developed for stabilizing stimuli on the retina so that presentation times can be
increased while maintaining lateralization. A dual-Purkinje-image eyetracker is used to monitor the
patient’s eye movements and deflect the retinal image to compensate for any changes in the patient’s
visual fixation. In other words, as the subject moves
his eyes, the system moves the display in tandem with the eyes so that the other hemisphere cannot see the display. These techniques provide effective ways of exploring the effects of severing the largest fiber tract in the human brain, the corpus callosum.

The corpus callosum

The corpus callosum has over 200 million axons passing through it, and along with the anterior commissure, it provides the only direct link between the cortices of the right and left hemispheres. Postmortem research on human and monkey brains has revealed that the organization of the corpus callosum is topographic. Anterior fibers connect frontal regions of the two hemispheres, and pass through the rostral portion of the corpus callosum, including the genu. Posterior fibers connect posterior cortical structures, and these fibers from regions such as the superior parietal lobule and the occipital cortex pass exclusively through the splenium (De Lacoste, Kirkpatrick and Ross, 1985; Myers, 1965; Pandya, Karr, and Heilbronn, 1971). Research has revealed that this anterior to posterior organization results in modality specific regions of the corpus callosum. Motoric information is transferred from one hemisphere to the other via fibers in the anterior midbody of the corpus callosum, somatosensory information via the posterior midbody, auditory information via the isthmus, and visual information via splenial fibers.

The functional architecture of the corpus callosum derived from anatomical studies has been supported by behavioral studies on patients who have had incomplete sections of the corpus callosum. In contrast, patients who underwent a more extensive anterior callosal section that spared only one third of the splenium demonstrated intact visual transfer but lack of interhemispheric transfer in all other modalities. When anterior regions of the corpus callosum remain intact and the splenium is lesioned, interhemispheric visual transfer is completely disrupted (Gazzaniga and Freedman, 1973). The results of investigations on patients with partial callosotomies provide evidence that regions of the corpus callosum have specific functional roles.

There is recent evidence that there is an even greater degree of functional specificity within the corpus callosum than was previously thought. Patient V.P. is a 46-year-old woman who underwent callosotomy at the age of 26. Although the surgical report at the time indicated that callosotomy was complete, subsequent magnetic resonance imaging revealed spared fibers in the rostrum and genu. Despite these spared fibers, V.P. performed like a split-brain patient in most experimental paradigms. Occasionally, however, her performance in a task would suggest that there was information being transferred between her two hemispheres. This hint of interhemispheric transfer was intriguing and Funnell, Corballis and Gazzaniga designed a series of experiments to explore the phenomenon (Funnell, Corballis and Gazzaniga, 2000). Consistent with most previous experiments, they found that V.P. showed no signs of information transfer for color, shape or size. The story changed, however, when V.P. was presented with words. Suddenly, she demonstrated robust signs of transfer (see Fig. 2). One of the most revealing experiments is the ‘secret word paradigm.’ In this experiment, two words are flashed to the same hemisphere. The patient is told: “When you see this word (secret word is flashed to one side of fixation), don’t say that word. Instead, when you see that word, say this one (substitute word is flashed to the same hemisphere)” (see Fig. 3). The patient is then shown a list of words flashed to either the right or left of fixation and is asked to read them. The secret word is shown first to the hemisphere that was not instructed so there is no opportunity for cross-hemispheric cuing to have occurred. Since only one hemisphere was given specific information about these words, the probability of the other hemisphere producing the correct ‘substitute’ word when
Fig. 2. Interhemispheric transfer of information in split-brain patient V.P. She is unable to transfer simple visual information such as color or shape (A), but can transfer visually-presented words from one hemisphere to the other (B).

When you see this word:
+ TREE

Say this word instead:
+ DESK

Fig. 3. The 'secret word' paradigm showing transfer of orthographic word information in split-brain patient V.P. One hemisphere is instructed to substitute one word for another in a forthcoming list. When the 'secret word' is presented to the other hemisphere, V.P. says the substitute word, indicating that the information is available to both hemispheres.

shown the 'secret' word is essentially zero if there is indeed no interhemispheric information transfer. Remarkably, V.P.'s other hemisphere was able to produce the substitute word in half of the test trials. In some additional trials, she did not produce the correct substitute word but indicated knowledge that the presented word was the secret word by raising her hand, hesitating, or producing an incorrect
substitute word. This is strong evidence that information is being transferred between hemispheres in this task.

Why does the secret word paradigm produce such strong evidence for interhemispheric information transfer whereas there is clearly no transfer in other tasks? The answer lies in the type of information presented to V.P. When the information is pictorial (e.g., shape, size, color), there is no evidence for transfer. When words are presented, there is robust evidence for transfer. Since research with other callosotomy patients has demonstrated that there is no transfer of word information with a complete lesion of the corpus callosum, the transfer seen in V.P. is likely occurring via her spared callosal fibers. Since the spared rostral fibers connect frontal regions, it is unlikely that they are contributing to transfer of visual information. The other spared fibers are in the tip of the splenium, specifically in the ventroposterior region. These fibers connect occipital regions and are likely the conduit by which interhemispheric transfer is occurring in V.P. But why is this transfer only seen when words are presented? A possible answer lies in a recent paper by Suzuki, Yamadori, Endo et al. (1998). They describe a patient with a lesion limited to the ventroposterior end of the splenium who showed transfer of picture information but not letter information. After reviewing the literature on patients with splenial lesions, Suzuki et al. (1998) speculate that the anterior to middle portion of the splenium is involved in transfer of picture information and the ventroposterior portion is involved in transfer of letter information. Investigations with V.P. are consistent with this speculation and suggest that these fibers in the ventroposterior region of the splenium may connect visual word form area to homologous regions in the contralateral hemisphere. This is consistent with previous research demonstrating that lesions of the splenium could disrupt word reading by disconnecting the inputs to the left angular gyrus (Damasio and Damasio, 1983; Dejerine, 1891; Geschwind, 1972).

These studies add to our growing knowledge of the functional architecture of the human brain. There is a remarkable degree of specificity in the corpus callosum and studies with callosotomy patients with spared callosal fibers can reveal this functional topography.

Subcortical interactions

Although patients who undergo complete callosotomy are referred to as split-brained, in fact it is only the cortex that is divided. The term split-brain implies that the two sides of the brain are truly separated with each hemisphere functioning independently of the other. The left and right cortices are indeed separated, but subcortical structures are untouched by the surgery and provide a possible pathway for integration between the hemispheres. The degree to which subcortical structures are capable of supporting interhemispheric information transfer has been disputed. Some researchers have reported transfer of perceptual information (e.g., Johnson, 1984a,b; Sergent, 1990; Sergent and Myers, 1985) such as location and orientation (Corballis and Trude, 1993). Evidence has also been reported for transfer of higher level cognitive information (Cronin-Golomb, 1986; Cronin-Golomb, Gabrieli and Keane, 1996; Lambert, 1991). Other investigators, however, dispute some of these claims (Corballis, 1994a; Kingstone and Gazzaniga, 1995; Seymour, Reuter-Lorenz and Gazzaniga, 1994). At first glance, it seems difficult if not impossible to draw any definitive conclusions from this body of literature.

Michael Corballis (1994b), however, reconsidered the literature on subcortical interactions and concluded that much of the evidence for subcortical transfer of higher level perceptual or cognitive information was not convincing, although there was some evidence for subcortical transfer of coarse perceptual information (e.g., large vs. small). He demonstrated that in many of the experiments reporting evidence for interhemispheric transfer, the experimental findings could be explained by information available to just one hemisphere rather than subcortical transfer. Having specific types of information available to one hemisphere could facilitate above-chance guessing in some paradigms and produce the appearance of subcortical information transfer. An example of this process is described by Gazzaniga, Holtzman and Smylie (1987). They presented the right hemisphere of a split-brain patient with digits and asked the patient to name them. Since this patient had no evidence of right-hemisphere speech, it was assumed that the verbal responses were produced by the left
hemisphere. When the right hemisphere was presented with one of two digits ('1' or '2'), the left hemisphere was able to name the digit if the left hemisphere was aware of what the two response choices were. If there were more than two response choices or the left hemisphere was not aware of what the response choices were, the patient was not able to name the digits accurately. This indicates that although some paradigms can produce the appearance of subcortical interactions, the results can often be explained via the strategies patients use in approaching tasks.

The issue of subcortical transfer of higher-level information was investigated by Kingston and Gazzaniga (1995) in patient J.W., who has a complete callosotomy verified by post-surgical MRI. They presented pairs of words with one word appearing in each visual field (e.g. tooth + brush). After each word pair was presented, J.W. was given a pad of paper and pen and asked to draw a picture of what he had seen. In this first version of this task, J.W. drew a significant number of pictures that combined the words presented to the two visual fields. It was noted, however, most of these were drawn when he was able to see the paper on which he was drawing. When the paper was hidden from view, his drawings generally reflected one of the presented words rather than a combination of the two. This finding raised the possibility that the integration of the two words was occurring on paper rather than in the brain. A second version of this task was then designed to investigate this issue. The word pairs were constructed so that the pair formed a compound word that was not suggested by either of the individual words in the pair (e.g. break + fast, head + stone). This time, J.W. never drew pictures that combined the information from both visual fields. The authors concluded that the integration seen in the first version of the task was not the result of subcortical connections and could instead be attributed to bilateral control of the same hand. This provides further evidence that there is no transfer of higher-order information between the two hemispheres of split-brain patients.

It can therefore be concluded that some crude information, such as binary information can be transferred via subcortical pathways, but evidence for transfer of more complex information is not compelling (Corballis, 1994b). Since interhemispheric transfer of higher-level perceptual, motor and cognitive information does not occur via subcortical pathways, studies of patients with surgically separated cortices can shed light on the role of each hemisphere in these higher-level functions.

**Hemispheric differences in language**

The most salient difference between the two cerebral hemispheres is speech. The left hemisphere is capable of producing speech while the right hemisphere in most callosotomy patients remains mute. In fact, the language abilities of the isolated left hemisphere are indistinguishable from the patient's pre-surgical linguistic abilities, suggesting that the left hemisphere is dominant for most if not all language abilities. Initially, it was assumed that since the right hemisphere could not talk that it had no capacity for language. Subsequent experiments, however, showed conclusively that this was not the case for some callosotomy patients (Gazzaniga, 1965; Gazzaniga and Sperry, 1967; Levy, Nebes and Sperry, 1971). For those patients who demonstrate language abilities in both hemispheres, there is a great deal of effort devoted to characterizing the linguistic capacities of the two hemispheres. These studies point to a distinction between grammar and the lexicon. In general terms, grammar refers to the system of rules we have for ordering words to enable communication. The lexicon can be described as the mind's dictionary in which words or groups of words are associated with certain meanings. Recent research has demonstrated that electrophysiological activation associated with grammatical aspects of language is localized over left anterior temporal regions. In contrast, activations to open-class, non-grammatical lexical items are more diffuse (Neville and Mills, 1997). This might suggest a left-hemisphere dominance for grammar and potentially more bilateral involvement in the lexicon.

Investigations with split-brain patients provide evidence for this dichotomy. There is abundant evidence that both hemispheres of split-brain patients are capable of supporting a lexicon, although the extent and organization of the lexicon may be different in the two hemispheres. The receptive vocabularies of several split-brain patients have been assessed using the Peabody Picture Vocabulary Test. Gazzaniga,
glycine, Baynes et al. (1984) tested patient J.W., and found comparable vocabularies in the right and left hemisphere. Zaidel (1976) tested patients N.G. and L.B. and found that although the left hemispheres of both patients had more extensive vocabularies than the right hemispheres, the difference between the hemispheres was judged to be relatively small.

Other research has probed the nature of the left and right hemisphere lexicons. Cronin-Golomb (1986) demonstrated that both hemispheres of split-brain patients can make abstract associations between visually presented pictures (e.g. clock/calendar linked by the concept of time). Although there were not many trials in each condition, there was some indication that the left hemisphere was better able to make these associations than the right. Gazzaniga and Smylie (1984), in a similar experiment, found that both hemispheres could make inferential judgments, but the left hemisphere performed significantly better than the right. Gazzaniga and Miller (1989) demonstrated that both hemispheres were able to make above chance judgments of antonymy, but the right hemisphere made significantly more errors on these judgments than did the left. In addition, the degree of association between the antonym pairs was considered. Direct antonyms were those that were strongly associated (e.g. fast/slow). Indirect antonyms were those which expressed the same conceptual contrast but which were not strongly associated (e.g. swift/slow). Normal subjects are slower to make judgments about the indirect than the direct antonyms. The left hemisphere of split-brain patients was also slower to make these judgments, but there was no significant reaction time difference in the right hemisphere. A left-hemisphere superiority for antonyms was also reported by Sidtis, Volpe, Wilson et al. (1981). Furthermore, they found that the right hemisphere was able to identify synonyms, functional relations among words, superordinates, and subordinates, but the left hemisphere was significantly better than the left in making all of these judgments. This suggests that both hemispheres can support a lexicon but the organization of the lexicon in the two hemispheres is different.

In addition, there is evidence that access to the lexicon in the two hemispheres is different. Reuter-Lorenz and Baynes (1992) investigated word recognition in the two hemispheres of split-brain patients to determine whether access to the visual lexicon is the same in both hemispheres. Based on a series of studies, they conclude that the right hemisphere employs a serial, letter-by-letter approach to reading. In contrast, the left hemisphere tends to use a more efficient parallel access mode. Therefore, access to the lexicon differs in the two hemispheres, as does the organization of the lexicon in each hemisphere. Both hemispheres, however, do have access to a lexicon.

Although both hemispheres of split-brain patients demonstrate lexical capabilities, the left hemisphere is clearly dominant for grammar. Although the right hemisphere can comprehend single words (Gazzaniga, LeDoux and Wilson, 1977) and commands (Gazzaniga and Hillyard, 1971; Gazzaniga et al., 1977), it has little or no syntactic capability. Zaidel (1977) demonstrated that the right hemisphere can match chips for color, shape, and size on the Token Test, but was significantly impaired relative to the left in overall performance. Although the right hemisphere can comprehend single words, it has difficulty combining the meanings of reference phrases (e.g. big red circle) (Zaidel, 1977). Gazzaniga and Hillyard (1971) asked the two hemispheres of split-brain patients match pictures to printed sentences. They found that the right hemisphere could not distinguish between active and passive constructions, future and present tense, and singular and plural nouns. The right hemisphere was, however, able to discriminate between affirmative and negative sentence constructions. In an interesting twist, Baynes and Gazzaniga (1988) demonstrated that it may not be a lack of grammatical knowledge that resulted in the right hemisphere's poor performance on Gazzaniga and Hillyard's tasks. They demonstrated that the right hemisphere was in fact able to make grammaticality judgments about a variety of violation types. Interestingly, the right hemisphere was unable to use this grammatical knowledge in comprehension tasks. Therefore, the right hemisphere may have more passive grammatical capabilities than some paradigms suggest.

Although the most salient difference between the two hemispheres is speech, this is not true for all callosotomy patients. Some patients have developed the capacity to generate speech from their right hemispheres following complete callosotomy. These patients demonstrate some unique features in relation
to other callosotomy patients. Kutas, Hillyard and Gazzaniga (1988) examined the semantic abilities of the two hemispheres using event-related brain potentials. They presented sentences to each hemisphere in isolation in which the last word of the sentence was either semantically congruent or anomalous. In neurologically normal subjects, an anomalous word at the end of a sentence elicits a specific cerebral potential known as the N400. In all five of the split-brain patients tested, the anomalous words resulted in an N400 in the left hemisphere. Only the two patients who were capable of speaking from the right hemisphere, however, produced N400 waves from their right hemispheres. This suggests that the language capabilities of the right hemispheres in these two patients is more fully developed than those of the patients who are capable of speech only from the left hemisphere (Kutas et al., 1988).

Asymmetries in visual perception

Most reports of hemispheric asymmetries in split-brain patients have concentrated on left-hemisphere advantages in language and higher cognition. However, one of the most striking of the early observations with split-brain patients was that the right hemisphere appeared to possess markedly superior visuospatial abilities than the left. Bogen and Gazzaniga (1965), who investigated split-brain patients’ performance on a standard block-design task, reported the first evidence for this asymmetry. Patients were able to arrange colored blocks to reproduce a given pattern when they used their left hands (controlled by the right hemisphere), but performed poorly with their right hands (controlled by the left hemisphere). Similarly, copies of drawings produced by the left hands of split-brain patients were considerably better than those produced by their right hands (see e.g. Gazzaniga, 1970). Copies made using the right hand contained some of the details of the original pictures but had no spatial coherence. In contrast, the drawings made using the left hand were recognizable facsimiles of the originals. Since the patients tested in these studies were all right-handed, it is unlikely that this right-hand deficit is the result of a motor problem. Rather, these observations suggest that at least some aspects of the visual representation of an object are superior in the right hemisphere than in the left.

In spite of the evidence that the right hemisphere outperforms the left on tasks such as copying and block design, it should not be concluded that the right has universally superior perceptual abilities. The left hemisphere clearly has sufficient perceptual acumen to read words and to recognize and name objects. Rather, perceptual asymmetries must arise at a fairly late level of processing. Gazzaniga and LeDoux (1978) argued that the right-hemisphere dominance exhibited in these tasks reflected a superiority for manipulospatial processing. That is, they suggested that the visual representations within each hemisphere were similar, and that the asymmetry is only manifested when the task requires active manipulation to produce the correct spatial arrangements. Although asymmetries may be magnified when manipulation is required, more recent evidence from a variety of sources suggests that there is a hemispheric asymmetry in visuospatial processing even when no manipulation is required (e.g. Hellige, 1993).

Although the exact nature of this visuospatial asymmetry remains unclear, recent research with split-brain patients confirms that it is indeed an asymmetry in spatial processing, and not an across-the-board visual asymmetry. For example, Funnell, Corballis and Gazzaniga (1999) found that the right hemisphere was considerably better than the left at detecting whether two otherwise identical pictures were mirror images of one another, despite the fact that the left hemisphere had no difficulty in identifying the objects pictured. In another study, Corballis, Funnell and Gazzaniga (1999b) compared the abilities of the divided hemispheres of two split-brain patients to make ‘spatial’ or ‘identity’ judgments on the same set of stimuli (see Fig. 4). When the patients were required to make spatial judgments, the right hemisphere outperformed the left. Conversely, when identity judgments were required, the right-hemisphere superiority disappeared. Although the scope of the right-hemisphere superiority for spatial processing is still unclear, these studies underscore the fact that both hemispheres are capable of sophisticated visual processing, and that asymmetries only appear once a considerable amount of processing has been accomplished.

The hemispheric asymmetry in visuospatial processing might be better characterized as a left-hemisphere deficit than as a right-hemisphere special-
hemisphere specialization for copying and name observation suggested that the left hemisphere was superior in visuospatial abilities. The functional difference in perceptual accuracy and name observation may have arisen at a stage where the left hemisphere, at least, gained dominance over the right hemisphere. Although the left hemisphere is generally thought to be only manipulative of visual information, it can manipulate to corresponding corners of the two squares. In the ‘identity’ condition they are asked to determine whether the two icons are the same or different (Corballis et al., 1999b).

Fig. 4. Sample stimulus used to investigate spatial and identity perception in split-brain patients. In the ‘spatial’ condition the patients are asked to determine whether the icons are in corresponding corners of the two squares. In the ‘identity’ condition they are asked to determine whether the two icons are the same or different (Corballis et al., 1999b).

Fig. 5. Perception of a square supported by illusory contours (A) and amodal boundary completion (B). Most observers perceive the arrangement in A as a white square superimposed on four black circles. The edges of the square are formed by illusory contours. The arrangement in B is most often perceived as a square behind four circular holes. Because the edges of the square are completed outside of the visual mode, the shape is said to be perceived by amodal completion.

perceive shapes by amodal completion (Kanisza, Renzi, Conte et al., 1993; Regolin and Vallortigara, 1995), which provides further evidence that the left hemisphere may have lost visuospatial abilities once possessed.

Attentional resources in the divided hemispheres

With the hemispheres divided, many researchers were left wondering how split-brain patients deploy attention. Can both hemispheres direct attention independently? If so, then severing the corpus callosum might result in significant confusion about where in space the patient should be attending at any given moment. Observation of these patients as well as their own reports suggest that this is not the case, and findings from a number of researchers corroborate this. Split-brain patients are able to orient to either side of visual space regardless of which hemisphere gets the cue (Holtzman, Sdits, Volpe et al., 1981) although the cues are more effective when directing attention to contralateral visual space rather than to ipsilateral space (Reuter-Lorenz and Fendrich, 1990). Recent research has qualified these findings. A number of investigators have demonstrated that the right hemisphere can deploy attention to the entire visual field whereas the left hemisphere attends only to the right field (Berlucchi, Mangun and Gazzaniga, 1997; Corballis, 1995; Mangun, Luck, Plager et al., 1994).
A second related question concerns attentional resources. Does each hemisphere have its own attentional resources, or are these resources shared between the hemispheres? The work of a number of researchers suggests that the latter possibility best accounts for the experimental findings. Holtzman and Gazzaniga (1982) designed a task in which the two hemispheres were each given a series of items to remember. In the 'easy' condition, the same stimulus was presented repeatedly. In the 'hard' condition, a series of different items were presented. They found that the performance of each hemisphere was affected by the difficulty of the task the other hemisphere was doing. For example, when the left hemisphere was doing the easy task, the right hemisphere's performance was better than when the left hemisphere was doing the hard task. Other investigators have subsequently provided additional evidence for this type of dual-task interference (Ivry, Franz, Kingston and Johnson, 1998; Pashler, Luck, Hillyard et al., 1994).

Interestingly, although the two hemispheres appear to compete for attentional resources, there are situations in which splitting the brain can actually improve performance in complex tasks. Holtzman and Gazzaniga (1985) presented a callosotomy patient with a complex spatial memory task in which some of the critical information was presented to one hemisphere and some to the other hemisphere. When neurologically intact controls were given this task, they integrated the visual information from the two visual fields and this made the task complicated. For the split-brain patient, however, each hemisphere perceived only half of the stimulus so each hemisphere performed a task that was much simpler than when the information was combined into a single task. The split-brain patient was therefore able to process the information twice as fast as the control subjects. Luck and colleagues (Luck, Hillyard, Mangun and Gazzaniga, 1989, 1994) have reported similar results for visual search tasks. As long as the stimulus array is divided between the two visual hemifields, visual search can proceed faster for split-brain patients than for neurologically intact controls.

Attentional mechanisms are clearly complex and research with split-brain patients has revealed some surprising truths. Two hemispheres share control of attentional resources. Several researchers have attempted to reconcile these findings. Kingstone and colleagues (Ens and Kingstone, 1997; Kingstone, Grabowecky, Mangun et al., 1997) suggest a resolution to this conflict by considering that the hemispheres interact quite differently in their control of reflexive (exogenous) and voluntary (endogenous) attentional processes. They propose that reflexive attentional orienting occurs independently in each hemisphere, while voluntary attentional orienting involves a single shared resource with control preferentially lateralized to the left hemisphere. Thus, when the left hemisphere is engaged in voluntary orienting, it over-rides voluntary orienting by the right hemisphere. This hypothesis explains not only low-level effects of attentional orienting, but also bears on more complex behaviors such as visual search. For example, when the number of items in a search array is small, attentional orienting is largely reflexive in nature, and the two hemispheres act independently. On the other hand when the number of items in the array is large, or the search is driven by strategic demands, attentional orienting is largely volitional and is lateralized to the left hemisphere (Kingstone, Ens, Mangun and Gazzaniga, 1995).

Another similar theory of attention has been proposed recently by Luck and Hillyard (1999). They suggest that there may be multiple attentional mechanisms with different patterns of hemispheric control. They propose that multiple mechanisms of attention operate at different stages of processing, some of which are shared across the disconnected hemispheres and others that might be independent.

The effects of callosotomy on memory

A great deal of research has been focused on memory processes and the ways in which the two hemispheres interact during the processes of acquisition and retrieval. Early studies on the effects of callosotomy on memory were often contradictory. One of the earliest studies on memory in callosotomy patients (Zaidel and Sperry, 1974) concluded that disconnecting the two hemispheres had significant and lasting effects on memory in these patients. Particularly affected were such functions as nonverbal memory and short story recall. The conclusions of that study, however, were based on comparison
A second related question concerns attentional resources. Does each hemisphere have its own attentional resources, or are these resources shared between the hemispheres? The work of a number of researchers suggests that the latter possibility best accounts for the experimental findings. Holtzman and Gazzaniga (1982) designed a task in which the two hemispheres were each given a series of items to remember. In the ‘easy’ condition, the same stimulus was presented repeatedly. In the ‘hard’ condition, a series of different items were presented. They found that the performance of each hemisphere was affected by the difficulty of the task the other hemisphere was doing. For example, when the left hemisphere was doing the easy task, the right hemisphere’s performance was better than when the left was doing the hard task. Other investigators have subsequently provided additional evidence for this type of dual-task interference (Ivy, Franz, Kingston and Johnson, 1998; Pashler, Luck, Hillyard et al., 1994).

Interestingly, although the two hemispheres appear to compete for attentional resources, there are situations in which splitting the brain can actually improve performance in complex tasks. Holtzman and Gazzaniga (1985) presented a callosotomy patient with a complex spatial memory task in which some of the critical information was presented to one hemisphere and some to the other hemisphere. When neurologically intact controls were given this task, they integrated the visual information from the two visual fields and this made the task complicated. For the split-brain patient, however, each hemisphere perceived only half of the stimulus so each hemisphere performed a task that was much simpler than when the information was combined into a single task. The split-brain patient was therefore able to process the information twice as fast as the control subjects. Luck and colleagues (Luck, Hillyard, Mangun and Gazzaniga, 1989, 1994) have reported similar results for visual search tasks. As long as the stimulus array is divided between the two visual hemifields, visual search can proceed faster for split-brain patients than for neurologically intact controls.

Attentional mechanisms are clearly complex and research with split-brain patients has revealed some of the ways the two hemispheres share control of attention while also competing for attentional resources. Several researchers have attempted to reconcile these findings. Kingstone and colleagues (Enns and Kingstone, 1997; Kingstone, Gruboweczy, Mangun et al., 1997) suggest a resolution to this conflict by considering that the hemispheres interact quite differently in their control of reflexive (exogenous) and voluntary (endogenous) attentional processes. They propose that reflexive attentional orienting occurs independently in each hemisphere, while voluntary attentional orienting involves a single shared resource with control preferentially lateralized to the left hemisphere. Thus, when the left hemisphere is engaged in voluntary orienting, it over-rules voluntary orienting by the right hemisphere. This hypothesis explains not only low-level effects of attentional orienting, but also bears on more complex behaviors such as visual search. For example, when the number of items in a search array is small, attentional orienting is largely reflexive in nature, and the two hemispheres act independently. On the other hand, when the number of items in the array is large, or the search is driven by strategic demands, attentional orienting is largely volitional and is lateralized to the left hemisphere (Kingstone, Enns, Mangun and Gazzaniga, 1995).

Another similar theory of attention has been proposed recently by Luck and Hillyard (1999). They suggest that there may be multiple attentional mechanisms with different patterns of hemispheric control. They propose that multiple mechanisms of attention operate at different stages of processing, some of which are shared across the disconnected hemispheres and others that might be independent.

The effects of callosotomy on memory

A great deal of research has been focused on memory processes and the ways in which the two hemispheres interact during the processes of acquisition and retrieval. Early studies on the effects of callosotomy on memory were often contradictory. One of the earliest studies on memory in callosotomy patients (Zaidel and Sperry, 1974) concluded the disconnecting the two hemispheres had significant and lasting effects on memory in these patients. Particularly affected were such functions as nonverbal memory and short story recall. The conclusions of that study, however, were based on comparisons between post-surgical patients and age- and intelligence-matched controls. These types of measurements are not clear to what extent memory deterioration was due to the operation and its sequelae or callosotomy. In some cases, improvement in performance was observed.

A comparison between pre- and post-surgical patients and controls would be most informative. Such a comparison was done by a recent study (Wilson, 1995). The study demonstrated that improvement in performance was not compensated for by equivalent deterioration in control conditions, suggesting that the memory loss was due to the operation and not to callosotomy per se.

The effects of callosotomy on memory are complex and depend on the nature of the task and the type of memory. Further research is needed to understand the underlying mechanisms and to develop effective therapeutic interventions.
and Gazzaniga (1995) studied the ability of the two hemispheres of a callosotomy patient to discriminate between items presented at study and items similar to studied items but that were not presented in the study session. They found that the right hemisphere is very good at this discrimination but the left hemisphere is not (see also Phelps and Gazzaniga, 1992). This pattern was found with abstract patterns, faces and words. If the visual/verbal dichotomy was correct, then the performance of the two hemispheres should have varied by stimulus type. Instead, each hemisphere appeared to have its own processing style regardless of whether the stimuli were verbal or pictorial. The data suggest that the right hemisphere stores what it sees without making inferences. Conversely, the left hemisphere stores inferences about the presented material and these inferences confuse judgments about similar items. This notion that the two hemispheres have different processing styles may have broader implications for the roles of the two hemispheres in other cognitive functions. It relates directly to the left-brain interpreter postulated by Gazzaniga.

The interpreter

In the early 1970s, testing on split-brain patients revealed an interesting phenomenon. In the single-field version of the task, one hemisphere is presented with a target picture followed by an array of pictures. The patient is instructed to point to the picture most closely associated with the target picture. If the right hemisphere is presented with the target, then the patient would point with the left hand - the hand that is controlled by the right hemisphere. If 'cherry' was the target picture and the pictures in the array were 'apple', 'toaster', 'chicken', and 'glass', then the patient should point to 'apple' since apples and cherries are both fruits (Gazzaniga and LeDoux, 1978). This paradigm revealed that both hemispheres of split-brain patients could make such associations. Although this sheds light on the cognitive capabilities of the two hemispheres, the more interesting experiment is the double-field version. In this task, a split-brain patient is shown two different pictures simultaneously, one in each visual field. For example, the right hemisphere might be shown a picture of a snow scene and the left hemisphere a chicken claw. Each hemisphere then responds by pointing to the associated picture with the contralateral hand. The patient is then asked to explain his response. The left hemisphere, dominant for speech in most split-brain patients, has knowledge of only one of the two presented pictures. But since each hand responds to the target presented to the contralateral hemisphere, he has pointed to two pictures. How will the patient explain his response? Without hesitation, patient P.S. responded to this example by saying, "I saw a claw and I picked the chicken, and you have to clean out the chicken shed with a shovel". The left hemisphere has no access to the snow scene that the right hemisphere has associated with the shovel, but immediately incorporates the shovel into its response. Based on observations like this, Gazzaniga postulated the existence of a left-hemisphere interpreter. The interpreter attempts to make sense of the world by forming beliefs and inferences about internal bodily states and about the actions of others (Gazzaniga, 1992).

The chicken and shovel example demonstrates the interpretation of actions. The interpretation of internal bodily states is illustrated in an experiment with patient V.P. She was shown film segments using the previously described dual-Purkinje-image eyetracker which permits extended lateralization of visually presented stimuli. Some of the film segments depicted violent scenes, such as one in which one person was throwing another into a fire. When this was shown to the right hemisphere of patient V.P., she responded, "I don't really know what I saw. I think just a white flash. Maybe some trees, red trees like in the fall. I don't know why, but I feel kind of scared. I feel jumpy. I don't like this room, or maybe it's you getting me nervous". She subsequently confided in one of the experimenters, "I know I like Dr Gazzaniga, but right now I'm scared of him for some reason" (Gazzaniga, 1992).

The tendency to seek explanations for emotional arousal has also been demonstrated in neurologically normal subjects. Schacter and Singer (1962) injected subjects with epinephrine, which activates the sympathetic nervous systems and causes increased heart rate, hand tremors and facial flushing. Some subjects were informed that the drug would cause these symptoms and other subjects were not. The subjects were then put into a waiting room with another
pointing to his forehead, and another, to his mouth.

This method, in most cases, led one of the participants to draw the line from his forehead to the anterior temporal lobe.

The paradigm assumes that when a person is asked to perform a task requiring the use of a specific brain hemisphere, they will be able to do so consistently.

The paradigm has been used in research to study the functioning of the two hemispheres in the brain.

In this paradigm, participants are asked to respond to a series of visual stimuli, with the stimuli presented to one hemisphere at a time.

The paradigm has been used to study a wide range of cognitive functions, including spatial processing, language, and emotional processing.

The paradigm has also been used to study the effects of brain lesions on cognitive function.

The paradigm is a useful tool for studying the functioning of the two hemispheres in the brain, and has been used in a variety of research studies.
tendency to create theories about random sequences is detrimental to performance. In many situations, however, there is an underlying pattern and in these situations the left hemisphere's drive to create order from apparent chaos would be the best strategy. In an intact brain, both of these cognitive styles are available and can be implemented depending on the situation. Although the interpreter allows for a great deal of cognitive flexibility that would otherwise not be available to us, it also opens the door to errors that are uniquely human.

"Mistakes are the very basis of human thought embedded there, feeding the structure like root nodules. If we were not provided with the knack of being wrong, we could never get anything useful done ... The hope is in the faculty of wrongness, the tendency toward error. The capacity to leap across mountains of information to land lightly on the wrong side represents the highest of human endowment ... The lower animals do not have this splendid freedom. They are limited, most of them, to absolute infallibility. Cats, for all their good side, never make mistakes. I have never seen a maladroit, clumsy or blundering cat. Dogs are sometimes fallible, occasionally able to make charming minor mistakes, but they get this way trying to mimic their masters (Thomas, 1979, p. 561)."

What can the split-brain tell us about consciousness?

Our brains are an infinitely complex series of neural networks subserving a myriad of functions. Decades of split-brain research have revealed some of the specialized functions of the two hemispheres. Lesion studies and functional brain imaging have further revealed regional specificity within each hemisphere. The remarkable degree to which specific functions can be localized within and between hemispheres has led some researchers to suggest that the human brain can be thought of as a set of modules, each of which is involved in specific functions - physiological, perceptual, and cognitive, among others. Although humans pride themselves on being the most sapient of all species, much of what our brains do remains entirely outside of our conscious awareness and control. Perceptual illusions provide striking demonstrations of the degree to which our brains process events without any conscious control on our part. In the optical illusion depicted in Fig. 6, we cannot help but perceive the parallelogram as a different size and shape than the parallelogram on the right. Even after confirming with a ruler that both parallelograms are in fact the same size and shape, we simply cannot perceive them that way. Similarly, we perceive the top line in Fig. 7 as distinctly longer than the bottom line even though we know for a fact that the two lines are the same length. These are both visual illusions, but illusions can occur across as well as within modalities. In the McGurk effect (McGurk and MacDonald, 1976), seeing a face mouthing the phoneme /ba/ causes us to perceive /ba/ even when told that the sound track...
has been dubbed and the phoneme we are actually hearing is /da/. When we close our eyes, we can clearly hear /da/. With our eyes open, however, we cannot help but hear /ba/. These illusions serve to illustrate that we have little conscious control over the way we perceive the world.

Despite the modularity of our minds and the number of things our brains do without our conscious knowledge, we retain the feeling that we are integrated and unified and that we have control over our thoughts and actions. Split-brain research gives us some insight into what underlies this feeling. Split-brain patients have occasionally been described as having two brains. Although this notion is intuitively appealing, the post-surgical reports of the patients themselves stand in direct contrast to this. They report no differences in their consciousness as a result of surgery. It is intriguing to consider how two isolated hemispheres can give rise to a unitary sense of consciousness. The left-hemisphere interpreter may provide the answer to this question. In the split-brain patient, the interpreter seamlessly provides explanations for behaviors generated by the right hemisphere. Because the left hemisphere has no knowledge of the source of the behavior, the explanations are often spurious. Nevertheless, they are generated easily with no apparent concern that they are necessarily post hoc. Schacter and Singer demonstrated that this same interpretative process is common in subjects whose hemispheres are connected. The interpreter, in its quest for order, generates hypotheses and explanations for a myriad of self- and other-generated actions and emotions. This module which can incorporate and ‘explain’ anything that happens to us or around us may provide the basis for our illusionary sense of personal integration and control over ourselves and the world around us. Thus the interpreter may be synonymous with, or at least be essential for, consciousness.

Conclusion

The story of the human split brain is remarkable in many ways. The discovery that two functionally independent hemispheres – in some sense two independent minds – could coexist in the same head remains as compelling now as when it was first reported. Stories of this nature in both the scientific and popular presses almost overshadowed the fact that commissural section was a successful surgical intervention that dramatically reduced seizures in most cases, and eliminated them in some. Nevertheless, it is the non-clinical sequelae of severing the cortical commissures that remain the most interesting findings to come from the human split brain.

Experiments with split-brain patients have provided dramatic confirmation of hemispheric asymmetries for language and visuospatial functions that had been suggested by lesion studies, as well as revealing more subtle differences that had hitherto been unsuspected. As a result, split-brain studies have informed our understanding of the cortical organization of almost every cognitive system. Many of the functional specializations of the two hemispheres would have been difficult or impossible to discover in the intact brain, since they can be masked by an intact corpus callosum.

In addition to the providing invaluable data about hemispheric asymmetries, split-brain studies have also revealed a great deal about the function of the corpus callosum. Comparisons between patients with varying degrees of callosal section have demonstrated that the topographical organization of the corpus callosum is reflected in the kinds of information that can pass through different callosal regions. Similarly, investigations with fully-sectioned patients have begun to elucidate the functions and limitations of the subcortical connections between the hemispheres.

It is doubtful whether any other surgical intervention has had such a dramatic impact on our understanding of so many diverse areas of human brain function. The relatively small group of split-brain patients has been studied extensively by hundreds of researchers over the last four decades. Despite — or perhaps because of — the volume of literature that has been generated to date, the study of split-brain patients continues to be an exciting and vibrant field.

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