

ESSAY

## Forty-five years of split-brain research and still going strong

Michael S. Gazzaniga

Abstract | Forty-five years ago, Roger Sperry, Joseph Bogen and I embarked on what are now known as the modern split-brain studies. These experiments opened up new frontiers in brain research and gave rise to much of what we know about hemispheric specialization and integration. The latest developments in split-brain research build on the groundwork laid by those early studies. Split-brain methodology, on its own and in conjunction with neuroimaging, has yielded insights into the remarkable regional specificity of the corpus callosum as well as into the integrative role of the callosum in the perception of causality and in our perception of an integrated sense of self.

In the 1970s, when the modern era of split-brain research began, the idea of mapping the cortical circuits of perception, memory and cognition was revolutionary. While Karl Lashley was heavily committed to the idea that neurons had little specificity<sup>1</sup>, Donald Hebb was strenuously arguing the opposite<sup>2</sup>. Roger Sperry's ongoing work on neural development<sup>3</sup>, which represented a frontal assault on Paul Weiss's idea that function precedes form, was well underway<sup>4</sup>. Split-brain research began in this context.

Although the 1970s marked the beginning of modern split-brain research, the first known callosotomy surgeries were carried out 30 years earlier (see [TIMELINE](#)). Van Wagenen and Herren introduced the concept of split-brain surgery in an effort to control the seizures of patients with intractable

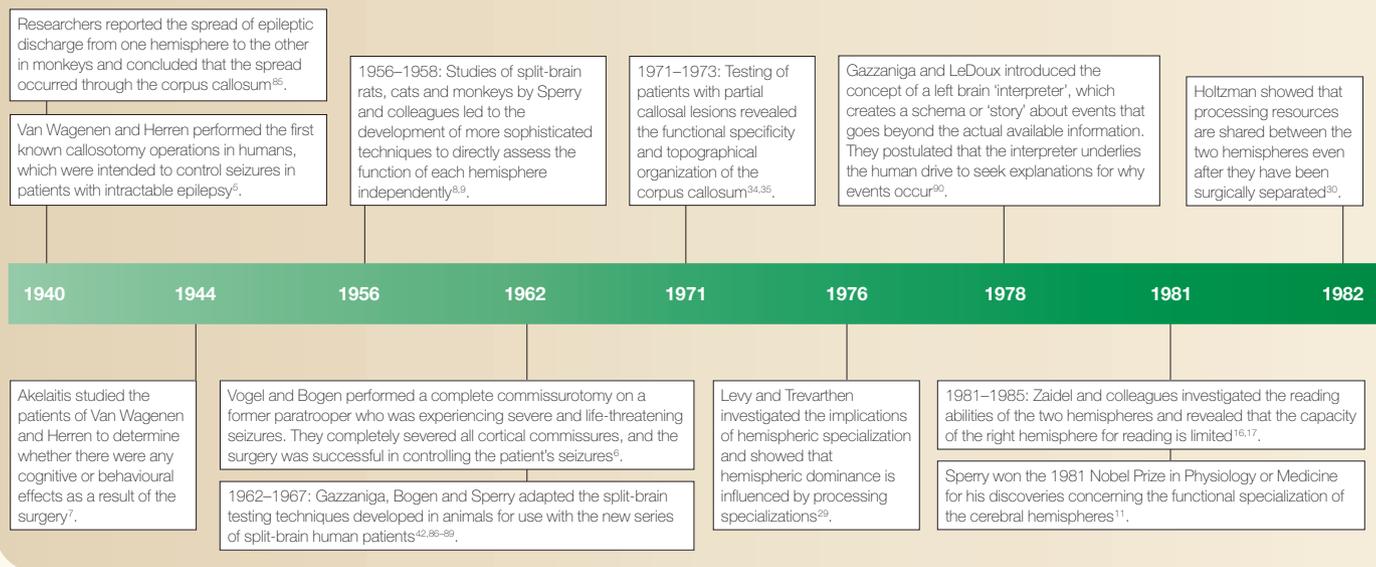
epilepsy<sup>5</sup>. However, the surgeries did not lead to a reduction in seizures and they stopped performing the procedure. Thirty years later, Philip Vogel and Joseph Bogen carried out a complete commissurotomy on a former paratrooper who was experiencing severe and life-threatening seizures<sup>6</sup>. They speculated that the earlier surgeries performed by Van Wagenen and Herren had been unsuccessful because the corpus callosum had not been fully severed. During surgery, Vogel and Bogen completely severed all cortical commissures, which was successful in controlling the patient's seizures<sup>6</sup>.

Van Wagenen and Herren's original patients were studied by A. J. Akelaitis at the University of Rochester in the 1940s, and he concluded that the disconnection of the two hemispheres did not result in any cognitive or behavioural effects<sup>7</sup>. In the intervening years, however, studies of split-brain rats, cats and monkeys by Sperry and colleagues resulted in the development of more sophisticated techniques with which to directly assess the function of each hemisphere independently<sup>8,9</sup>. The Caltech (California Institute of Technology) environment was teeming with experiments showing that severing the cerebral commissures in non-human animals profoundly limited the exchange of information between hemispheres. However, a huge problem remained for those committed to the idea of the importance of specific neural circuits: Akelaitis claimed that, in humans, severing the corpus callosum has none of the dramatic effects seen in animals<sup>7</sup>. How could this be?

During my senior year at Dartmouth College I tried to study Van Wagenen and Herren's original patients. I designed many experiments in an effort to reveal the effects of callosal disconnection in humans, only for them to go unused on the Rochester patients. The effort was not lost, however. By the time I arrived at Caltech, Joseph Bogen, then a neurosurgical resident at Loma Linda Medical School, had developed an argument and rationale for once again introducing callosal surgery as a reasonable approach for controlling otherwise intractable epilepsy<sup>5</sup>. He was extremely familiar with the work of the Sperry laboratory, and asked Sperry if a researcher might be interested in testing such patients both pre- and post-operatively. When I walked in the front door for my first day of graduate work, the assignment was given to me. The split-brain experiments I had designed during my senior year at Dartmouth would finally be implemented, but on the Caltech, rather than the Rochester, patients. Nothing can possibly replace a singular memory of mine: that of the moment when I discovered that case W.J. could no longer verbally describe (from his left hemisphere) stimuli presented to his freshly disconnected right hemisphere. An experiment I had designed, executed and carried out alone as a mere graduate student at Caltech had worked<sup>10</sup>. With it, the modern split-brain story was born, and I was to spend the next 5 years in a sort of sublime state, working every day at the finest scientific institution in the world with one of the greatest biologists of all time, Roger Sperry<sup>11</sup>.

Over the years, split-brain research has afforded important insights into neural mechanisms, as the function of each hemisphere can be tested independently of the other. Patients studied not only at Caltech, but also at Harvard, Yale, the Medical College of Ohio, Dartmouth, UC Davis and, more recently, in Italy, have all revealed and confirmed the overall pattern of results. Severing the entire callosum blocks the interhemispheric transfer of perceptual, sensory, motor, gnostic and

Timeline | Major milestones in the history of split-brain research



other forms of information in a dramatic way, allowing us to gain insights into hemispheric differences as well as the mechanisms through which the two hemispheres interact (for reviews, see REFS 12–14). Akelaitis got it wrong, probably because his tests were not sophisticated enough and/or his patients did not have complete callosal sections<sup>7</sup>. Myers and Sperry, and many others got it right<sup>8,9</sup>. Their split-brain work in animals paved the way for split-brain work in humans.

The most obvious functional hemispheric asymmetry in humans is in the domain of language. In the vast majority of the population, the left hemisphere is dominant for language, and speech is generated only from the left hemisphere<sup>15</sup>. The left hemisphere is also specialized for processing written language, although the right hemisphere does have a limited capacity for reading. It is able to read whole words (ideographic lexical/semantic access) but is unable to convert graphemes to phonemes, a task that is easily accomplished by the language-dominant left hemisphere<sup>16,17</sup>.

Although most findings from work with split-brain patients were consistent with previous studies of patients with unilateral lesions, some studies have changed our view of the neural organization of language, and have revealed unexpected modularity of function. One such example is the left-handed split-brain patient V.J., who is able to generate speech from her left hemisphere but not from her right<sup>18</sup>, and, conversely, is able to generate written language from her right hemisphere but not her left. Previously, it had been assumed that spoken and written

language relied on similar cognitive mechanisms, and were therefore controlled by the same hemisphere. However, studies with V.J. indicate that spoken and written language output can be controlled by independent hemispheres<sup>18</sup>.

The left hemisphere's dominance for language is complemented by the right hemisphere's specialization for visuospatial processing. Studies with split-brain patients have revealed right hemisphere superiority for various tasks involving such components as part-whole relations<sup>19</sup>, spatial relationships<sup>20</sup>, apparent motion detection<sup>21</sup>, mental rotation<sup>22</sup>, spatial matching<sup>23</sup> and mirror image discrimination<sup>24</sup>. Despite hemispheric differences in the performance of these tasks, the two hemispheres are equally able to perform many visual tasks that lack a spatial component<sup>25</sup>.

Despite cortical disconnection, the two hemispheres are connected through sub-cortical pathways in split-brain patients. In some cases, the two hemispheres seem to function completely independently. For example, using visual search tasks, it has been shown that in patients who have undergone complete callosotomy, each hemisphere maintains an independent focus of attention<sup>26</sup>. Bilateral stimulus arrays can, therefore, be scanned faster by split-brain patients than by neurologically normal individuals. However, in other cases there is evidence for interhemispheric integration, even when the cortical commissures have been severed<sup>27</sup>. Binary information is transferred between the two hemispheres of split-brain patients<sup>28</sup>, and there is evidence

that processing resources are also shared by the two hemispheres.

Hemispheric dominance in split-brain patients is influenced by processing specializations such that the hemisphere that is specialized for a given task will dominate processing in that task<sup>29</sup>. In addition, task difficulty influences interhemispheric integration. Increasing the difficulty of a task in one hemisphere draws resources away from the other and results in poorer performance by that other hemisphere<sup>30</sup>. The effect of task difficulty on hemispheric integration has also been shown in the intact brain by Banich and colleagues<sup>31–33</sup>. They propose that simpler tasks are best processed in one hemisphere, whereas more complex tasks benefit from the increased computational power provided by interhemispheric cooperation. Their studies show that when the processing capabilities of a single hemisphere are inadequate for a given task, the processing resources of the other hemisphere are recruited<sup>31–33</sup>.

Whereas studies of patients with complete callosotomies provide insights into callosal versus non-callosal interhemispheric integration, studies of patients with partial lesions of the corpus callosum have yielded insights into the functional specificity of the callosum<sup>34–36</sup>. Damage to particular callosal regions blocks the transfer of particular types of information. Therefore, there are areas of the callosum dedicated to the transfer of visual information, somatosensory information, motor information and so on. Testing patients with partial callosal lesions revealed the functional specificity and

Corballis introduced the concept of a right hemisphere 'interpreter' on the basis of the right hemisphere's superiority for visuospatial processing. As visual perception is fundamentally ambiguous, the right hemisphere interpreter uses perceptual information to create a veridical representation of the world<sup>91</sup>.

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Luck and co-workers showed that each hemisphere of patients who have undergone complete callosotomy maintains an independent focus of attention<sup>26</sup>.

topographical organization of the corpus callosum<sup>34–36</sup>.

This brings us to the present era and to why there is new excitement about unearthing the networks of the brain and developing a deeper understanding of the mind. The evolution of split-brain testing has led us to new frontiers (for reviews of split-brain research, see REFS 12–14,37–39). In the early days of split-brain testing, research with split-brain patients was at the cutting edge and revealed previously unknown aspects of hemispheric specialization and interhemispheric interaction. As the pace of scientific discovery quickened, the focus of split-brain research became aimed at confirming and extending findings from other methodologies. What is exciting about the present era is that split-brain research is now leading the way again, rather than following in the wake of other methodologies. Split-brain research is informing neuroimaging studies and is providing the basis for interpreting neuroimaging results. Not only can these powerful clinical cases be used to elucidate facts about cerebral lateralization, but we can now, through modern brain imaging techniques, identify processing networks that involve both hemispheres, and also identify the actual neuronal tracts that are involved in connecting the processing sites. Combining new neuroimaging techniques with well-established neuropsychological methodologies offers powerful advances in our understanding of the cerebral mechanisms of cognition. Below, I review three such advances from our laboratory that encompass a wide range of issues.

### Callosal transfer in the intact brain

One of the clear consequences of split-brain surgery is the specific nature of which types of information can and cannot be transferred between hemispheres following the lesion. First, there are marked differences between species. A monkey with a severed corpus callosum easily transfers visual information of all types through the remaining anterior commissure<sup>40</sup>. In humans, a severed callosum precludes all such visual communication, even though the anterior commissure remains intact<sup>41–44</sup>. This simple fact alerts us to the differences that exist among homologous structures as we attempt to build animal models of human mechanisms.

Although in humans full callosal disconnection causes a general breakdown of interhemispheric transfer, can local callosal lesions reveal an underlying modality-specific organization? Studies of patients with partial callosal lesions show that the callosum is organized in a specific way, with the more posterior regions transferring basic sensory information that relates to vision, audition and somatosensory information<sup>35,45,46</sup>, whereas the more anterior regions seem to be involved in the transfer of attentional resources and higher cognitive information<sup>47</sup>. This general framework captures the first order of callosal processes. However, with modern brain imaging a much more dynamic picture of callosal function and organization is beginning to emerge.

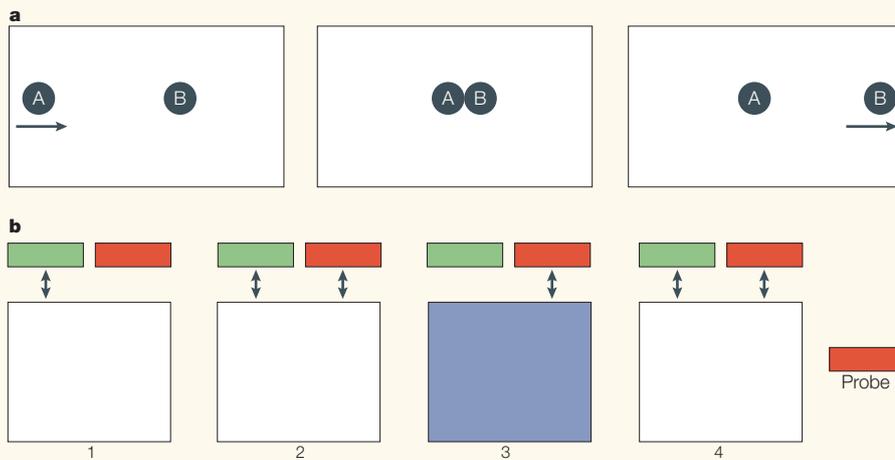
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Diffusion tensor imaging (DTI) is leading to major advances in understanding callosal mechanisms in healthy individuals. This neuroimaging technique provides a way of characterizing the structural organization of the corpus callosum and other white matter tracts, which cannot be seen in such detail on conventional structural MRI. Essentially, DTI provides information about water diffusion in three-dimensional space during a given period of time. In the brain, water diffusion depends on microstructural tissue properties<sup>48–50</sup>. In white matter, water diffusion is faster in parallel with the axonal

direction than perpendicular to the axonal direction (for a review, see REF 51). Fractional anisotropy (FA) is a measure obtained from DTI data that represents the extent to which the movement of water molecules is restricted by the axonal microstructure — that is, higher FA values indicate more restricted diffusion. Studies of FA measurements in patients with degenerative diseases indicate that axon myelination is a major contributing factor to FA values<sup>52</sup>, although axon density, the presence of crossing fibres and other factors also influence the measurement of the direction and magnitude of water diffusion<sup>48,53</sup>. Therefore, FA values can be used to indirectly assess the structural integrity of the corpus callosum.

Baird and colleagues recently combined DTI, functional imaging and behavioural data that were collected during the performance of a task that required interhemispheric transfer to explore individual differences in callosal transmission<sup>54</sup>. Healthy participants were asked to identify objects presented from unusual viewpoints. Successful completion of this task requires information transfer from the right parietal cortex, which is responsible for recognizing objects in unusual orientations<sup>55</sup>, to the left inferior frontal cortex, which is responsible for object naming<sup>56</sup>. Naming times were correlated with relative signal changes on functional MRI (fMRI) data to localize regions of cortical activity in superior parietal and inferior frontal regions that were more active with longer reaction times. The degree of blood oxygen level dependent (BOLD) signal change within these cortical regions (assessed with fMRI) was used to predict individual differences in FA values through the corpus callosum (assessed with DTI). We found that shorter naming times were associated with increased FA in the splenium of the corpus callosum, whereas longer reaction times were associated with increased FA in the genu<sup>54</sup>. These findings indicate that there are two callosal pathways for transferring information from the right parietal cortex to the left inferior frontal cortex: an efficient posterior pathway between the parietal cortices, and a slower anterior pathway between the inferior frontal cortices. More importantly, this study showed that DTI, functional imaging and behavioural performance measures can be combined to investigate the functional connectivity between the two hemispheres of an intact brain.

At present, Molly Colvin is expanding this work by combining DTI with behavioural measures of interhemispheric transfer time (IHTT) to research the functional specificity



**Figure 1 | Causal perception and causal inference in two split-brain patients. a** | Perceptual task. The stimuli for the collision experiment consisted of three panels that depicted the motion of a ball (A) towards another ball (B), and the subsequent motion of B. The movements of the two balls were either contiguous in space and time, or included a small spatial or temporal gap. Note that the labels A and B are for illustrative purposes only and did not appear on the actual stimuli. In both of the split-brain patients, the right hemisphere performed better than the left in judging the causal nature of the collisions. **b** | Inferential task. Stimuli for the causal inference experiment consisted of the sequential presentation of four stimulus interactions (1–4) and a response probe, which represented one trial. Arrows indicate the movement of one or both of the coloured ‘switches’ on each presentation. One switch turned on the ‘lightbox’ (large square) on each trial. In presentation 3, the lightbox was not illuminated. After observing four interactions between the switches and the lightbox, participants were required to judge whether the response probe represented the switch that had caused the illumination of the box. In both patients, the left hemisphere performed better than the right in drawing simple causal inferences. Data from REF. 66.

Specifically, it was expected that low callosal FA values would be associated with greater activity in the non-dominant hemisphere during memory encoding of words (a task that is thought to normally depend on the left hemisphere), thereby impairing subsequent recognition. As expected, during word encoding, the group with low callosal FA values showed greater right inferior frontal lobe activity. However, right inferior frontal lobe activity was associated with impaired word recognition only in individuals with high callosal FA values, which indicates that high FA values in the callosum are associated with greater interference between the two hemispheres when one hemisphere is specialized to perform the task. Therefore, individual differences in callosal organization might determine rates and routes of interhemispheric integration, and influence functional lateralization<sup>62,63</sup>.

This new evidence from neuroimaging is, therefore, causing us to rethink earlier conclusions about interhemispheric interaction and recruitment that were drawn from split-brain testing alone. Converging evidence from the two methodologies is likely to continue to advance our knowledge of the way in which the hemispheres interact. Combining DTI, fMRI and behavioural IHTT measures promises to provide a powerful method for investigating callosal function in the intact, living brain.

### Understanding causality

Understanding cause and effect is fundamental to making sense of the dynamic physical world. For example, expectations about interactions between objects, such as collisions, are already apparent in 6-month-old infants<sup>64</sup>. It has been argued that understanding causality depends on both perceptual and inferential components. According to Michotte, simple two-dimensional displays of objects ‘colliding’ evoke an illusion of causality that is constructed by the visual system in a manner similar to the construction of other high-level percepts, such as three-dimensional object structure from motion<sup>65</sup>. However, the evidence for causal perception is taken from observers’ reports, which are open to post-perceptual interpretation. Split-brain patients provide a means of teasing apart the processes that are involved in the perception of causation.

Matt Roser and colleagues<sup>66</sup> investigated whether causal perception and causal inference rely on common or distinct processes by testing two split-brain patients and a group of neurologically normal participants. In one experiment, participants observed collision

of the corpus callosum<sup>57</sup>. Because FA measures are sensitive to the axonal properties that are thought to be related to the type of information being transferred between the two hemispheres<sup>58,59</sup>, it was expected that FA measures obtained from specific callosal sub-regions would correlate with different measures of IHTT. She found significant correlations between FA measures and IHTT in the expected callosal regions, which provides strong evidence for the functional specificity of callosal sub-regions in the intact human brain. For example, correlations between FA values through the midbody of the corpus callosum — a region thought to connect the motor cortices — were found when the task required rapid visuomotor integration. Furthermore, the relationship between callosal FA values and IHTT seemed to depend on task demands. For tasks that required rapid interhemispheric integration (for example, transfer of visual information to the hemisphere directing a motor response), individuals with high callosal FA values had faster IHTTs. For tasks that benefited from intrahemispheric processing before interhemispheric integration (for example, some cases of bilateral stimulus presentations), individuals with low callosal FA values had faster IHTTs<sup>57</sup>.

Colvin has gone on to explore how callosal organization relates to lateralized cortical activity. In recent years, there have been several intriguing studies showing bilateral neural activation in the ageing brain for tasks that are strongly lateralized to one hemisphere in the brains of young adults<sup>31,60</sup>. One explanation for this phenomenon is that the bilateral activation occurs in response to a diminishing capacity for neuronal processing in one hemisphere that results from the ageing process. A task that one hemisphere could solve or accomplish in a younger brain takes both hemispheres working together to complete in the ageing brain<sup>61</sup>. Indeed, a similar model seems to apply to individual variations in the performance of young adults. As task difficulty increases, young adults tend to show a performance benefit from involving both hemispheres<sup>31,60</sup>.

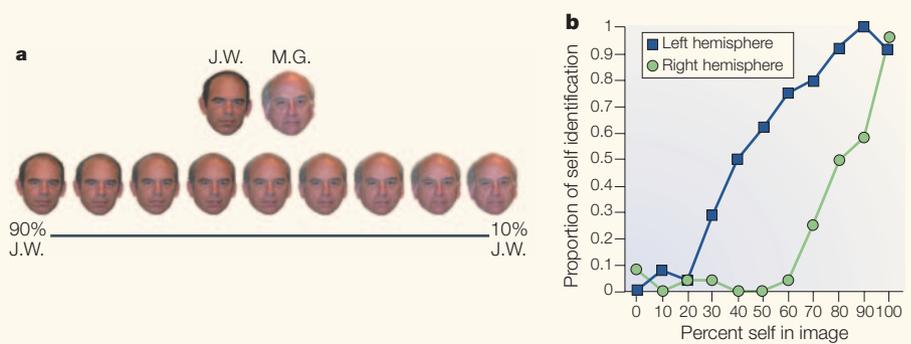
Explanations for using two hemispheres instead of one for harder tasks introduce the issues of how the corpus callosum allocates processing resources between hemispheres. In this regard, Colvin has made some intriguing observations about the relationship between callosal organization and activity in the non-specialized hemisphere, as well as about the impact of non-specialized cortical activity on performance of a lateralized task in healthy young adults<sup>62,63</sup>.

events, in which the spatial or temporal contiguity of the movements of the colliding objects was manipulated, and responded according to whether they thought the second movement was caused by the first (FIG. 1a). In a second experiment, participants observed a short sequence of events (the movement of switches and the illumination of a light) and had to infer, on the basis of contingencies between events, whether one event caused the other (FIG. 1b). The central question was whether the more inferential task (the second experiment) would be lateralized to the same hemisphere as the more purely perceptual judgement (the first experiment).

Interestingly, they found that the direct perception of causality and the ability to infer causality depended on different hemispheres in the divided brain. In both patients, the left hemisphere was able to draw simple causal inferences, but was unable to use this capacity to determine the causal nature of collision events. Conversely, the right hemisphere was sensitive to the causal nature of collision events but was unable to draw simple causal inferences. This finding implies that understanding causality is not a unitary process and that causal perception and causal inference can proceed independently. Therefore, causal perception did not depend on the ability to perform inference or interpretation at the simple level required by the inferential task.

Using fMRI in healthy participants, Fugelsang, Roser and colleagues<sup>67</sup> continued their investigations by identifying regions in the right hemisphere involved in perceiving causality. There were significantly higher levels of relative activation in the right middle frontal gyrus and the right inferior parietal lobule for causal relative to non-causal events. They manipulated both spatial and temporal contingencies, and found that some neural regions were activated by both factors (right prefrontal), whereas other regions were uniquely activated by one or other factor (right parietal cortex for spatial manipulations and right temporal cortex for temporal manipulations).

These data, combined with the results of the split-brain experiments<sup>66</sup>, allow for several observations about the nature of causal perception. They indicate that perception of physical causality is the result of cortical processes mediated by the right hemisphere. Conversely, higher-order causal inferences are based on left hemispheric processes. Therefore, in the intact brain, the coordinated activities of both hemispheres allow for a full understanding of causality in the physical world.



**Figure 2 | Face recognition of self versus a familiar other in a split-brain patient.** **a** | Nine faces were created by morphing an image of split-brain patient J.W.'s face with an image of M.G.'s face (a familiar other to J.W.) in 10% incremental shifts. Images were randomly presented to each of J.W.'s separated hemispheres. J.W. was asked to determine whether the image was himself or whether the image was M.G. **b** | J.W. showed a bias for self-recognition in the left hemisphere, which tended to recognize 'self' with only 40% of 'self' in the image. The right cerebral hemisphere required at least 80% of 'self' in the image for self-recognition to occur. Modified, with permission, from REF. 83 © (2002) Macmillan Magazines Ltd.

### Self-recognition

Severing the corpus callosum in humans has raised a fundamental question about the nature of the self: does each disconnected half brain have its own sense of self? Research with split-brain patients quickly established that each half brain is specialized for certain functions and is capable of processing stimuli without the obvious help or awareness of the opposite half brain. But could it be that each hemisphere has its own point of view, its own self-referential system that is truly separate and different from the other hemisphere<sup>68</sup>?

Early observations of split-brain patients indicated that this could be the case<sup>69</sup>. There were moments when one hemisphere seemed to be belligerent while the other was calm. There were times when the left hand (controlled by the right hemisphere) behaved playfully with an object that was held out of view while the left hemisphere seemed perplexed about why. However, of the dozens of instances recorded over the years, none allowed for a clear-cut claim that each hemisphere has a full sense of self. Although it has been difficult to study the 'self' *per se*, there have been intriguing observations about perceptual and cognitive processing relating to the self.

Research has revealed much about the processes and brain structures that support the recognition of familiar others (for example, friends, family members and movie stars). Both functional imaging and patient studies show that face recognition is typically reliant on structures in the right cerebral hemisphere. For example, we have shown that split-brain patients perform significantly better on tests of face recognition when familiar faces are presented to the right hemisphere compared with the left hemisphere<sup>70</sup>. Similarly, damage to specific

cortical areas in the right hemisphere impairs the ability to recognize others<sup>71–75</sup>.

But is the right hemisphere similarly specialized for self-recognition? Although some support has been garnered for this idea<sup>76–78</sup>, the available evidence is inconclusive. Neuroimaging studies have revealed that highly self-relevant material (for example, autobiographical memories) activates a range of cortical networks in the left hemisphere that could, potentially, support self-recognition and a host of related cognitive functions<sup>79–82</sup>. Therefore, whereas the recognition of familiar others relies primarily on structures in the right hemisphere, self-recognition might be supported by additional left-lateralized cognitive processes. To investigate this possibility, David Turk and colleagues assessed face recognition of self versus a familiar other in a split-brain patient<sup>83</sup>.

Patient J.W. viewed a series of facial photographs that ranged from 0% to 100% self images. A photograph of me (M.G.), a long time associate of J.W. (that is, a 'highly familiar' other), was used to represent 0% self and a photograph of J.W. was used to represent 100% self. Nine additional images were generated using computer-morphing software, with each image representing a 10% incremental shift from M.G. to J.W. (FIG. 2a). In one condition (self-recognition), J.W. was asked to indicate whether the presented image was himself; in the other condition (familiar other recognition), he was asked to indicate whether the image was M.G. The only difference across the two conditions was the judgement that was required ('Is it me?' versus 'Is it Mike?').

The results revealed a double dissociation in J.W.'s face recognition performance. His left hemisphere showed a bias towards

recognizing morphed faces as self (FIG. 2b), whereas his right hemisphere showed the opposite pattern; that is, biased recognition in favour of a familiar other. In short, the left hemisphere is quick to detect a partial self image, even one that is only slightly reminiscent of the self, whereas the right brain needs an essentially full and complete picture of the self before it recognizes the image as such. In the left hemisphere, there was, essentially, a linear relationship between the amount of self in the image and the probability of detecting self. The right hemisphere, on the other hand, did not recognize the image as self until the image contained more than 80% self. The finding that the left hemisphere requires less self in the image for self-recognition might reflect a key role of the left hemisphere in the retrieval of self-knowledge, or might depend on the left-brain interpreter taking whatever information is available and making a judgement call on the basis of that information.

Overall, the data indicate that a sense of self arises out of distributed networks in both hemispheres<sup>68,84</sup>. It is likely that both hemispheres have processing specializations that contribute to a sense of self — and that sense of self is constructed by the left hemisphere interpreter on the basis of the input from these distributed networks.

### Final perspectives

The saga continues for those interested in how studying patients with surgical or natural lesions, as well as healthy individuals, in a brain-imaging environment can illuminate basic mechanisms of human cognition and personal conscious experience. One approach feeds off the other, and together new observations can be made. I see no end to the possibilities. We have moved from a static view of what happens in a particular cortical region to a much more interactive view of how the whole cortex, interacting through white matter fibre systems, orchestrates the entire cerebral network into coherent and apparently seamless cognitive action. In the past, we more or less assumed that this was going on. Now, we are becoming enlightened as to how it occurs. It is, of course, not lost on me to also observe how the entire field has moved from studying basic transfer processes of simple modality-specific stimuli to complex experimental designs that investigate the nature of the mechanisms of self. I have no doubt that the interplay between split-brain research and other methodologies such as neuroimaging will continue to shed light on the human mind and brain.

**Michael S. Gazzaniga is at the Center for Cognitive Neuroscience, 6162 Moore Hall, Dartmouth College, Hanover, New Hampshire 03755-3547, USA.**  
e-mail: michael.s.gazzaniga@dartmouth.edu

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#### Competing interests statement

The author declares no competing financial interests.

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