

INVITED REVIEW

Cerebral specialization and interhemispheric communication

Does the corpus callosum enable the human condition?

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Summary

The surgical disconnection of the cerebral hemispheres creates an extraordinary opportunity to study basic neurological mechanisms: the organization of the sensory and motor systems, the cortical representation of the perceptual and cognitive processes, the lateralization of function, and, perhaps most importantly, how the divided brain yields clues to the nature of conscious experience. Studies of split-brain patients over the last 40 years have resulted in numerous insights into the processes of perception, attention, memory, language and reasoning abilities. When the constellation of findings is considered as a whole, one sees the cortical arena as a patchwork of specialized processes. When this is considered in the light of new studies on the lateralization of functions, it becomes reasonable to suppose that the corpus callosum has enabled the development of the many specialized systems by allowing the reworking of existing cortical areas while preserving existing functions. Thus, while language emerged in the left hemisphere at the cost of pre-existing perceptual systems, the critical features of the bilaterally present perceptual system were spared in the opposite

half-brain. By having the callosum serve as the great communication link between redundant systems, a pre-existing system could be jettisoned as new functions developed in one hemisphere, while the other hemisphere could continue to perform the previous functions for both half-brains. Split-brain studies have also revealed the complex mosaic of mental processes that participate in human cognition. And yet, even though each cerebral hemisphere has its own set of capacities, with the left hemisphere specialized for language and speech and major problem-solving capacities and the right hemisphere specialized for tasks such as facial recognition and attentional monitoring, we all have the subjective experience of feeling totally integrated. Indeed, even though many of these functions have an automatic quality to them and are carried out by the brain prior to our conscious awareness of them, our subjective belief and feeling is that we are in charge of our actions. These phenomena appear to be related to our left hemisphere's interpreter, a device that allows us to construct theories about the relationship between perceived events, actions and feelings.

Keywords: cerebral specialization; callosum; interhemispheric; interpreter

Abbreviations: HERA = hemispheric encoding/retrieval asymmetry; LVF = left visual field; RVF = right visual field; SOA = stimulus-onset asynchrony

Introduction

In the pages of this journal much of the original work on disconnection syndromes has been described, especially the effects of surgical section on the corpus callosum. Over 30 years ago, Norman Geschwind's magnificent two-part review article on disconnection syndromes (Geschwind, 1965*a, b*) launched not only a thousand research ships but provided

the intellectual basis for a new behavioural neurology, particularly in the USA. In what follows I review progress in studying patients with surgical disconnection of the cerebral hemispheres. I concentrate on research over the past 40 years, especially as it relates to current views of the human brain's neurological organization. This work is of a particular kind

in that each cerebral hemisphere is examined with the help of specialized stimulus lateralization techniques. These techniques have evolved over years of testing and they allow unique ways of interpreting the neuropsychological assessment of these surgical cases. As a consequence, studies that do not use these testing procedures are limited and will not be reviewed.

General background

The human brain is a bizarre device, set in place through natural selection for one main purpose—to make decisions that enhance reproductive success. That simple fact has many consequences and is at the heart of evolutionary biology. Once grasped, it helps the brain scientist to understand a major phenomenon of human brain function—its ubiquitous lateral cerebral specialization. Nowhere in the animal kingdom is there such rampant specialization of function. Why is this, and how did it come about?

What emerges from split-brain research is a possible insight to these questions. It may turn out that the oft-ignored corpus callosum, a fibre tract that is thought merely to exchange information between the two hemispheres, was the great enabler for establishing the human condition. Non-human brains, by contrast, reveal scant evidence for lateral specialization, except as rarely noted, for example, by Hamilton and Vermeire while they were investigating the macaque monkey's ability to perceive faces (Hamilton and Vermeire, 1988). In that study, they discovered a right hemisphere superiority for the detection of monkey faces.

With the growing demand for cortical space, perhaps the forces of natural selection began to modify one hemisphere but not the other. Since the callosum exchanges information between the two hemispheres, mutational events could occur in one lateralized cortical area and leave the other mutation-free, thus continuing to provide the cortical function from the homologous area to the entire cognitive system. As these new functions develop, cortical regions that had been dedicated to other functions are likely to be co-opted. Because these functions are still supported by the other hemisphere, there is no overall loss of function. In short, the callosum allowed a no-cost extension; cortical capacity could expand by reducing redundancy and extending its space for new cortical zones.

This proposal is offered against a backdrop of new findings in cognitive neuroscience, findings that strongly suggest how important local, short connections are for the proper maintenance and functioning of neural circuits (Cherniak, 1994; Allman, 1999). Long fibre systems are relevant—most likely for communicating the products of a computation—but short fibres are crucial for producing the computation in question. Does this mean that as the computational needs for specialization increase there is pressure to sustain mutations that alter circuits close to a nascent site of activity?

One of the major facts emerging from split-brain research is that the left hemisphere has marked limitations in perceptual

functions and that the right hemisphere has even more prominent limitations in its cognitive functions. The model thus maintains that lateral specialization reflects the emergence of new skills and the retention of others. Natural selection allowed this odd state of affairs because the callosum integrated these developments in a functional system that only got better as a decision-making device.

Another aspect of this proposal can be seen when considering possible costs to the right hemisphere. It now appears that the developing child and the rhesus monkey have similar cognitive abilities (Hauser and Carey, 1998). It has been shown that many simple mental capacities, such as classification tasks, are possible in the monkey and in the 12-month-old child. Yet many of these capacities are not evident in the right hemisphere of a split-brain subject (Funnell and Gazzaniga, 2000). It is as if the right hemisphere's attention-perception system has co-opted these capacities, just as the emerging language systems in the left hemisphere co-opt its capacity for perception.

With these changes ongoing, one might predict that there would be an increase in local intrahemispheric circuitry and a reduced interhemispheric circuitry. With local circuits becoming specialized and optimized for particular functions, the formerly bilateral brain need no longer keep identical processing systems tied together for all aspects of information processing. The communication that occurs between the two hemispheres can be reduced, as only the products of the processing centres need be communicated to the opposite half-brain. Recently, Rilling and Insel have reported that there is a differential expansion of cerebral white matter relative to the corpus callosum in primates (Rilling and Insel, 1999). Humans show a marked decrease in the rate of growth of the corpus callosum compared with intrahemispheric comparisons of white matter.

There is also new evidence that could lead the way to discovering how new functions, exclusively human in nature, arise during cortical evolution. Neurons in the monkey's prefrontal lobe respond not only when the animal is going to grasp a piece of food but also when the human experimenter is about to grasp the same piece of food (Rizzolatti *et al.*, 1996). It would appear that circuits in the monkey brain make it possible for the monkey to represent the actions of others. Rizzolatti (Rizzolatti, 1998) suggested that such a system might be the seed for the uniquely human theory of a mind module (Baron-Cohen, 1995).

It is against this backdrop—one in which developmental and evolutionary time come into play and a dynamic cortical system establishes adaptations that become laterally specialized systems—that I review research on hemispheric disconnection syndromes. First, I examine basic neurological systems related to the senses, and then I consider issues in motor control. The evolutionary perspective creeps in early as we see similarities and differences in organization between the monkey and human visual systems. Building on these aspects, I survey perceptual and cognitive issues that have

been studied intensely over the past 35 years, and I present them from an evolutionary perspective as well.

Patient population

Over the years, two major patient populations have been investigated in split-brain studies. The first surgical series originated with Bogen and colleagues in California (Bogen *et al.*, 1965). These patients purportedly had their corpus callosum and anterior commissure sectioned in one operation. The case histories of the most frequently studied patients have been reported elsewhere and include the history of patients L.B., N.G., A.A., N.Y., C.C. and N.W. A 20-year follow-up MRI of these six patients confirmed the callosal section but not the section of the anterior commissure (Bogen *et al.*, 1988).

The second surgical series was undertaken at Dartmouth Medical School by Donald Wilson and David W. Roberts (e.g. Wilson *et al.*, 1977). This series included several patients who have been studied extensively, including patients P.S., J.W., and D.R. Another patient has been patient V.P., who was operated on by Dr Mark Rayport at the Medical College of Ohio. Finally a new patient, V.J., was operated on in California by Stephen Nudik. She had a post-operative MRI and the entire callosum had been successfully sectioned (Baynes *et al.*, 1998). Extensive clinical histories for most of the foregoing patients have been reported elsewhere (Gazzaniga *et al.*, 1984).

The studies reported below make use of all of these patients. Most experiments report results in which at least two of the patients reported above were examined. Overall, it can be said that the broad description of the split-brain syndrome applies to all patients who have undergone either full callosal surgery or section of the forebrain commissure. In what follows, experiments that bring out differences in performance between patients note which patients are being characterized.

Finally, the large literature on callosal agenesis is not reviewed. Massive brain reorganization takes place in these patients, and while some deficits of interhemispheric transfer on some limited tests have been observed (Aglioti *et al.*, 1993; Lassonde *et al.*, 1995), they show few of the dramatic deficits that occur following surgical section of the corpus callosum (Jeeves and Silver, 1988).

Methodological approaches

Over the years, several methodological advances have improved the perceptual and cognitive testing of patients who have undergone commissurotomy. In the original testing, mechanical timing devices were used to back-project 35 mm slides tachistoscopically. In more recent times, computer-driven stimulus presentation systems have been used. Throughout the progression of research, new technologies have given a boost to testing perceptual and cognitive aspects

of the two separated or partially separated hemispheres (Fig. 1).

Basic neurological mechanisms

For sensory systems, dramatic similarities and differences are evident in how the subhuman primate and human visual system are organized. The simple and compelling fact is that the two systems contrast significantly with each other. These differences may reflect an overarching principle of brain evolution: cortical space is co-opted for new purposes.

With the remarkable separation of sensory information and with the lateralization of corticospinal motor systems, the split-brain animal and human raise interesting questions about the neural mechanism by which motor activities occur. In particular, in recent years, these patients have provided the opportunity to test theories about the nature of the neural pathways that coordinate hands and arms. As we know, the ability to manipulate the environment reached a pinnacle when the fully opposable thumb evolved in humans. Not surprisingly, the brain contains specialized circuitry to exploit this capacity for prehension. In what follows, I examine the relevant sensory and motor research.

The anterior commissure does not transfer visual information in the human but does in the monkey

A major difference between the visual system of monkey and human is that the intact anterior commissure in the monkey transfers visual information of all kinds (Gazzaniga, 1966) (Fig. 2). The intact human anterior commissure appears to transfer nothing visual (Seymour *et al.*, 1994; Gazzaniga *et al.*, 1965; Funnell *et al.*, 2000a, b). The fact that visual information remains lateralized to one hemisphere after callosal section in humans was first demonstrated by using quick-flash tachistoscopic presentation methods. It was clear that visual information presented to the right visual field projected exclusively to the left hemisphere and information presented to the left visual field projected exclusively to the right hemisphere. These observations have now been confirmed by employing prolonged stimulation with the Purkinje eyetracker and image stabilizer (Gazzaniga *et al.*, 1996).

One possible explanation for the differences between the visual systems of the two species can be found in the manner in which the visual system developed in humans. It is now known that the cortical fields of origin for neurons of the anterior commissure fibres are extensive in the monkey and reach far into the temporal lobe. By contrast, the projection fields of these neurons are more limited and include only the anterior third of the temporal lobe (Zeki, 1973; Jouandet and Gazzaniga, 1979). While the pattern of projections is not known for the human, it is interesting to speculate that the caudal projections through the anterior commissure were

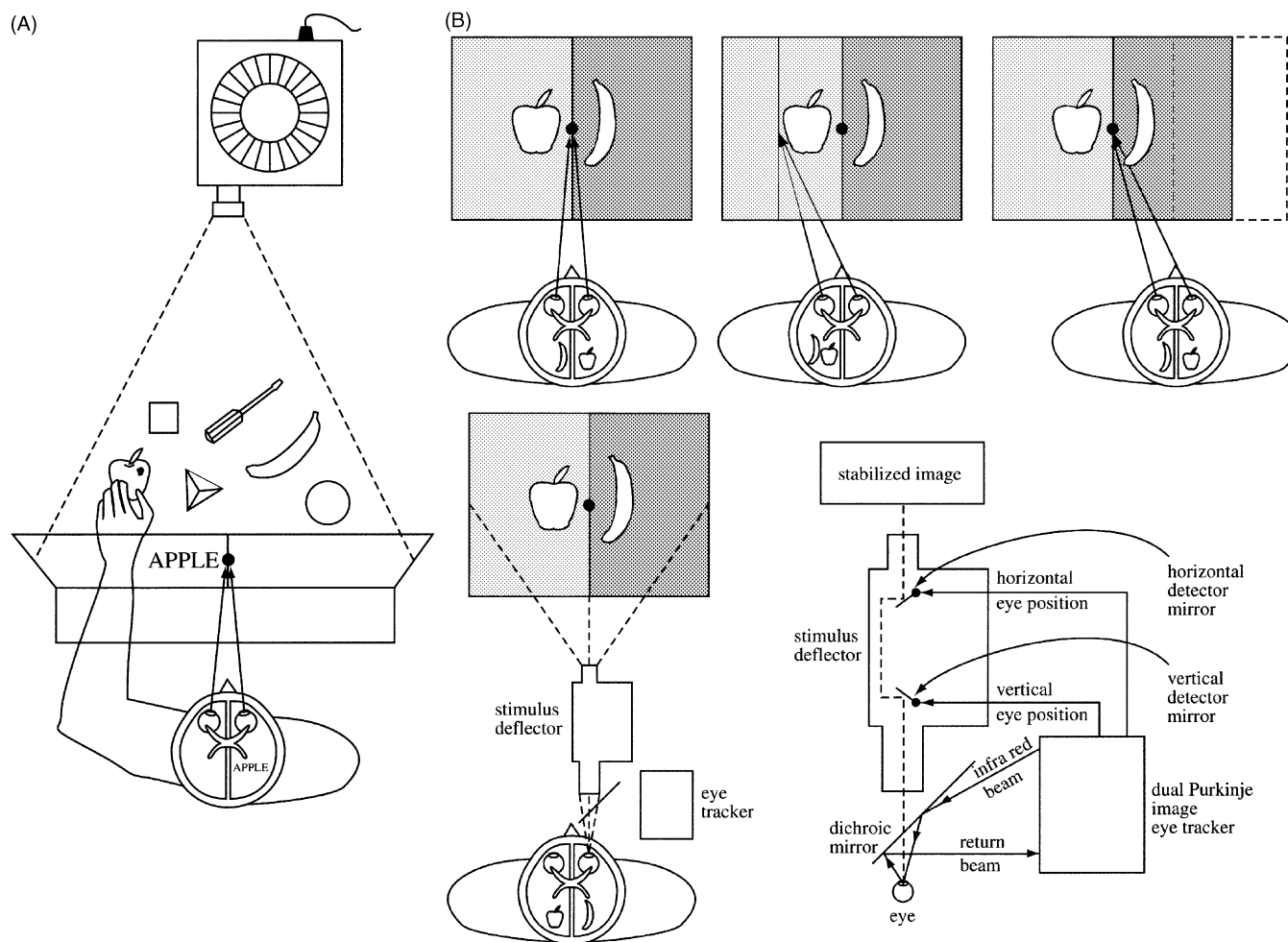


Fig. 1 To examine hemispheric processing differences differentially it is necessary to lateralize stimuli within the left and right visual fields. In early studies this was managed with a mechanically driven tachistoscope, as depicted in **A**. Tactile stimuli were also presented out of view to either hand. More recently, lateralized computer presentations have replaced the tachistoscope (shown in **B**). As shown in the centre panel, however, proper lateralization is not achieved if the subject makes an eye movement during the stimulus presentation (*upper middle*). The development of retinal stabilization procedures makes it possible now to counteract the effects of such eye movements. The Purkinje eye-tracking and image-stabilizing device is depicted in the right panel of **B**. Coupled with a mirror stimulus deflector, this dual Purkinje image eyetracker allows retinal stabilization. As eye movements occur, horizontal and vertical deflection mirrors move to counteract these movements, maintaining proper lateralization.

crowded out by the addition of specialized regions that developed in the anterior regions of the visual system. This left the anterior commissure for olfactory and non-visual communication. Regions involved in early stages of visual processing would remain unaffected by the addition of these new functional regions. This is consistent with the view that there are no major interspecies differences in the early stages of the visual system.

Humans have visual midline overlap phenomena

Nasotemporal overlap at the retinal vertical meridian in cat and monkey is readily evident (Stone, 1966; Stone *et al.*, 1973; Bunt and Minkler, 1977; Leventhal *et al.*, 1988). In a 1–2° stripe that straddles the two visual half-fields, visual information is sent to the left and right visual cortices.

Whether the anatomical projections have any functional significance has never been established, but there has been speculation that this zone might be responsible for the phenomenon of 'macular sparing' (Bunt and Minkler, 1977; Leventhal *et al.*, 1988). Strokes affecting the primary visual cortex in either hemisphere produce blindness in the opposing visual field, but within the blind field a small region of central vision is frequently preserved. Sparing can be explained by the assumption that, because of nasotemporal overlap, the entire fovea is represented in both hemispheres. By contrast, in neurologically normal subjects, attempts to demonstrate this zone psychophysically have failed consistently (e.g. Harvey, 1978; Lines and Milner, 1983). Fendrich and colleagues have examined this in split-brain subjects (Fendrich and Gazzaniga, 1989; Fendrich *et al.*, 1994). Using an image stabilizer in combination with a Purkinje eyetracker, careful assessment of the visual midline of two split-brain

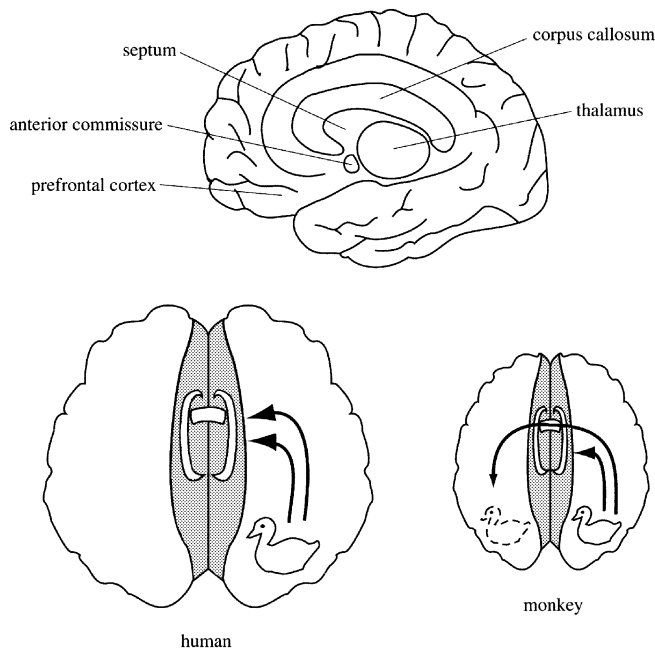


Fig. 2 Only the corpus callosum is sectioned in most split-brain operations performed on humans. In the split-brain patients who underwent surgery in California, however, the anterior commissure was also sectioned. Behavioural testing on patients with and without sparing of the anterior commissure reveals no evidence for visual transfer of information in any of these patients. The anterior commissure, therefore, does not appear to support any functional transfer in humans. In split-brain monkeys, however, leaving the anterior commissure intact does allow the interhemispheric transfer of visual information, even when the body of the corpus callosum is sectioned.

patients has revealed an area no more than 2° wide at the vertical midline where some visual information appears available to each half-brain (Fig. 3). This contrasts with the findings of Sugishita and colleagues, who found no evidence of overlap in hemianopic subjects but did not have the advantage of image stabilization and were restricted to only brief stimulus presentations (Sugishita *et al.*, 1994). The strip of overlap does not encompass the entire fovea. Within this strip the signals conveyed to each hemisphere from the contralateral hemiretina appear to be weak or degraded. Stimuli could not be compared across the vertical meridian if the comparisons required detailed information on shape. Moreover, Fendrich and colleagues found no indication of overlap when stimuli were presented for only 200 ms. Only longer presentations indicated a dual representation of the retinal midline. The callosotomy research thus supports other work showing that macular sparing cannot be explained by nasotemporal overlap.

Somatosensory processes are largely lateralized

The classic observations of the somatosensory system for a split-brain patient have not changed significantly. Following callosal section, stereognostic information processed by one

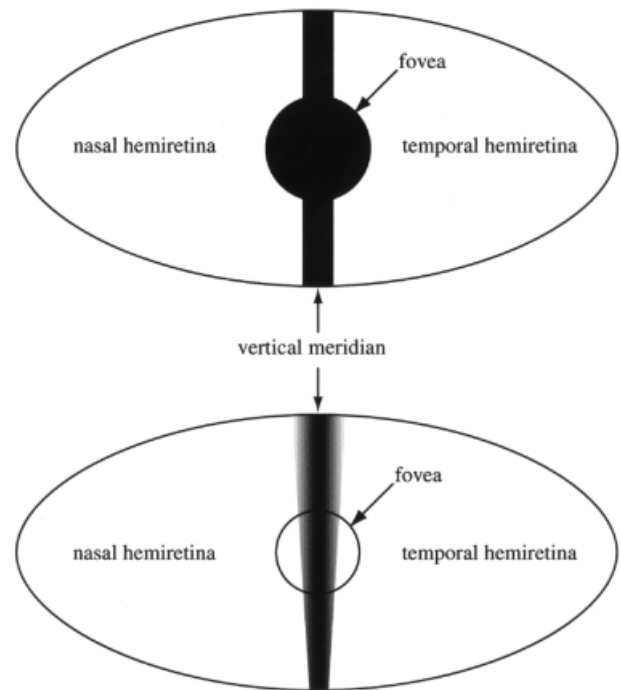


Fig. 3 The clinical phenomenon of macular sparing by nasotemporal overlap has been explained traditionally by hypothesizing a zone of overlap that encompasses the entire fovea. In contrast, data from callosotomy patients suggest that the zone does not encompass the entire fovea but rather remains narrow as it crosses the fovea. There is additional evidence that it may be wider in the upper hemiretina (lower visual field) than in the lower hemiretina.

hand is not available to the ipsilateral hemisphere (Gazzaniga *et al.*, 1963). Moreover, the presence or absence of light or deep touch can be detected by either hemisphere from both sides of the body, even though the ipsilateral stimulus is often ignored under conditions of bilateral stimulation.

More recent investigations have examined whether noxious stimuli can be represented bilaterally after unilateral stimulation (Stein *et al.*, 1989). The conclusion was that, when noxious heat stimuli ($43\text{--}47^\circ\text{C}$) were presented ipsilaterally to the responding hemisphere and were rated by the subject on a visual analogue scale, the ipsilateral hemisphere perceived the stimuli as far less intense than they actually were. The contralateral hemisphere perceived the stimulus intensity as in normal subjects, who rated it highly unpleasant. But when the stimuli reached the highest levels of heat intensity used in pain studies ($49\text{--}51^\circ\text{C}$), the ipsilateral hemisphere perceived the stimulus intensity correctly (as does that of normal subjects) and the subjects rated the stimuli as highly unpleasant. Therefore, the emotional responses of the two hemispheres to the same stimulus are simultaneous but can be quite different. Thus, a variety of emotions evoked by at least some types of sensory stimuli are tightly coupled (sensory-affective coupling) to each hemisphere's perception of the attributes of the same sensory stimulus.



Fig. 4 The motor pathways originating from one hemisphere have a strong contralateral projection that manages both the proximal and the distal musculature. The ipsilateral projections are not as strong and are involved in only proximal responses.

A disconnected hemisphere can control both arms but exerts only dominant control over the opposite hand

One of the enduring findings of split-brain research has been the distinction between a disconnected hemisphere's capacity for controlling proximal muscles versus distal muscles. Sectioning the callosum impairs the left hemisphere's ability to control the left hand and the right hemisphere's ability to control the right hand (Gazzaniga et al., 1967). These ipsilateral sensory-motor combinations need the intact callosum to integrate information from the cortical sensory areas to the motor cortex that controls distal hand movement. Either hemisphere can guide and control ipsilateral and contralateral movements involving the more proximal musculature of the shoulder, the upper arm, and of course the legs (Fig. 4).

Prehension requires both the proximal musculature to transport the arm to the location of the desired object (i.e. reaching) and the distal musculature to adjust the shape of the hand to the intrinsic properties of the target (i.e. grasping) (Jeannerod, 1981). Consequently, coordinating reaching and grasping may require that circuits lateralized to the ipsilateral and contralateral hemispheres interact. Johnson supports this hypothesis and goes on to say that this organization extends to motor planning as well as execution (Johnson, 1998; Johnson et al., 1999). Consistent with earlier work on motor control (e.g. Gazzaniga et al., 1967; Milner and Kolb, 1985), the left and right hemispheres have a knack for selecting the right way to grasp a target object with the contralateral hand. By contrast, only the left hemisphere evinces an advantage for choosing appropriate reaching movements. These results imply that the cerebral organization of motor planning is similar, but not identical, to those for motor control. In particular, the motor-dominant left hemisphere may be responsible for planning movements that include the proximal musculature of both arms. With the right arm, movements can be transferred via the corpus callosum to control mechanisms in the right hemisphere. Grasping, by contrast, can be planned and controlled only by the hemisphere

contralateral to the relevant effector (Johnson et al., 1999). In the context of earlier motor control research, the apparent specialization of the left hemisphere for planning proximal movements reveals the pivotal role played by the corpus callosum in coordinating motor planning and control.

Support for the hypothesis that each hemisphere is specialized to represent movements of the contralateral hand is contained in a study of hand identification in callosotomy patients (Parsons et al., 1998). When asked to identify whether line drawings depict left or right hands—a task that involves imagining one's own hands in the position of the stimuli—each hemisphere displayed an advantage for identifying the contralateral versus the ipsilateral hand.

Split-brain patients can move their two arms in coordinated fashion

While the two arms can be individually governed by either hemisphere, it was uncertain whether bimanual coordination was possible. Split-brain patients can use their two hands in a seemingly coordinated fashion when performing tasks that require the integrated activity of the two hands. For example, patient J.W. is expert at the assembly of model cars, an activity that requires bilateral coordination. The production of actions requires planning at multiple levels in terms of the psychological processes and the underlying neural correlates of the processes. The central goal of current investigations has been to explore the extent of independence and interaction after callosotomy in components associated with the ability to carry out these coordinated movements.

There is decoupling of spatial but not temporal processes after callosotomy

Franz and colleagues (1996) showed that commissurotomy patients could coordinate two conflicting spatial programmes, whereas a normal control was impaired (Fig. 5). In effect, the spatial maps associated with a movement could be localized and isolated in each separated hemisphere. At the same time, while spatial information between the limbs remained separate, the temporal coordination of a bimanual movement remained largely intact.

In following up a partially sectioned patient, Eliassen and colleagues discovered that the integration of direction information for two-handed movements takes place exclusively across the posterior corpus callosum (Eliassen et al., 1999). They showed that the timing of a movement's initiation is affected by anterior and posterior callosotomy. The ability of the two hands to move simultaneously was affected by the callosal surgery. Thus, the distribution of spatial and temporal signals to integrate bimanual movement is dissociable with regard to callosal topography. Posterior cortical areas, the parietal lobes, are the source of a spatial motor signal used during bimanual movements. Eliassen and colleagues went on to show that

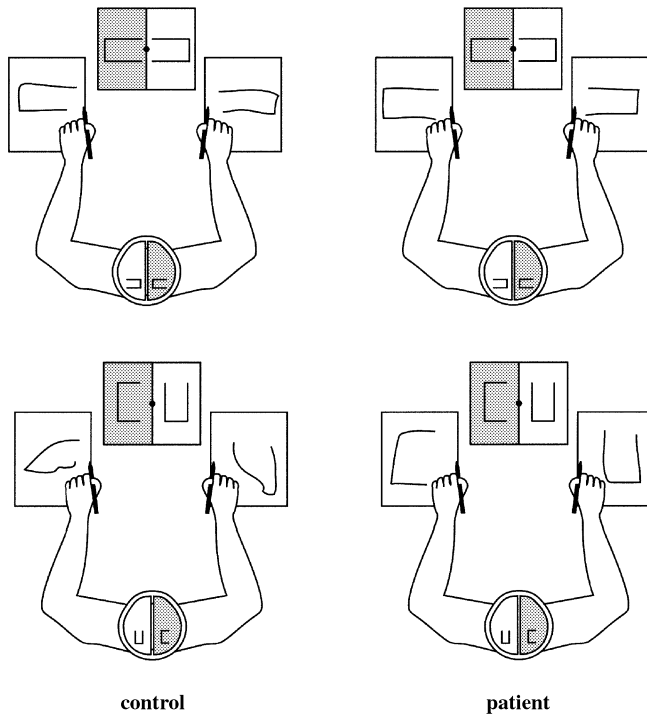


Fig. 5 The disconnection between the spatial maps of the two hemispheres in split-brain patients is illustrated in this paradigm. Subjects are shown two figures, one in each visual field, and asked to draw the stimuli with both hands simultaneously. Neurologically normal subjects are able to perform this bimanual task when the two stimuli are identical or mirror-reversed but not when the stimuli result in incompatible spatial maps. Split-brain patients, however, show no deficit in this latter condition and their performance is strikingly better than that of normal subjects. The split-brain patient is able to carry out conflicting motor programmes, indicating that the spatial representations of movements are clearly maintained and isolated to each hemisphere (adapted from Franz *et al.*, 1996).

anterior and posterior fibres are not equipotential (Eliassen *et al.*, 2000). Anterior callosotomy disrupts the simultaneity of self-initiated bimanual movements more than it does the production of bimanual movements in response to a visual stimulus.

There is a subcortical locus for temporal coupling in bimanual movements after callosotomy

In studies by Tuller and Kelso and by Franz and colleagues, patient V.J. showed temporal coupling when asked to produce rhythmic bimanual movements (Tuller and Kelso, 1989; Franz *et al.*, 1996). This observation has been replicated and extended by Ivry and colleagues (e.g. Ivry and Hazeltine, 1999). They discovered that the within-hand temporal variability of each hand was reduced (i.e. became more consistent) during bimanual tapping compared with unimanual tapping. This refutes neurological models that maintain that bimanual coupling arises from a common control signal isolated in one hemisphere. Rather, these

results are consistent with the hypothesis that separable timing mechanisms are associated with each hand and are linked by a common subcortical signal for a response.

Either hemisphere can initiate saccadic eye movements

In contrast to the inability of a disconnected hemisphere to initiate ipsilateral hand movements with accuracy, each hemisphere can direct the eyes either contraversively or ipsiversively (Hughes *et al.*, 1992). This capacity would not be predicted by dozens of studies showing that, in each hemisphere, the frontal eye fields control only contraversive eye movements (Wurtz and Albano, 1980; Bruce and Goldberg, 1984). What is more, preliminary evidence (Fendrich *et al.*, 1998) shows that, despite the absence of a corpus callosum, either hemisphere can monitor the amplitude of saccades initiated by the other hemisphere even when no visual feedback is available. This finding is noteworthy because it is generally thought that saccades are primarily monitored via a 'corollary discharge' derived from the motor commands sent to the eye muscles. In this instance, regardless of which hemisphere issues the commands, the corollary discharge is routed to both hemispheres from a subcortical locus. Fendrich and colleagues similarly found that each hemisphere can initiate both an ipsiversive and a contraversive oculomotor pursuit (Fendrich *et al.*, 1990). Such results reveal how psychophysical studies of patients with discrete lesions can illuminate neural pathways that might otherwise not be evident.

Attentional, perceptual and cognitive interaction after hemisphere disconnection

The attentional and perceptual abilities of split-brain patients have been explored extensively. It now appears that function is duplicated between the hemispheres in basic perceptual processes; this may proceed independently in the two hemispheres, even in the absence of the corpus callosum. However, the situation is more complicated for attentional processes, where some forms of attention are integrated at the subcortical level and other forms act independently in the separated hemispheres. In contrast, higher-level cognitive and linguistic processes involve hemispheric specialization, so callosal pathways are necessary to integrate these functions.

Simple perceptual interactions are not seen

Split-brain patients cannot cross-integrate visual information between their two half visual fields. When visual information is lateralized to either the left or the right disconnected hemisphere, the unstimulated hemisphere cannot use the information for perceptual analysis. This is also true for stereognostic information presented to each hand. While the presence or absence of touch stimulation is noted in any part

of the body by either hemisphere, patterned somatosensory information is lateralized. Thus, an object held in the left hand cannot help the right hand find an identical object. Although some have argued that certain higher-order perceptual information is integrated at some level by way of subcortical structures (Cronin-Golomb, 1986; Sargent, 1990), these results have not been replicated by others (McKeever *et al.*, 1981; Corballis *et al.*, 1993; Corballis, 1994; Seymour *et al.*, 1994; Funnell *et al.*, 1999).

Subcortical transfer of higher-order information is more apparent than real

Kingstone and Gazzaniga found that split-brain patients will sometimes draw a picture that combines word information presented separately to the two hemispheres. For example, from a left visual field (LVF) stimulus of 'ten' and a right visual field (RVF) stimulus of 'clock', the subject draws a picture of a clock set at 10 o'clock (Kingstone and Gazzaniga, 1995). Although this outcome initially seemed to imply the subcortical transfer of higher-order information between the hemispheres, subsequent observations revealed that it reflects dual-hemisphere control of the drawing hand (biased to the left hemisphere). Conceptually ambiguous word pairs, such as 'hot' + 'dog', were always depicted literally (e.g. a dog panting in the heat) and never as emergent objects (e.g. a frankfurter; Fig. 15). Moreover, right- and left-hand drawings often depicted only the words presented to the left hemisphere.

Interhemispheric transfer is seen for crude spatial location information

Unlike visual and somatosensory cues, crude information concerning spatial locations can be cross-integrated (Trevarthen, 1968; Trevarthen and Sperry, 1973; Holtzman, 1984). In one experiment, a four-point grid was presented to each visual field (Fig. 6A). On a given trial, one of the positions on the grid was highlighted and one condition of the task required the subject to move his eyes to the highlighted point within the visual field stimulated. In the second condition, the subject was required to move his eyes to the relevant point in the opposite visual field. Split-brain subjects could do this at above-chance levels, perhaps because of crude cross-integration of spatial information. This was true even if the grid was positioned randomly in the tested field.

Spatial attention can be directed but not divided between the hemispheres

The finding that some type of spatial information remains integrated between the two half-brains raises a question: are the attentional processes associated with spatial information affected by cortical disconnection surgery? Using a modification of a paradigm developed by Posner and colleagues (Posner *et al.*, 1980) that capitalizes on priming

phenomena, Holtzman and colleagues (Holtzman *et al.*, 1981) found that either hemisphere can direct attention to a point in either the left or right visual field (Fig. 6B). Posner first showed that the response latency to a peripheral visual target is reduced when observers have prior information regarding its spatial locus, even when eye movements are prevented. The spatial cue presumably allows observers to direct their attention to the location prior to the onset of the target. When this paradigm was used in split-brain patients to measure how much attentional cues affect performance, the separated hemispheres were not strictly independent in their control of spatial orientation. Rather, the two hemispheres relied on a common orienting system to maintain a single focus of attention. Thus, as with normal people, a cue to direct attention to a point in the visual field is used no matter which hemisphere gets the cue.

The discovery that spatial attention can be directed with ease to either visual field raised another question: can each separate cognitive system in the split-brain patient independently direct attention to a part of its own visual field (Holtzman *et al.*, 1984)? Can the right hemisphere direct attention to a point in the left visual field while the left brain simultaneously attends to a point in the right visual field? Normal subjects cannot so divide their attention. Can split-brain patients do so?

The split-brain patient cannot divide spatial attention between the two half-brains (Reuter-Lorenz and Fendrich, 1990). There appears to be only one integrated spatial attention system that remains intact after cortical disconnection (Fig. 6B). This is consistent with electrophysiological studies showing that event-related potentials associated with simultaneous target detections in the two visual fields are not elicited independently in the separated hemispheres (Kutas *et al.*, 1990). Thus, like neurologically intact observers, the attentional system of split-brain patients is unifocal. They cannot prepare for events in two spatially disparate locations.

Attentional resources are shared

Even though there seems to be but one focus of attention, the dramatic effects of disconnecting the cerebral hemispheres on perception and cognition might suggest that each half-brain possesses its own attentional resources. If this were true, one would predict that the cognitive operations of one half-brain, no matter what the difficulty, would have only a slight influence on the other's cognitive activities. The competing view is that the brain has limited resources for managing such processes; if resources are being applied to task A, fewer are available for task B. This model maintains that the harder one hemisphere works on a task, the worse the other hemisphere does on a task of constant complexity.

Many investigations have focused on this issue; all confirm the notion that the central resources are limited (Holtzman and Gazzaniga, 1982; Reuter-Lorenz *et al.*, 1996). In the original experiment, two series of geometrical shapes were displayed concurrently to the left and right of central fixation

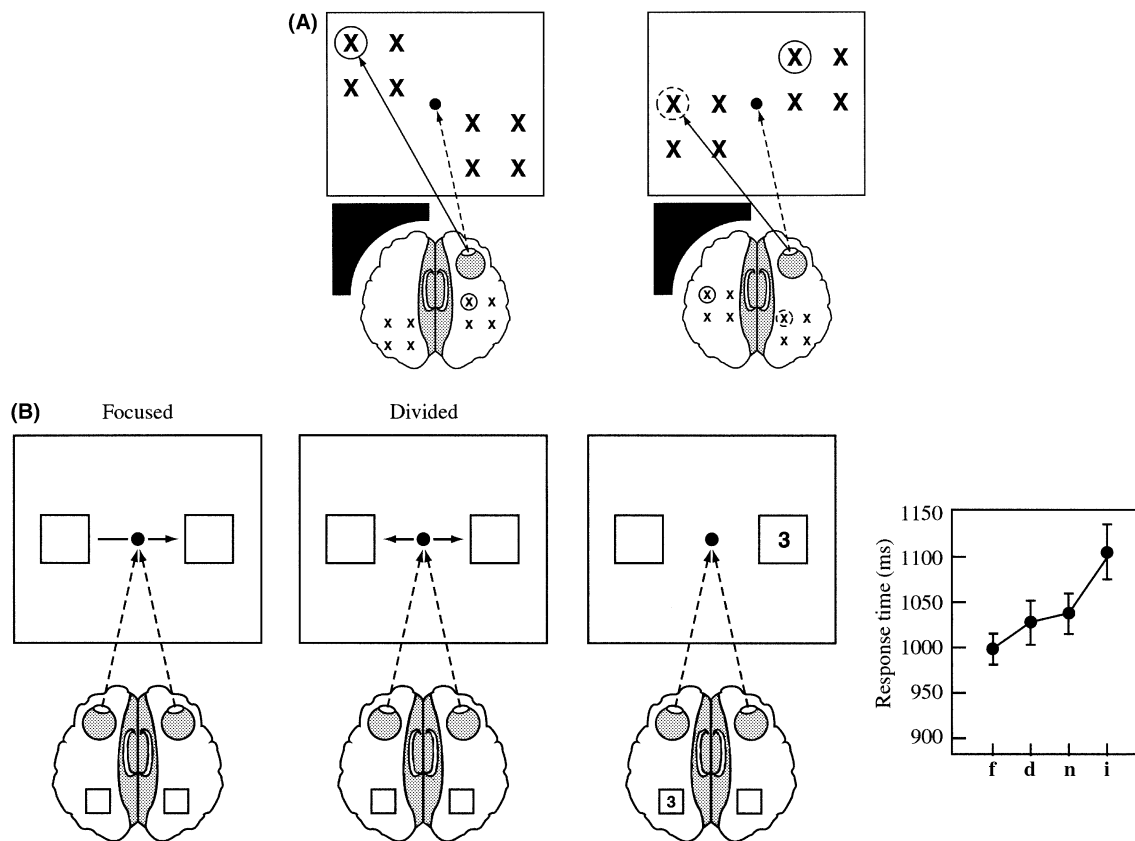


Fig. 6 (A) A spatial cueing task demonstrating crude transfer of spatial information. On 'within-field' trials, the eyes moved to the stimulus that was surrounded by the probe. On 'between-field' trials, the eyes also moved to the corresponding stimulus in the other hemifield. (B) The experimental paradigm for studies on 'focused' and 'divided' attention. On each trial, a spatial cue appeared 1.5 s before the target stimulus was presented. There were four cue conditions. In the focused condition, the cue directed attention to one hemifield. In the divided attention condition, both hemifields were cued. In the 'neutral' condition neither hemifield was cued. In the 'invalid' condition, one hemifield was cued (as in the focused condition) but the target was subsequently presented in the non-cued location. Average response latencies (± 1 standard error) are shown for focused (f), divided (d), neutral (n) and invalid (i) cue trials (adapted from Gazzaniga, 1995).

and hence were lateralized to the right and left hemispheres (Fig. 7). A unilateral probe figure appeared subsequently, and the observer indicated with a forced-choice key press whether it matched any of the field's items. In half of the trials the same three figures were displayed in the two fields—the hard condition. In the other half, one hemisphere saw three items while the other saw only one stimulus presented three times, the latter being the easy condition. The results proved that when one half-brain was working on processing only one repeated stimulus, the opposite hemisphere was better at recalling whether the probed stimulus was part of the original three stimuli. When both hemispheres were trying to process three stimuli, the performance of each hemisphere was impaired. These findings have been replicated in a monkey model of the tasks (Lewine *et al.*, 1994).

Other experiments address attentional sharing (Pashler *et al.*, 1994; Ivry *et al.*, 1998). Split-brain patients have a psychological refractory period effect between the two hemispheres, an indication that tasks being presented to each half-brain alone are being correlated. When one hemisphere discriminates a stimulus and makes a choice, this delays the

other hemisphere in making a similar choice. At the same time, the patients fail to exhibit attentional costs between the hemispheres. For example, split-brain patients do not show the cost that normal subjects reveal when they use two hands for the two responses: they maintain incompatible response codes for each hand.

Division of cognitive resources can improve performance

In the callosum-sectioned patient, no measurable interactions happen between the two hemispheres during the processing of perceptual information. Identical and simple visual patterns of all kinds can be presented to each separate half-brain and the patient cannot say whether the stimuli are the same or different. This raises the possibility that, in a memory test of visual retention, a split-brain subject might perform at a higher level than a normal subject if the perceptual information were distributed between the two visual half fields. For example, a complex spatial memory task was

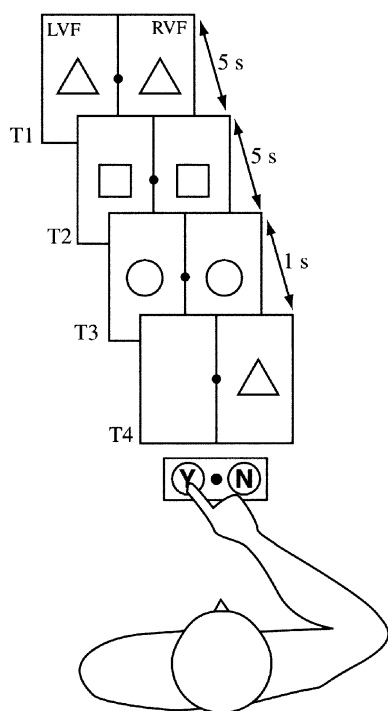


Fig. 7 An experiment showing that common, and therefore limited, cognitive resources are available to split-brain subjects. The figure shows the sequence of events for a redundant three-condition trial. Two series of geometrical shapes were shown concurrently to each hemisphere, followed by a unilateral probe. Split-brain patients were faster to decide whether the probe was presented in the series when the non-probed hemisphere had been shown only one shape than when it had been shown several different shapes (adapted from Holtzman and Gazzaniga, 1982).

administered to a split-brain patient and normal controls; critical information was presented in each visual half-field (Holtzman and Gazzaniga, 1985). For normal subjects, the visual information was automatically combined and perceived as one large problem. For the split-brain patient, each hemisphere perceived a problem that remained separate from the perceptual information presented to the other half-brain; thus, each hemisphere perceived a much simpler task. The results were clear: the split-brain patient outperformed the normal subjects. The callosum-sectioned patient benefited from the fact that the perceptual array under one of the test conditions did not seem to be more difficult because the work was distributed to each separate hemisphere, even though the sensory array was identical to that experienced by the normal subjects.

There is no question that disconnection of the cerebral hemispheres allows a unique cognitive state. In a sense it turns a unified perceptual system into two simpler perceptual systems that do not interact and therefore do not interfere with each other. It allows the breaking down of a large perceptual problem into smaller, more manageable problems that a half-brain can solve. From the observer's point of view, though, it looks as if the patient's total information processing capacity has increased and is superior to that of

normal subjects. Yet, as we noted for attention, split-brain patients do not have more resources to call on to solve problems. The human brain has a set number of resources it can allocate to cognitive tasks, and these resources remain constant after commissurotomy. How, then, do we explain these two different results? Performance seems better than normal yet perceptual and cognitive tasks have limited resources.

The conundrum forces the issues of where in a perceptual-motor task the resources are applied. Are they, for example, applied during the early phases of information processing, which deal with the complexity of the visual stimulus itself? Or are the resources applied at later loci of the information processing sequence to handle more cognitive aspects? Interactions between the hemispheres on resource limits may occur when the task is more cognitive and requires a working memory. Lewine and colleagues have proposed a similar scheme and suggest that the site of subcortical interaction may be the brainstem (Lewine *et al.*, 1994).

Visual search may proceed independently in separated half-brains

While the resources a brain commits to a task appear constant, their method of deployment can vary. The more items to be analysed in a visual array, the longer it takes. After a baseline reaction time has been established it takes normal controls an additional 70 ms to respond to two more items, another 70 ms for an additional two items, and so on. In split-brain patients, when the items are distributed across the midline of the visual field, as opposed to being in one visual field, the reaction time to added stimuli is cut in half (Fig. 8) (Luck *et al.*, 1989, 1994).

This notion was extended by Kingstone and colleagues when they discovered that the strategy differs according to which hemisphere examines the contents of its visual field (Kingstone *et al.*, 1995). The left-dominant hemisphere uses a 'guided' or 'smart' strategy whereas the right hemisphere does not. This means that the left hemisphere adopts a helpful cognitive strategy in solving the problem whereas the right hemisphere does not possess those extra cognitive skills. But it does not mean that the left hemisphere is always superior to the right hemisphere in attentional orienting.

Kingstone and colleagues have demonstrated that the right hemisphere, which is superior to the left hemisphere for processing upright faces, shifts attention automatically to where someone is looking (Kingstone *et al.*, 2000). The left hemisphere does not demonstrate a similar attentional response to gaze direction.

The act of independent scanning in the hemispheres of split-brain patients during visual search appears contrary to the sharing of attentional resources. At this time, this issue remains unresolved and more research is needed. However, it should be mentioned that this apparent discrepancy may reflect the fact that multiple mechanisms of attention appear

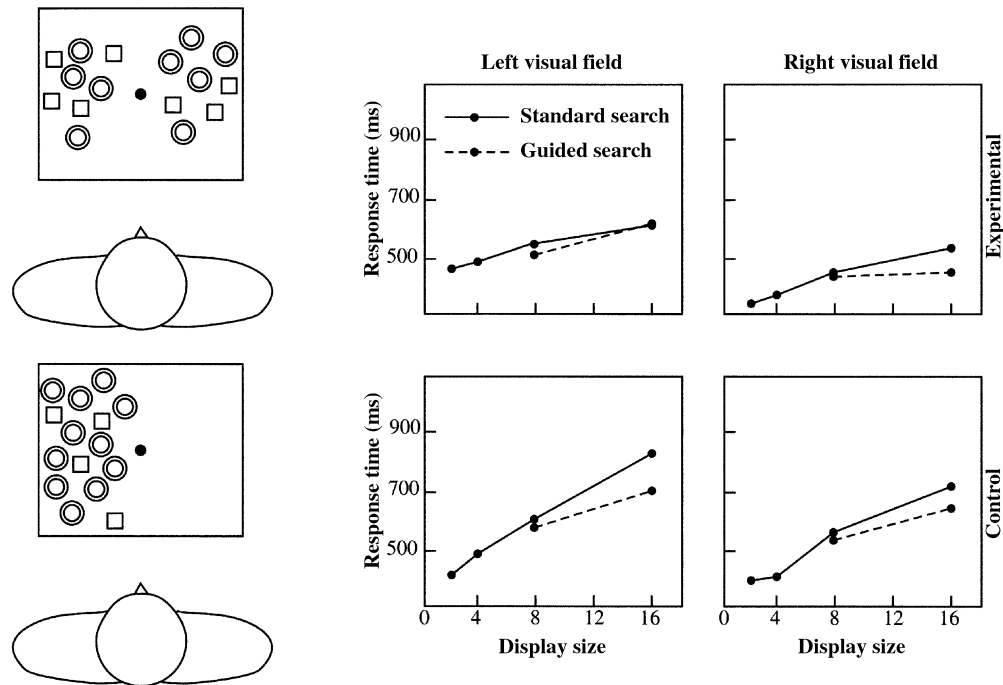


Fig. 8 Bilateral (*top left*) and unilateral (*bottom left*) search arrays with set size equal to 16. Bilateral ('standard') search and unilateral ('guided') search response times for split-brain patient J.W. ('Experimental', *top panel*) and the normal control group (*bottom panel*) as a function of visual field and set size. Patients V.P. and D.R. showed the same results as J.W. (adapted from Kingstone *et al.*, 1995).

to operate at different stages of processing, some of which might be shared across the disconnected hemispheres and others of which might be independent (Luck and Hillyard, 2000). Luck and Hillyard describe evidence that the psychological refractory period paradigm reflects a late attentional mechanism, whereas visual search reflects an early attentional mechanism.

Attentional orienting differs qualitatively between the hemispheres

Kingstone and colleagues have noted that the hemispheres interact quite differently in their control of reflexive (exogenous) and voluntary (endogenous) attentional processes (Enns and Kingstone, 1997; Kingstone *et al.*, 1997, 2000). The evidence suggests that reflexive attentional orienting happens independently in the two hemispheres, while voluntary attentional orienting involves hemispheric competition with control preferentially lateralized to the left hemisphere. These data explain not only the low-level sensory effects of attentional orienting but also bear on more complex behaviours, such as visual search. For instance, when the number of items to be searched is small, attentional orienting is largely reflexive in nature, and the two hemispheres perform independently (Luck *et al.*, 1989, 1994). But when the number of items to be searched is large, or the search is strategic, attentional orienting is largely volitional and attentional orienting is lateralized to the left hemisphere

(Kingstone *et al.*, 1995). Mangun and colleagues have also shown that the right hemisphere has a predominant role in attentional orienting (Mangun *et al.*, 1994). Indeed, even in callosally sectioned patients, the right hemisphere attends to the entire visual field whereas the left hemisphere attends only to the right field. This finding has also been noted by Berlucchi and colleagues (Berlucchi *et al.*, 1997) and by Corballis (Corballis, 1995).

Perceptual asymmetries following cerebral disconnection

Hemispheric asymmetries in visuospatial processing have long been observed (e.g. Gazzaniga *et al.*, 1967). Nevertheless, the fundamental nature of these asymmetries and how they arose remain unclear. Initial studies with split-brain patients found that the right hemisphere outperformed the left at a variety of visuospatial tasks such as block design and drawing three-dimensional objects (Bogen and Gazzaniga, 1965; Gazzaniga *et al.*, 1965). These findings contributed to the popular notion that the right hemisphere is specialized for visuospatial processing. Subsequently, a number of researchers proposed dichotomies suggesting that the two hemispheres process information in different, though complementary, ways. For example, Sergent suggested that the left hemisphere selectively processes the high-spatial-frequency information in a stimulus and the right hemisphere selectively processes the low-spatial-frequency information

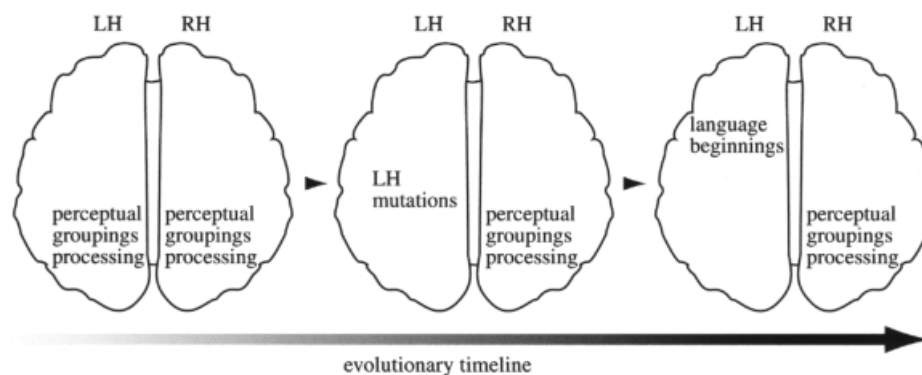


Fig. 9 Schematic representation of the hypothesis suggesting that lateral specialization in both hemispheres may originate from unilateral mutations to one hemisphere. In the example depicted here, the left hemisphere gives up the capacity for perceptual groupings—presumably present in each hemisphere of lower animals—as it changes to accommodate the development of language. Because the corpus callosum connects the two hemispheres there is no overall cost to the cognitive/perceptual system.

(Sergent, 1982). Similarly, Lamb and colleagues proposed that the left hemisphere processes the local details of a stimulus, whereas the right hemisphere processes its global layout (Lamb *et al.*, 1989). Finally, Kosslyn and colleagues proposed that the left hemisphere tends to represent visuospatial information ‘categorically’ (representing the relations between stimuli descriptively: above, below, left, right) (Kosslyn *et al.*, 1989). The right hemisphere, by contrast, was posited to represent visuospatial information in a finer-grained, ‘coordinate’ framework.

Each of these dichotomies suggests that the hemispheres both contribute their expertise to the overall processing of the stimulus, effectively dividing the workload between them. While these theories have each received some empirical support, there has been relatively little effort to test them directly in the split brain. Fendrich and Gazzaniga, though, did examine the Sergent hypothesis concerning hemispheric differences in sensitivity to differing spatial frequencies (Fendrich and Gazzaniga, 1989). In this study, split-brain patients compared the orientations of two grating patches presented briefly within a single visual hemifield. Performance declined with increasing spatial frequency in both visual fields. The data failed to support the hypothesis that the right hemisphere is specialized for processing low spatial frequencies and the left for high spatial frequencies.

An alternative view is that perceptual asymmetries do not necessarily reflect a division of labour between the hemispheres, but are a consequence of other, more primitive, hemispheric specializations (Gazzaniga, 1970, 1998; Corballis *et al.*, 2000). As left-hemisphere specialization for linguistic (and temporal) processing evolved, cortical tissue that had been dedicated to visuospatial processing was co-opted, resulting in the loss of visuospatial abilities in the left hemisphere (Fig. 9). This cost is illustrated in a series of experiments we have conducted recently.

There is right-hemisphere superiority for perceptual grouping processes

In order to perceive objects in the environment as unified wholes, the visual system must often extrapolate from incomplete information about contours and boundaries. For example, there are conditions in which object contours are perceived in areas of completely homogeneous stimulation. Because these object boundaries are not present in the physical stimulus, they are referred to as ‘illusory contours’. Illusory contours are often perceived when the edges of elements in the visual array are consistent with the presence of a superimposed surface or object, despite the lack of a brightness transition to signal an object contour (Kanizsa, 1976, 1979). Similarly, the shape of an object can often be perceived correctly in spite of the fact that some other object or surface occludes a significant proportion of its contour. The process underlying the perception of the shape in this case is termed ‘amodal completion’ (Michotte, 1964; Kanizsa, 1979).

Several authors have suggested that the same mechanism is responsible for both illusory contour perception and amodal completion (Kellman and Loukides, 1987; Kellman and Shipley, 1991; Ringach and Shapley, 1996). Furthermore, there is some evidence that this mechanism is preferentially lateralized to the right cerebral hemisphere. Illusory contours and amodal completion are often cited as examples of the Gestalt ‘closure’ principle, which refers to the experience of a bounded perceptual unit from partial or disorganized information (e.g. Koffka, 1924). Several studies have suggested that the right hemisphere plays a critical role in perceptual closure processes (e.g. De Renzi and Spinnler, 1966; Wasserstein *et al.*, 1987; Hirsch *et al.*, 1995).

Corballis and colleagues investigated boundary completion by illusory contours and amodal completion in split-brain subjects (Corballis *et al.*, 1999). These processes were assessed using a lateralized shape discrimination task similar

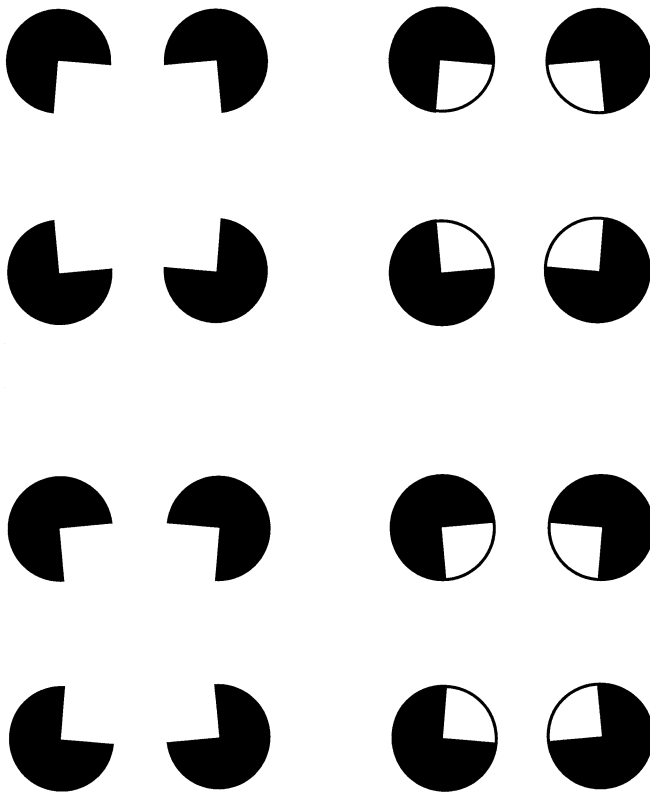


Fig. 10 Illusory contours reveal that the human right hemisphere can process some things better than the left. Both hemispheres can decide whether the illusory shapes (*left column*) are 'fat' or 'thin'. When outlines are added to the inducers so that the shapes can be perceived only by amodal completion (*right column*), only the right hemisphere can still tell the difference (adapted from Corballis *et al.*, 1999).

to that employed by Ringach and Shapley (Ringach and Shapley, 1996). In this task the subject is required to judge whether a deformed Kanizsa rectangle appears 'thin' or 'fat' (Fig. 10). Performance is compared with that in a control task in which the pacmen all face in the same direction and the participant is required to judge whether they are tilted 'up' or 'down'. Ringach and Shapley showed that neurologically intact observers are significantly better at the shape discrimination task than the control task, which indicates that the boundary-completion process assists in making the discrimination. The difference in performance between the two conditions provides an index of the perceptual strength of the boundary completion.

The first experiment (Corballis *et al.*, 1999) investigated the generation of illusory contours by the isolated hemispheres of two right-handed callosotomy patients, J.W. and V.P. Patient J.W.'s performance for both left-hemifield and right-hemifield stimuli was significantly improved by the presence of illusory contours. This indicates that J.W.'s two hemispheres are equally capable of generating illusory contours. Patient V.P. also showed improved discrimination accuracy when illusory contours were present, although this was restricted to stimuli presented to the right hemifield. This indicates that V.P.'s left hemisphere, at least, is capable

of generating illusory contours. Her discrimination performance for left-hemifield stimuli was good, so it seems likely that the lack of an advantage for illusory contour stimuli was the result of a ceiling effect. Overall, the results of this experiment suggest that, although the right hemisphere is better at the angular discrimination task, the two hemispheres profit equally from the presence of illusory contours.

Corballis and colleagues also compared the generation of illusory contours with amodal boundary completion in each hemisphere of patients J.W. and V.P. (Corballis *et al.*, 1999). If both tasks were mediated by the same neural mechanism there should be no systematic differences in performance between the two hemispheres. Both patients showed marked asymmetry in performance when discrimination depended on amodal completion. Amodal completion was performed well by the right hemisphere, but was poor in the left hemisphere. This finding strongly suggests that some aspect of the mechanism supporting amodal completion is lateralized to the right hemisphere. Taken together, these data suggest that several dissociable mechanisms contribute to boundary completion, and that these mechanisms are lateralized differently.

An intriguing aspect of this finding is that mice can apparently perceive shapes by amodal completion (Kanizsa *et al.*, 1993), which suggests that the grouping process that is lateralized to the right hemisphere is not a recent evolutionary adaptation. This has led to the current speculation that the right-hemisphere 'specialization' for visuospatial processing may be the result of the left hemisphere losing the visuospatial abilities it once possessed.

There is a left-hemisphere matching deficit for visual stimuli

Recently, we have been studying the hypothesis that the left hemisphere is capable of sophisticated visual processing but represents spatial information relatively crudely compared with the right hemisphere (Corballis *et al.*, 1999; Funnell *et al.*, 1999). The implication of this hypothesis is that pattern recognition is a function of both hemispheres but the right hemisphere is further specialized for processing spatial information. Several recent results support this hypothesis. First, Funnell and colleagues discovered that the left hemisphere of split-brain patient J.W. was impaired relative to the right hemisphere in deciding whether two visually presented objects were identical or mirror-reversed (Funnell *et al.*, 1999). This deficit was similar in magnitude for a variety of stimulus manipulations. In a follow-up study, Corballis and colleagues (unpublished results) found similar left-hemisphere deficits in patients J.W. and V.P. for judgements requiring spatial discriminations (size, orientation and vernier acuity) but not for those requiring non-spatial discrimination (luminance).

Corballis and colleagues conducted a more explicit test of

the hypothesis that the major difference in visual function between the hemispheres is a right-hemisphere specialization for representing spatial relationships (Corballis *et al.*, 1999). They presented patients J.W. and V.P. with pairs of stimuli within a single visual hemifield. These stimuli consisted of a square frame that contained a small icon in one corner. In one condition (the 'identity' condition), the task was to judge whether the icons were the same in each square. In the other condition (the 'spatial' condition), the task was to judge whether the icons were in the same relative position in the two squares. There was a suggestion in the data that the left hemisphere may perform the identity task better than the right, although both hemispheres performed this task well. In contrast, the right hemisphere was consistently better than the left in the spatial condition.

The results of this series of experiments indicate that the left hemisphere demonstrates striking deficits in simple visuospatial tasks. It is noteworthy that experiments with split-brained monkeys have sometimes revealed superiority of the *left* hemisphere for spatial judgements (e.g. Hamilton and Vermeire, 1991; Vogels *et al.*, 1994). The studies by Funnell and colleagues (Corballis *et al.*, 1999; Funnell *et al.*, 1999), as well as the preponderance of previous evidence from our laboratory and others, suggest that this is reversed in humans. Although this difference should not be over-interpreted, it is consistent with the idea that the evolution of language in the left hemisphere has resulted in the loss of some visuospatial abilities it once possessed.

There are hemispheric differences in the perception of sequentiality and apparent motion

When two spatially displaced visual stimuli are presented in rapid sequence, an observer may perceive a single stimulus moving between the two locations. This phenomenon is known as apparent motion. Whether apparent motion is perceived depends critically on the timing of the stimulus presentations. For example, Kolers has reported that the percept of apparent motion between successive flashes breaks down at a stimulus-onset asynchrony (SOA) somewhere between 150 and 200 ms, given a spatial separation of 3.3° (Kolers, 1972). Nevertheless, subjects are typically able to discriminate which of two flashes occurs first at much lower SOAs (e.g. Corballis, 1996; Forster *et al.*, 2000). Thus, the perception of apparent motion can be dissociated from the ability to discriminate sequentiality from simultaneity. Recent findings suggest that the neural representations of these processes may also be dissociable. Rorden and colleagues have reported that parietal lesions that disrupt the judgement of successiveness can leave motion perception unimpaired (Rorden *et al.*, 1997). In two recent papers, Corballis and colleagues (Corballis, 1996; Corballis *et al.*, 2000) report a RVF/left-hemisphere advantage in sequentiality/simultaneity discrimination in one split-brain patient (L.B.) when the SOA was below the threshold for the perception of apparent

motion. In contrast, more recent studies from three split-brain patients (L.B., J.W. and V.P.) suggest a LVF/right-hemisphere advantage for the same judgement when the SOA is long enough to support the perception of apparent motion (Forster *et al.*, 2000). All these studies employed similar methods.

The dissociation between the perception of apparent motion and the detection of sequentiality was obtained within a single patient (L.B.), which suggests that it cannot be accounted for by differences between subjects. The results imply that the perception of sequentiality is performed better by the left hemisphere, but that apparent motion, i.e. a more 'visuospatial' phenomenon with a longer time constant, is perceived better by the right hemisphere. These findings are consistent with the notion that the left hemisphere has finer temporal resolution than the right, as the percept of apparent motion, which may be lateralized to the right hemisphere, requires a longer SOA than the discrimination of sequentiality, which appears to be lateralized to the left hemisphere.

Monitoring and producing facial expressions are managed by different hemispheres

In the perceptual domain, it appears that the right hemisphere has special processes devoted to the efficient detection of upright faces (Gazzaniga, 1989). Although the left hemisphere can also perceive and recognize faces and can reveal superior capacities when the faces are familiar, the right hemisphere appears to be specialized for unfamiliar facial stimuli (Levy *et al.*, 1972; Gazzaniga and Smylie, 1983). This pattern of asymmetry has also been shown for the rhesus monkey (Hamilton and Vermiere, 1988).

Since the right hemisphere is superior in the perception of faces, it would be reasonable to suppose it is also specialized for the management of facial expressions (Fig. 11). Recent studies have shown, however, that while both hemispheres can generate spontaneous facial expressions, only the dominant left hemisphere can generate voluntary facial expressions (Gazzaniga and Smylie, 1990). It was also shown that when the left hemisphere carried out a command to smile or frown, the right side of the face responded ~180 ms before the left side. This latter finding is consistent with the fact that the callosum is involved in the execution of voluntary facial commands.

Hemispheric specialization for sensory-motor tasks

There are some tests that bring out hemispheric superiorities in some of the patients. The block design test from the Wechsler Adult Intelligence Scale is one such test. Here, the simple task of arranging some red and white blocks to match those of a given pattern results in the left hemisphere performing poorly while the right triumphs (Bogen and Gazzaniga, 1965). However, in other patients both

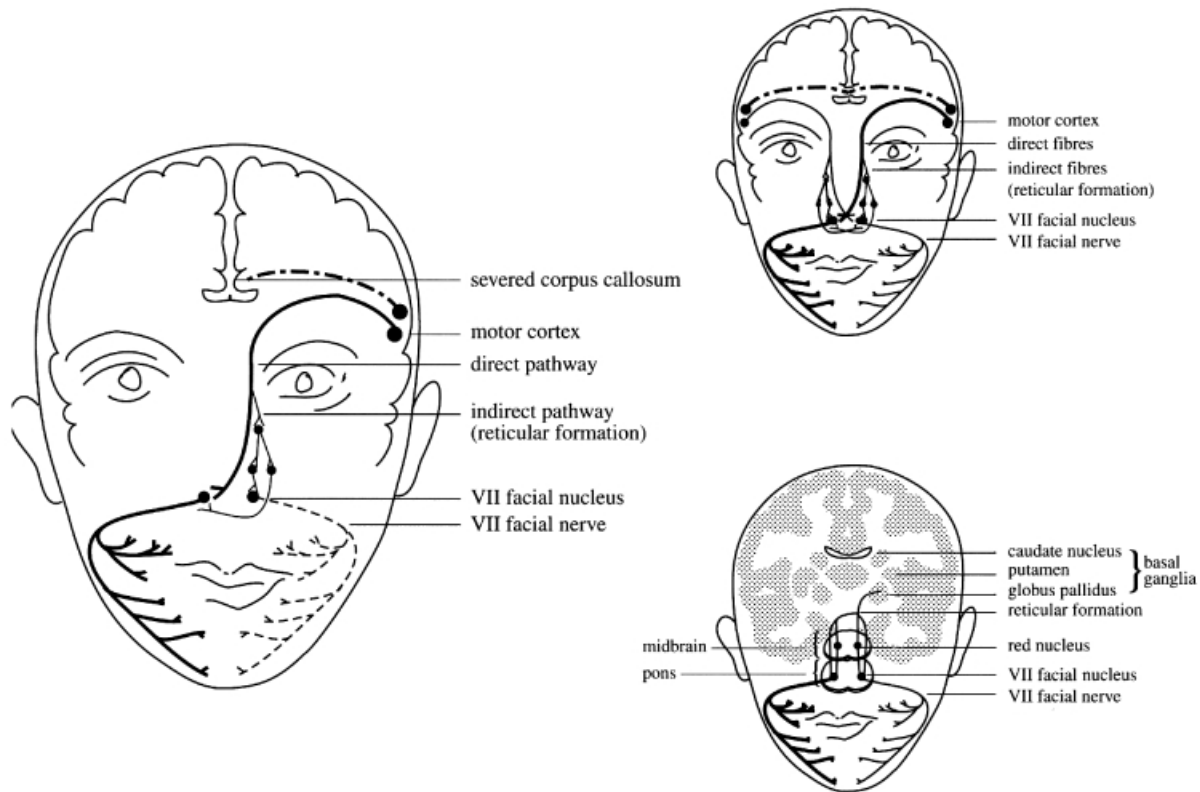


Fig. 11 The control of lower facial expressions is contralateral, so that the left hemisphere controls the right side of the face and *vice versa* (right panels). A command to the left hemisphere of a split-brain patient to 'smile' results in an asymmetrical response, the right side of the face smiling and the left side remaining neutral (left panel). The right hemisphere is apparently unable to carry out commands to smile or to frown (adapted from Gazzaniga and Smylie, 1990).

hemispheres appear impaired, and in still others the left hemisphere, in addition to speaking and thinking, performs this task well.

The same pattern of results is also seen for other tests such as the nonsense wire figure test (Milner and Taylor, 1972). The ability underlying these tests frequently seems to be localized to the right hemisphere. When the capacity happens to be lateralized in this way, it should be easier to analyse than when the processes involved are shared between the two half-brains.

The components of the block design task have not yet been identified. We do know that a patient who demonstrates right hemisphere superiority for this kind of task can show no superiority on the perceptual aspects of the task. If a picture of the block design pattern is flashed to either hemisphere, each can easily find the match from a series of pictures. And since each hand is demonstrably dexterous, the right for writing and the left for this kind of task, the crucial link must be in the mapping of the sensory message onto the capable motor system. It remains for future research to understand this superiority in performance when it is seen in one hemisphere.

Many low-level perceptual actions, such as anorthoscopic perception, can be carried out by both hemispheres

Not all perceptual activities are asymmetrical. An anorthoscopic display presents an image by moving it past a viewing slit that is too narrow to permit identification. In the right viewing conditions, a figure percept occurs and the viewer suddenly perceives a coherent moving image (Parks, 1965; Rock, 1981). Such percepts require the integration of spatial information over time. Since the right hemisphere is specialized for spatial processing, one might expect anorthoscopic percepts to be right-hemisphere-mediated. Fendrich investigated this possibility by presenting lateralized anorthoscopic displays to two callosotomy patients, J.W. and V.P. The stimuli consisted of 56 complex $4^\circ \times 4^\circ$ Lissajous figures (Fig. 12), which were swept horizontally back and forth across a $15'$ slit at $4^\circ/\text{s}$ (Fendrich *et al.*, 1996). The medial edge of the slit was 1.5° from the vertical meridian in the subject's LVF or RVF. To ensure sustained lateralization and eliminate retinal painting, the Purkinje image eyetracker was used to retinally stabilize the slit on the horizontal axis. Subjects indicated the moment when they perceived an

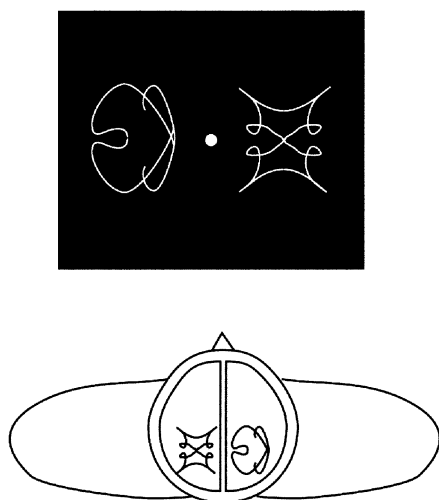


Fig. 12 Sample Lissajous figures used to test anorthoscopic shape perception in each hemisphere. These stimuli were presented to each hemisphere, moving behind a narrow slit so that only part of the figure was visible at any time, and the representation of the shape had to be constructed over time. Both hemispheres of patient J.W. were capable of perceiving shapes in this fashion (adapted from Fendrich *et al.*, 1996).

identifiable figure and then selected the figure from eight pictures inspected in free viewing conditions. The number of correct choices and the time required to attain correct figure percepts was recorded. The result was that both hemispheres could generate anorthoscopic percepts, the right hemisphere having only a minimal advantage. Thus, the synthesis of anorthoscopic figures occurs at a low level in the cortical visual processing hierarchy, where the processing of visual information does not depend on lateralized mechanisms.

Partial callosal section reveals specificity of commissure function

In animal studies, sectioning the entire corpus callosum and anterior commissure prevents the interhemispheric transfer of a wide range of modal and motor information. Partial sectioning of the commissures could also prevent some functions transferring across the callosum (Black and Myers, 1966; Sullivan and Hamilton, 1973; Hamilton and Vermeire, 1988). In humans, comparable studies were not possible until we found patients who had not undergone full callosal section; when we found them it became apparent that specific regions of the callosum were responsible for transferring specific types of information. This work was enhanced when MRI enabled investigators to describe cut and uncut fibre systems.

MRI-verified lesions of partial sections reveal modal functions

When the corpus callosum is fully sectioned, there is little or no perceptual or cognitive interaction between the

hemispheres. Surgical patients where callosal section is either limited or where there is inadvertent sparing of a part of the callosum enable one to examine functions of the callosum by region. For example, when the splenial region (posterior area of the callosum that interconnects the occipital lobe) is spared, there is normal transfer of visual information between the two cerebral hemispheres (Fig. 13). In such instances, pattern, colour, and linguistic information presented anywhere in either visual field can be matched with information presented to the other half-brain. Yet such patients do not transfer stereognostic information, and they also display a left ear suppression to dichotically presented auditory stimuli. Such observations are consistent with other human and animal data which reveal that the callosum's major subdivisions are organized in functional zones where the posterior regions are more concerned with visual information; the anterior regions transfer auditory and tactile information (Hamilton, 1982; Gazzaniga, 1989).

The anterior callosum is involved in higher-order transfer of semantic information

Patients who have undergone staged callosal section have also provided glimpses into what the anterior callosal regions transfer between the cerebral hemispheres. When the posterior half of the callosum is sectioned, the transfer of visual, tactile and auditory information is severely disrupted, but the remaining intact anterior callosum can transfer higher-order information. In one study the corpus callosum was sectioned in two stages (Sidtis *et al.*, 1981). After the first stage of sectioning the posterior callosum, the patient was unable to name stimuli presented to the right hemisphere. Over a 10-week period, though, he began to name some stimuli. Upon close inspection of this capacity it was discovered that the right hemisphere was transmitting to the left hemisphere gnostic cues about the stimulus but not the actual stimulus (Fig. 14). In short, the anterior callosum transfers gnostic representations of the stimulus rather than the real stimulus. After section of the anterior callosum, this capacity ceased.

Callosal specificity for orthographic transfer

Patient V.P. experienced inadvertent sparing of a band of fibres in the splenium and rostrum. These splenial fibres, seen in MRI, are functionally active in electrophysiological experiments and early behavioural experiments (Gazzaniga *et al.*, 1989; Mangun *et al.*, 1991). Funnell and colleagues (Funnell *et al.*, 2000a, b) report that, while there is no evidence for transfer of colour, shape, or size information, there is robust evidence for transfer of words presented visually. This is consistent with research by Suzuki and colleagues, who report dissociation between the interhemispheric transfer of word and picture information (Suzuki *et al.*, 1998). They speculate that transfer of word information is supported by fibres in the ventroposterior region of the splenium, which

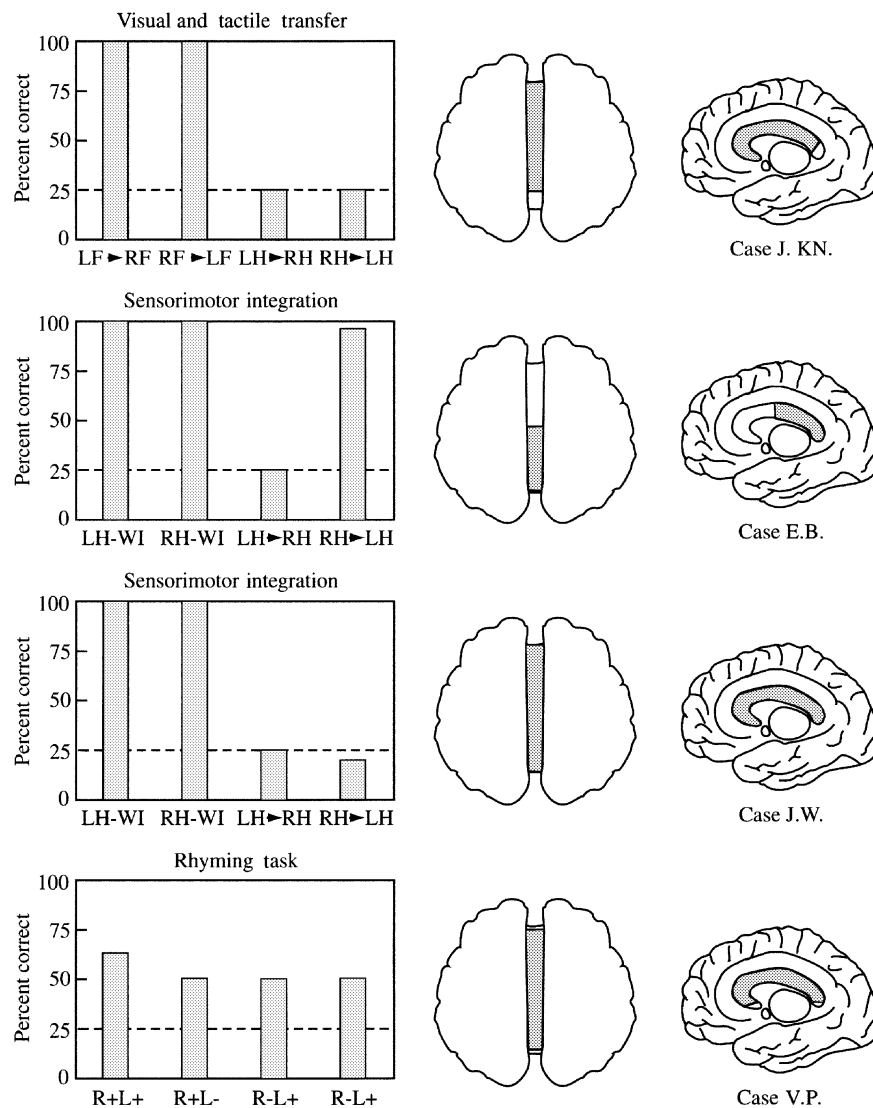


Fig. 13 Spared fibres in the corpus callosum allow the modality-specific transfer of perceptual and cognitive information. Patient J.KN. had some spared fibres in the splenium and was able to transfer visual information easily but performed at chance level for tactile information. Patient E.B. had a posterior callosotomy only, and was able to transfer sensorimotor information in one direction but not the other. This suggests that the neural fibres involved in transmitting the motor information to the opposite hemisphere were sectioned for only one direction of transfer. In contrast, patient J.W., who has a complete callosotomy, was unable to transfer any sensorimotor information. Patient V.P. has spared fibres at both ends of the corpus callosum. She is able to transfer some information about visually presented words from one hemisphere to the other, but otherwise appears fully split. For example, she is able to determine whether bilaterally presented words rhyme only if the two words look and sound alike (R+L+), but performs at chance level for all other conditions.

is the same region in which V.P. has callosal sparing (Fig. 15). The results for patient V.P. support the claim that remarkable functional specificity resides within the corpus callosum. V.P.'s spared splenial fibres appear to support the transfer of word information but not visual information.

Memory studies after cerebral disconnection

The most powerful impression one has when observing patients who have had their hemispheres divided is how

unaffected they appear to be in their general cognitive awareness, affect and sense of self (Gazzaniga, 1970). At a superficial level of observation, separating half of the neocortex from the other half appears to have little effect on cognition. Verbal IQ remains intact, as do within-hemisphere reaction times to perceptual stimuli and problem-solving capacity. Yet standardized memory tests administered postoperatively hint at an impairment of short-term memory (Zaidel and Sperry, 1974). Recent studies have extended these observations.

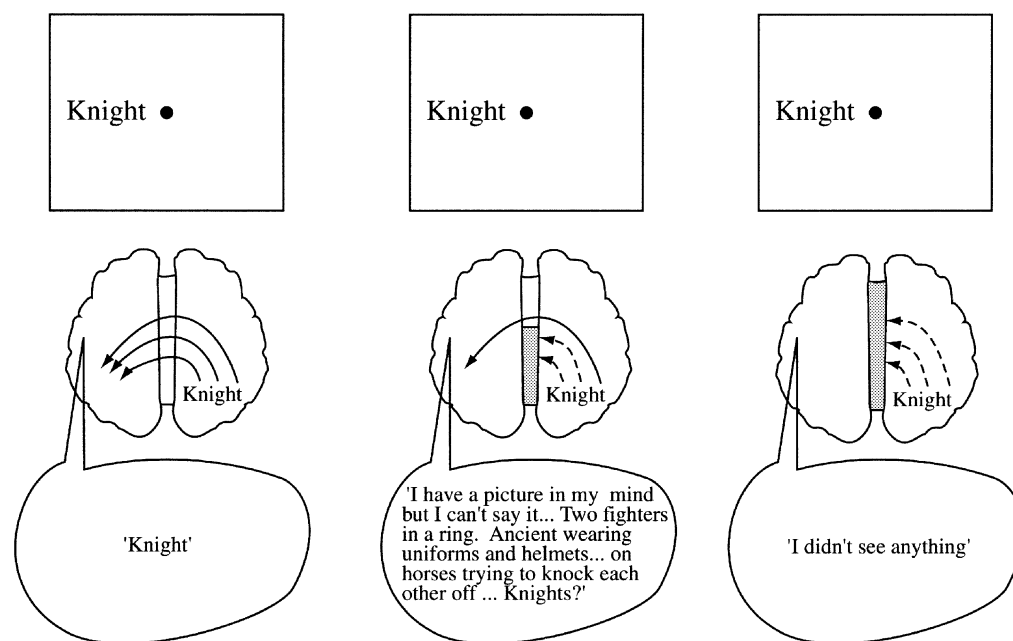


Fig. 14 Patient J.W. underwent a staged callosal section in which the posterior half of the callosum was sectioned before the anterior half. Prior to the surgery, J.W. had no difficulty reading words presented to the left visual field (*left panel*). Following posterior callosotomy, he was unable to read these words but could transfer semantic information about them (*centre panel*). After complete callosotomy, he was no longer able to transfer any information about the words (*right panel*). These results are consistent with the notion that anterior regions of the callosum are involved in the transfer of higher-order information (adapted from Sidtis *et al.*, 1981a).

Free recall but not recognition memory is impaired in each cerebral hemisphere

We have recently looked into information-processing capacities and sometimes have been able to compare postoperative performance with preoperative capacity. In these new tests, an interesting picture emerges: commissurotomy affects free recall mechanisms but recognition memory remains largely unchanged (Phelps *et al.*, 1991). Free recall requires a subject, with no cueing, to recall prior information such as a previously studied word list. Recognition tasks merely require a subject to judge whether a stimulus such as a printed word has been seen before on a list. Moreover, only posterior callosal-sectioned patients have a free recall deficit; patients with their anterior callosum sectioned behave normally. Since sectioning the posterior callosum inevitably involves sectioning the hippocampal commissure, this structure may play a crucial role in memory deficit. It is as if the resources for encoding a stimulus that contributes to free recall are less available after disconnection involving the hippocampal commissure.

There are multiple memory systems

The dominant theme in the cognitive neuroscience of memory is that memory is not a unitary system but is rather composed of multiple systems. Researchers generally agree on the existence of many of these systems, including explicit ones such as episodic or declarative memory, implicit ones such

as procedural memory and perceptual priming, and short-term ones such as working memory. Yet the widely studied distinction between episodic and semantic memory (Tulving, 1986) has been debated. Some argue that semantic memory is only a subsystem of a broader declarative memory system (Squire and Knowlton, 1995; Squire and Zola, 1998).

Compelling evidence in favour of a distinction between episodic and semantic memory systems comes from studies of brain-damaged patients, who show a dissociation between these two types of memory systems. There are many reports in the literature of patients who have virtually no episodic memory but do have intact semantic memory (Tulving *et al.*, 1988). For example, patient K.C. can remember how to change a tyre, but he cannot recall an incident in which he did so. Despite the lack of episodic memory, patients like K.C. can acquire new explicitly accessible semantic information (Kitchener *et al.*, 1998). Conversely, there are patients who exhibit the reverse pattern of memory deficit, such as patients with damaged anterior sections of the temporal lobe and elderly patients with semantic dementia (De Renzi *et al.*, 1987). These patients often have difficulty understanding the meaning of common words or the properties of common objects. Even so, they can sharply recall when items occurred. Hence, the patients have impaired semantic memory yet intact episodic memory.

Split-brain patients offer the opportunity to see a double dissociation within one brain. Many semantic and linguistic processes are known to be lateralized to the left hemisphere

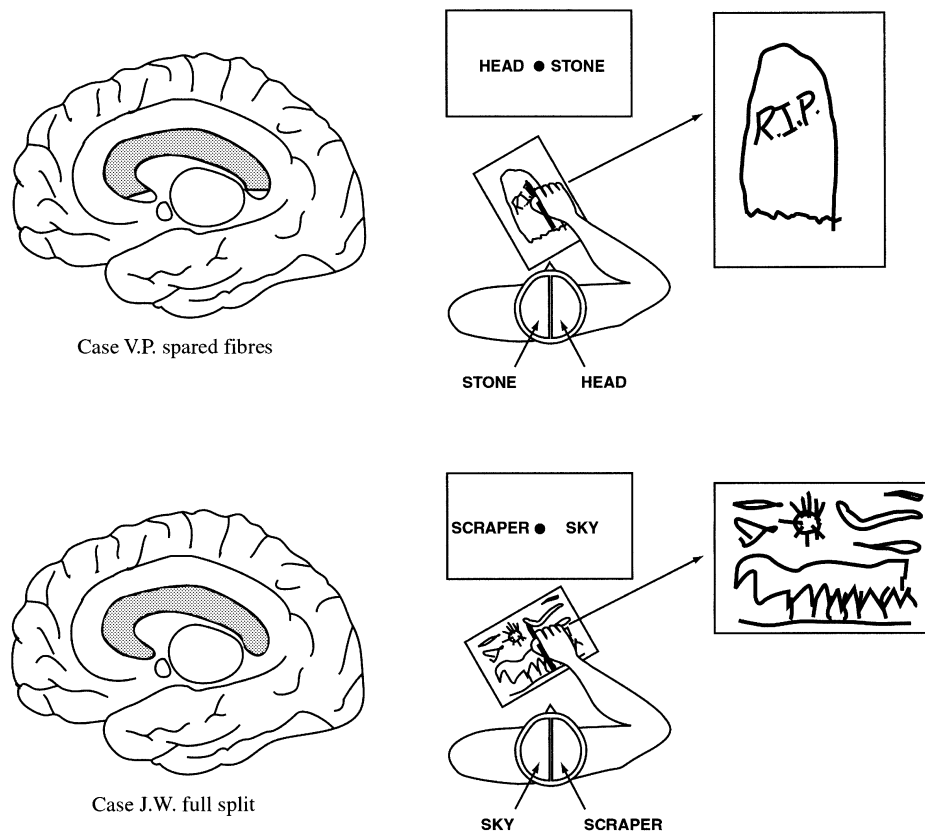


Fig. 15 Patient V.P., who has spared fibres at both ends of the corpus callosum, is able to integrate words presented to both visual fields to create a concept that is not suggested by either word. For example, when presented with the words 'head' and 'stone' she combines the information presented in the separate fields into the integrated concept of a tombstone (top panel). In contrast, patient J.W. (bottom panel) is unable to integrate information from the two visual fields. When presented with the words 'sky' and 'scraper' he simply draws a picture of the sky and of a scraper in serial order (adapted from Kingstone and Gazzaniga, 1995 and Funnell *et al.*, 2000).

in most people (Kutas *et al.*, 1988; Petersen *et al.*, 1988; Metcalfe *et al.*, 1995). These processes include, but are not limited to, word and object knowledge, semantic elaboration and judgements, and semantic priming (Warrington and Shallice, 1984; Demb *et al.*, 1995; Patterson and Hodges, 1995). Despite the left hemisphere's superiority in semantic processing, however, the left hemisphere also appears to be inferior in episodic memory tasks. This impairment is revealed in the high rate of false alarms in the left hemisphere as opposed to the right hemisphere for semantically related material (Phelps and Gazzaniga, 1992; Metcalfe *et al.*, 1995). It is as though the left hemisphere has impaired episodic memory but intact semantic memory.

Conversely, the right hemisphere is poor at semantic tasks even though it can have a robust lexicon and an intact episodic memory system (Gazzaniga *et al.*, 1962, 1965; Gazzaniga and Sperry, 1967; Baynes *et al.*, 1992; Metcalfe *et al.*, 1995). Despite the right hemisphere's deficit in semantic processing (i.e. simple problem-solving; LeDoux *et al.*, 1977a; Gazzaniga and Smylie, 1984), it recognizes words, pictures and abstract figures. Further, its performance in an array of episodic memory tasks is often better than the left

hemisphere's because of its much lower rate of false alarms. The right hemisphere's episodic memory is much more veridical in nature (Phelps and Gazzaniga, 1992; Metcalfe *et al.*, 1995; Miller *et al.*, 1998). It is as if the right hemisphere's episodic memory is intact but its semantic memory is impaired.

Studies of split-brain patients, therefore, provide support for the distinction between semantic and episodic memory (Fig. 16). These hemispheric memory dissociations are not true double dissociations in that one system is present and another is not; rather, the one system is relatively impaired while the other remains relatively intact. As I point out in the next section, episodic memory may be functioning quite well in each hemisphere, but its form or the nature of the representations may depend on the output of earlier systems.

Some hemispheric encoding asymmetries are material-specific and some are independent of material

The preceding research suggests a hemispheric difference in semantic and episodic memory. It has been further suggested

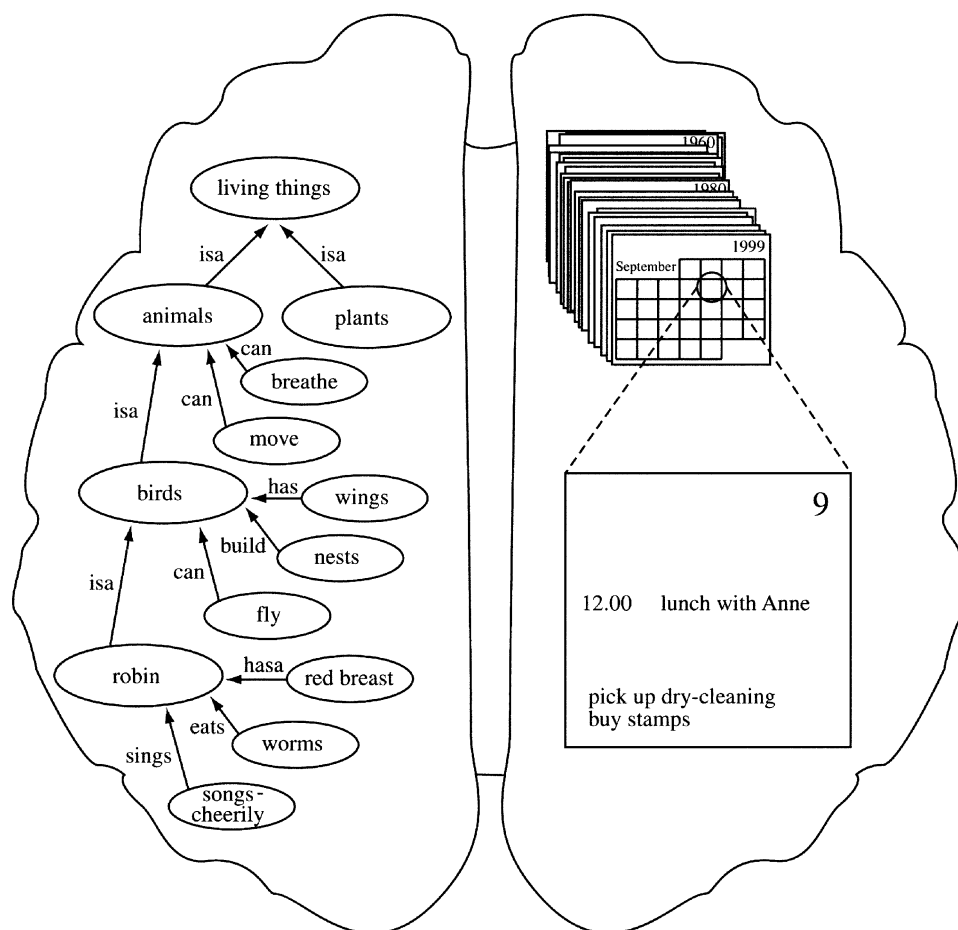


Fig. 16 Schematic drawing showing how the left hemisphere differs from the right in mnemonic functions. The left is specialized for semantic processing while the right appears to be specialized for episodic memory.

that within episodic memory, there is a hemispheric difference between encoding and retrieval. The memory model HERA (Hemispheric Encoding/Retrieval Asymmetry) proposed by Tulving and colleagues (Tulving *et al.*, 1994) suggests that episodic encoding is predominantly a left-hemisphere function while episodic retrieval is predominantly a right-hemisphere function. Semantic retrieval, however, is thought to rely on left-hemisphere regions. The model is based on examination of activations in PET and functional MRI (fMRI) investigations of memory functions (Kapur *et al.*, 1994; Demb *et al.*, 1995; Kapur *et al.*, 1996; Nyberg *et al.*, 1996; Cabeza *et al.*, 1997; Dolan and Fletcher, 1997; Buckner and Koutstaal, 1998). Although many neuroimaging studies have provided support for the model, the results of other studies have not been compatible with the model.

Because this model attributes specific memory functions to the two hemispheres, the split-brain patient provides an ideal opportunity to test aspects of the model. If episodic encoding and retrieval each rely on a different hemisphere, then dividing the hemispheres should have a devastating effect on episodic memory. As already noted, however, one of the most striking things about patients whose corpus

callosum is severed is that they do not demonstrate significant deficits in memory. What does the split-brain patient reveal about the neural substrates of memory processes?

A recent neuroimaging study suggests that the fundamental hemispheric difference in memory may be the nature of the to-be-remembered material. Kelley and colleagues found that words produced activations in the left prefrontal cortex, nameable objects produced bilateral activations in the prefrontal cortex and faces produced activations in the right prefrontal cortex (Kelley *et al.*, 1998). This possibility has been investigated by looking for hemispheric differences in memory for verbal and perceptual stimuli in split-brain patients (Miller *et al.*, 1997). In one task, the patients' two hemispheres were tested for memory of previously presented words. In the study phase, the patients engaged in either a shallow encoding task (whether the words contained the letter 'A') or a deep encoding task (whether the word represented a living object). The left hemisphere benefited from the deeper encoding whereas the right hemisphere did not. This is consistent with the suggestion, arising from the HERA model, that episodic memory is predominately a left-hemisphere function.

A second experiment, however, belies this interpretation. The design of the study was the same but the stimuli were faces instead of words. The shallow encoding task was to decide whether the face was male or female, and the deep encoding task was to judge whether the face was that of a healthy person. This time, the right hemisphere benefited from the encoding manipulation and the left did not. This study suggests that the basic difference between the two hemispheres of the brain may not be encoding versus retrieval, but is rather based on the nature of the material to be remembered. Further evidence for this conclusion is derived from a follow-up fMRI study in which college students studied faces, alternating between shallow encoding, deep encoding and rest conditions. In all of the subjects, the right fusiform gyrus and the right prefrontal cortex were active when the subject was comparing general face encoding with a control. When deep encoding of faces was compared with shallow encoding of faces, only areas of the right prefrontal cortex were active. This is consistent with the notion that it is the nature of the material to be encoded that lies at the root of the hemispheric difference in memory.

Although the foregoing studies provide evidence that the two hemispheres are specialized for processing different types of material, other research suggests that there are hemispheric processing differences that are independent of material. Metcalfe and colleagues demonstrated that the right hemisphere of split-brain patients is better than the left at discriminating between previously presented items and similar items that were not previously presented (Metcalfe *et al.*, 1995; see also Phelps and Gazzaniga, 1992). The left hemisphere tends to falsely 'recognize' these similar items, although it is able to correctly reject new items that are not similar to previously presented items. The critical point is that this hemispheric difference is independent of the material. The pattern of right hemisphere memory superiority was found with words, faces and abstract designs.

If two processes (such as encoding and retrieval) depend on each other for a cognitive task (such as episodic memory) and each of these processes is thought to be predominantly in a single hemisphere, then disconnection of the two hemispheres should have a catastrophic effect. What we find in split-brain patients, though, is not catastrophic impairment but mild impairment. Experimental evidence from split-brain patients suggests that the two hemispheres do play different roles in memory, but models such as HERA do not seem to characterize these differences accurately. The well-documented left-hemisphere superiority for verbal information and right-hemisphere superiority for visual information are shown to extend to hemispheric differences in memory for these materials. Interestingly, however, there are hemispheric processing differences independent of these material-specific effects. Evidence shows that the right hemisphere is specialized for veridical processing whereas the left hemisphere tends to process things in a more elaborative, less veridical manner. Thus each hemisphere is specialized for particular processes, but the roles of the two

hemispheres in memory cannot be captured by a simple dichotomy.

Language and speech processes of the left and right hemispheres

A dichotomy that is useful when trying to understand the neural substrates of language is the distinction between how the brain enables grammar and how it enables a lexicon. The grammar–lexicon distinction (Pinker, 1994) is different from the more traditional syntax–semantic distinction commonly invoked to understand the differential effects of brain lesions on language.

In general terms, grammar refers to the rule-based system humans have for ordering words to facilitate communication. The lexicon is the mind's dictionary in which words or groups of words are associated with certain meanings. The reason for using the grammar–lexicon distinction is that it takes into account the existence of units like idioms that can be learned by rote and form a single entry in the lexicon. While the lexicon (memory) cannot underlie most phrases and sentences because there is an endless number of unique sentences, such as the one I am currently writing, memory does play a role in the use of many short phrases ('how are you?' 'what's up?' 'get a life'). Thus, when uttered, such word strings do not reflect an interaction of syntax and semantic systems. They are, instead, an entry in the lexicon.

A modern view would predict that there ought to be brain areas wholly responsible for grammar. Moreover, evidence about localization of the lexicon ought to be more elusive since it reflects learned information and should be part of a brain's memory–knowledge system. The grammar system ought to be finite and hence localizable. The lexicon should be distributed and thus more difficult to completely damage. This is not to say that the grammar system is in a certain area of the brain. A syntax system is a complex entity that depends on the interaction of numerous subsystems for it to function.

Language and speech processes can rarely be present in both hemispheres

Right-hemisphere language has a different organizational structure compared with left-hemisphere language. Whereas the separated left hemisphere is fully capable of producing and comprehending all aspects of language, the right hemisphere can possess a lexicon but with scant grammar. In callosotomy patients who show evidence of right-hemisphere language, the disconnected right hemisphere is severely limited in its range of language behaviour (Gazzaniga, 1970; Zaidel, 1991).

Over the last 30 years, few patients have been added to the group that demonstrate some kind of language in the right hemisphere (for review see Baynes, 1990; Baynes and Eliassen, 1998). In the early 1980s only five split-brain

patients had demonstrated evidence of a lexicon in the right hemisphere. Since then we have found only one right-handed and one left-handed patient with a lexicon in both the left and the right hemisphere (Lutsep *et al.*, 1995; Baynes *et al.*, 1998).

The left and the right lexicons of these special patients can be nearly equal in their capacity, but they may be organized quite differently. For example, there are limited priming phenomena in the disconnected right hemisphere, and letter processing appears to be serial, not parallel, in nature (Reuter-Lorenz and Baynes, 1992; Baynes *et al.*, 1996, 1997a). In addition, they have other deficiencies such as not recognizing whether one word is subordinate to another (Gazzaniga *et al.*, 1984) and making judgements about antonyms (Gazzaniga and Miller, 1989). Although there appears to be a passive semantic network, it does not support a normal range of semantic judgments.

In summary, there can be two lexicons, one in each hemisphere, but this lexical organization is rare (Gazzaniga, 1983). When present, the right hemisphere's lexicon appears to be organized differently from the left hemisphere's lexicon. These observations are consistent with the view that lexical knowledge reflects general learning processes and, as such, can have a wider distribution in the cerebral cortex. Still, it is important to note that in the general population the lexicon appears to be in the left hemisphere. A right hemisphere lexicon is rarely present; when it is, it may be limited, perhaps because of organization differences that we have barely begun to characterize.

Generative syntax is present in only one hemisphere

While the right hemisphere of some patients clearly has a lexicon, these right hemispheres perform erratically in other aspects of language, such as understanding verbs, pluralizations, possessives and active-passive differences (Gazzaniga, 1970). The right hemisphere in patients who possess some language has not been able to use word order to understand phrases (Gazzaniga *et al.*, 1984). At the same time these right hemispheres can indicate when a sentence ends with a semantically odd word (Kutas *et al.*, 1990). In addition, right hemispheres that reveal language capacities can make judgements about grammaticality (Baynes and Gazzaniga, 1988). Thus, even though they cannot use syntax to understand sentences, they can judge that some utterances are grammatical while others are not. If we are correct that the right hemisphere has the means to encode static lexical information but not productive grammar, this unexpected finding would indicate that patterns of speech are learned by rote. Yet, recognizing the surface sound pattern of acceptable utterances does not mean that a neural system can use this information to assist in deriving meaning from a sentence. In both lexicon and grammar, the right hemisphere possesses some passive recognition abilities but does not employ them productively.

Generative phonology is present in only one hemisphere

The prototypical split-brain patient not only lacks right hemisphere control of speech mechanisms but cannot demonstrate systematic phonology (i.e. the system of rules that governs the way sounds are combined into words). Despite good auditory comprehension of single words, the right hemisphere of these patients lacks categorical perception of phonemes (Sidtis *et al.*, 1981b) and cannot match rhyming words and pictures (Zaidel and Peters, 1981). This inability to match rhyming words from printed text persists even after some control of speech mechanisms develops (Baynes *et al.*, 1995). Although many investigators document both whole-word and sublexical reading mechanisms, this dual-route hypothesis is not generally extended to the spoken lexicon. One exception is the hypothesis that tensed forms of regular verbs are generated but that tensed forms of irregular verbs are stored as lexical items (Pinker, 1994).

It is possible that the right-hemisphere auditory lexicon is composed of whole-word rather than sublexical units. One study that demonstrated right-hemisphere sensitivity to phonological units at the level of integrating visual and auditory discrepant input (the McGurk effect) employed whole-word stimuli rather than the more usual consonant-vowel syllables that demonstrate this effect (Baynes *et al.*, 1994). Such a whole-word lexicon may be adequate for comprehending auditory words but inadequate for articulatory mechanisms.

Some right hemispheres can develop speech

One of the hallmarks of most split-brain patients is that they speak out of the left hemisphere and not the right. This observation is consistent with the neurological literature and Amytal (amylobarbitol) studies, in which the left hemisphere is the dominant hemisphere for language and speech (Lenneberg, 1967).

There are now three and possibly four split-brain patients who can speak out of each hemisphere. While there is always an initially dominant hemisphere after brain bisection, some patients have developed the capacity to make one-word utterances from the disconnected right hemisphere (Gazzaniga *et al.*, 1979; Gazzaniga *et al.*, 1984; Zaidel and Seibert 1997). This rather startling development shows that two of the three major systems in human language can be managed by either hemisphere. Whereas patients P.S. and V.P. could speak in response to stimulation of the left visual field soon after the completion of surgery, patient J.W. did not develop this right-hemisphere capacity until ≥ 10 years after his surgery (Baynes *et al.*, 1995; Gazzaniga *et al.*, 1996). This change so long after surgery opens up new questions regarding behavioural plasticity in the adult brain.

Some right hemispheres can develop a writing system

A passive writing system can develop in the right hemisphere. One left-handed patient became agraphia (could not write

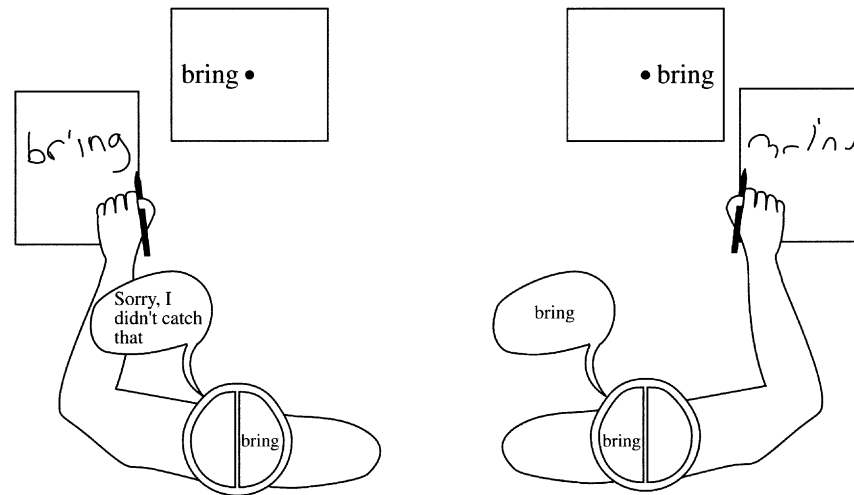


Fig. 17 Unique representations for the distributions of language processes in patient V.J. Following full callosal section she was able to verbalize material presented to her left hemisphere but not material presented to her right hemisphere. At the same time, she was unable to write words presented to her left hemisphere but was able to write words presented to her right hemisphere. This dissociation suggests that an intact phonological system is not a prerequisite for writing (adapted from Baynes *et al.*, 1998).

with either hand) following surgery. Five years after the surgery she remains unable to write at will, although she can produce her signature. When words are flashed to her dominant left hemisphere, she can say them out loud but she cannot write them (Fig. 17). When words are flashed to her right hemisphere, she cannot say them but her left hand can usually write them (Baynes *et al.*, 1998). She cannot write the names of objects when pictures are lateralized, although she can match words and pictures accurately. This patient also shows semantic priming in her right hemisphere (i.e. she is faster at recognizing words if they are preceded by related words), indicating a semantic network in her right hemisphere. Nonetheless, without the executive skills of her dominant left hemisphere, her writing remains isolated (modular) and useless in the non-dominant hemisphere.

Studies related to issues of consciousness

Classical split-brain research has revealed the many distinctive functions of the left and right hemispheres. By testing each disconnected hemisphere, one can assess the different capacities each might possess. The left hemisphere is specialized for language, speech and intelligent behaviour, while the right is specialized for such tasks as recognizing upright faces, focusing attention and making perceptual distinctions. Although split-brain research has elucidated many hemispheric differences in basic attentional, perceptual and cognitive functions, what have we learned about how the two hemispheres interact to make us integrated, sentient beings? Can split-brain patients perhaps give us a window into the nature of human consciousness?

The left hemisphere is specialized for intelligent behaviour

After the human cerebral hemispheres have been disconnected, the verbal IQ of a patient remains intact (Nass and Gazzaniga, 1987; Zaidel, 1991) and the problem-solving capacity, such as seen in hypothesis-formation tasks, remains unchanged for the left hemisphere (Ledoux *et al.*, 1977). While there can be deficits in free recall capacity and in other performance measures, the capacity for problem-solving appears unaffected. In other words, isolating essentially half of the cortex from the dominant left hemisphere causes no major change in cognitive functions. The left remains unchanged from its preoperative capacity, yet the largely disconnected, same-size right hemisphere is seriously impoverished in cognitive tasks. While the right hemisphere remains superior to the isolated left hemisphere for some perceptual and attentional skills, and perhaps also emotions, it is poor at problem-solving and many other mental activities. A brain system (the right hemisphere) with roughly the same number of neurons as one that easily cogitates (the left hemisphere) is incapable of higher order cognition—convincing evidence that cortical cell number by itself cannot fully explain human intelligence (Gazzaniga, 1995).

The left hemisphere is dominant for hypothesis formation

The difference between the two hemispheres in problem-solving is revealed in a probability-guessing experiment. In this paradigm, subjects try to guess which of two events will happen next. Each event has a different probability of

occurrence (e.g. a red stimulus might appear 75% of the time and a green 25% of the time) but the order of occurrence of the events is entirely random. There are two possible strategies for responding in this task: matching and maximizing. In the red/green example, frequency matching would involve guessing red 75% of the time and guessing green 25% of the time. Since the order of occurrence is entirely random, this strategy could potentially result in a great deal of error. The second strategy, maximizing, involves simply guessing red every time. That ensures an accuracy rate of 75% since red appears 75% of the time. Animals such as rats and goldfish maximize. Humans match. The result is that non-human animals perform better than humans in this task. The human's use of this suboptimal strategy has been attributed to a propensity to try to find patterns in sequences of events, even when told the sequences are random. Wolford and colleagues (2000) tested the two hemispheres of split-brain patients in this type of probability-guessing paradigm. They found that the left hemisphere used the frequency-matching strategy whereas the right hemisphere maximized (Fig. 18). Their interpretation was that the right hemisphere's accuracy was higher than the left's because the right hemisphere approaches the task in the simplest possible manner with no attempt to form complicated hypotheses about the task. The left hemisphere, on the other hand, engages in the human tendency to find order in chaos. The left hemisphere persists in forming hypotheses about the sequence of events even in the face of evidence that no pattern exists. Why would the left hemisphere do this even when it can be non-adaptive?

The left hemisphere possesses a unique capacity to interpret behaviour and unconsciously driven emotional states

Several years ago we observed how the left, dominant-speaking hemisphere dealt with behaviours we had elicited from the disconnected right hemisphere. We came upon the phenomenon by using a simultaneous concept test. The patient was shown two pictures, one exclusively to the left hemisphere and one exclusively to the right, and was asked to choose from an array of pictures placed in full view in front of him those that were associated with the pictures lateralized to the left and right brain. In one example of this kind of test, a picture of a chicken claw was flashed to the left hemisphere and a picture of a snow scene to the right hemisphere. Of the array of pictures placed in front of the subject, the obviously correct association is a chicken for the chicken claw and a shovel for the snow scene. Patient P.S. responded by choosing the shovel with the left hand and the chicken with the right. When asked why he chose these items, his left hemisphere replied 'Oh, that's simple. The chicken claw goes with the chicken, and you need a shovel to clean out the chicken shed'. Here the left brain, observing the left hand's response, interprets that response in a context consistent with its sphere of knowledge—one that does not

include information about the left hemifield snow scene. We called this left hemisphere process 'the interpreter' (Fig. 19).

This same general idea has been observed when the left brain interpreter struggles to cope with mood shifts produced experimentally by manipulating the disconnected right hemisphere. A positive mood shift triggered by the right hemisphere finds the left interpreting its current experience in a positive way. In a similar manner, when the right triggers a negative mood, the left interprets a previously neutral situation in negative terms. For example, in the first observation of this kind, an arousing stimulus was shown to the silent right hemisphere. The patient denied seeing anything, while at the same time suddenly claiming she was upset and that the experimenter was upsetting her. Here, the left hemisphere felt the valence of the emotional response but was unable to say what it was. Nonetheless, it immediately constructed a theory to explain the emotional state

The relationship between the interpreter and conscious experience

Decades of split-brain research have revealed the specialized functions of the two hemispheres, as well as providing insights into specialization within each hemisphere. Our large human brains have countless capacities. Our uniquely human skills may well be produced by minute, circumscribed neuronal networks, sometimes referred to as 'modules', but our highly modularized brain generates a feeling in all of us that we are integrated and unified. If we are merely a collection of specialized modules, how does that powerful, almost self-evident feeling come about? The answer may lie in the left hemisphere interpreter and its drive to seek explanations for why events occur.

In 1962, Schachter and Singer injected epinephrine into subjects participating in a research experiment (Schachter and Singer, 1962). Epinephrine activates the sympathetic nervous system and the result is an increased heart rate, hand tremors and facial flushing. The subjects were then put into contact with a confederate who behaved in either a euphoric or an angry manner. The subjects who were informed about the effects of the epinephrine attributed symptoms such as a racing heart to the drug. The subjects who were not informed, however, attributed their autonomic arousal to the environment. Those who were with the euphoric confederate reported being elated and those with the angry confederate reported being angry. This finding illustrates the human tendency to generate explanations for events. When aroused, we are driven to explain why. If there is an obvious explanation we accept it, as did the group informed about the effects of epinephrine. When there is not an obvious explanation, we generate one. The subjects recognized that they were aroused and immediately attributed some cause to it. This is a powerful mechanism; once seen, it makes one wonder how often we are victims of spurious emotional-cognitive correlations. Split-brain research has shown us that

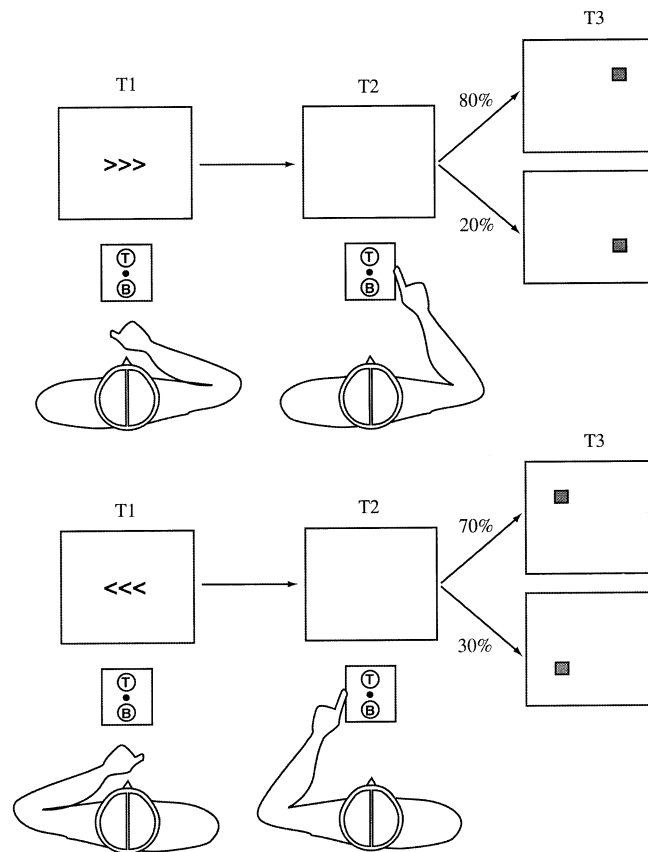


Fig. 18 Each hemisphere responds differently when challenged with the simple problem of trying to predict whether a light will appear above or below the horizontal meridian. The position of the light is determined randomly on each trial, the top position occurring 80% of the time for right-field/right-hand trials and 70% of the time for left-field/left-hand trials. After several blocks of trials the left hemisphere, like normal controls, distributes its responses between the two alternatives by matching the probability that each will occur (i.e. guesses 'top' ~80% of the time and 'bottom' ~20% of the time). As a result, it guesses less accurately than if a simple strategy of maximizing (always choosing the more probable alternative) were implemented. The right hemisphere, by contrast, does tend to choose the more probable alternative on each trial, which maximizes performance in the long term (adapted from Wolford *et al.*, 2000).

this tendency to generate explanations and hypotheses—to interpret—lies within the left hemisphere.

Although the left hemisphere seems driven to interpret events, the right hemisphere shows no such tendency. A reconsideration of hemispheric memory differences suggests why this dichotomy might be adaptive. When asked to decide whether a series of stimuli appeared in a study set or not, the right hemisphere is able to identify correctly items that have been seen previously and to reject new items. The left hemisphere, however, tends to falsely recognize new items when they are similar to previously presented items, presumably because they fit into the schema it has constructed (Phelps and Gazzaniga, 1992; Metcalfe *et al.*, 1995). This finding is consistent with the hypothesis that the left hemisphere interpreter constructs theories to assimilate perceived information into a comprehensible whole. By going beyond simply observing events to asking why they happened, a brain can cope with such events more effectively should they happen again. In doing so, however, the process of

elaborating (story-making) has a deleterious effect on the accuracy of perceptual recognition, as it does with verbal and visual material. Accuracy remains high in the right hemisphere, however, because it does not engage in these interpretive processes. The advantage of having such a dual system is obvious. The right hemisphere maintains a veridical record of events, leaving the left hemisphere free to elaborate and make inferences about the material presented. In an intact brain, the two systems complement each other, allowing elaborative processing without sacrificing veracity.

The probability-guessing paradigm also demonstrates why an interpreter in one hemisphere and not the other would be adaptive. The two hemispheres approach problem-solving situations in two different ways. The right hemisphere bases its judgements on simple frequency information, whereas the left relies on the formation of elaborate hypotheses. In the case of random events, the right hemisphere's strategy is clearly advantageous and the left hemisphere's tendency to create nonsensical theories about random sequences is

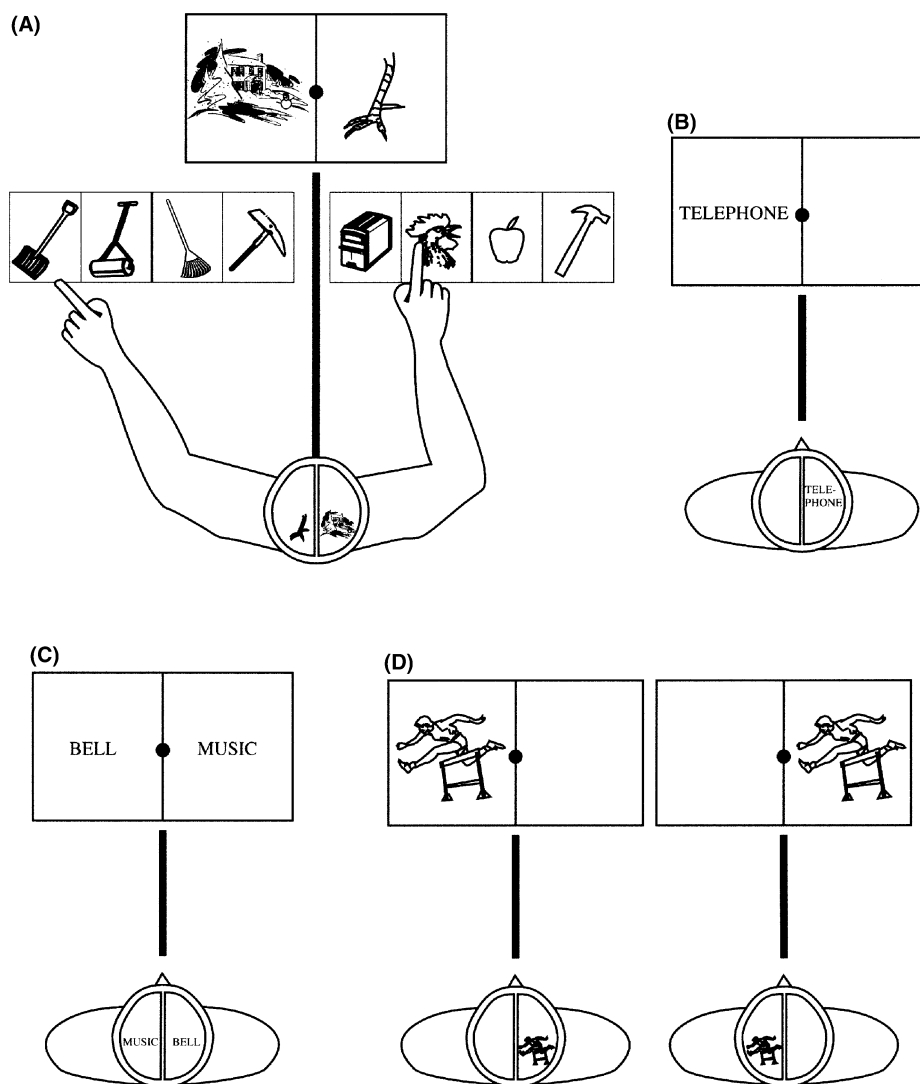


Fig. 19 Four examples of how the left brain tries to interpret the actions of both hemispheres. (A) In a classical test, a chicken claw was shown to the (speaking) left hemisphere and a snow scene was shown to the (silent) right hemisphere. Patient P.S. easily picked out related pictures from a set of eight choices. His left hand chose a snow shovel and his right hand chose a chicken. When asked why he had picked those particular pictures, P.S. said, 'Oh, that's simple. The chicken claw goes with the chicken, and you need a shovel to clean out the chicken shed'. (B) In another instance of the interpreter at work, patient J.W. was flashed the word 'telephone' to the right hemisphere. He said, 'I'm not sure I got that one. I think it's clap—that wouldn't be right, would it?' He was then asked to draw what he had seen and with his left hand he drew a telephone. When he was finished he said 'Telephone. I don't know where I got clap out of telephone'. He was then asked, 'You said clap but you drew a phone. Do you know why you drew a phone?' He responded 'No. Too many pills—it makes me feel high'. (C) Patient J.W. was flashed the word 'bell' to his silent right hemisphere and the word 'music' to his left hemisphere. Again, each hemisphere was free to choose related pictures from a group. J.W. pointed to a picture of a bell, and when asked why said 'Music—last time I heard any music was from the bells outside here, banging away'. J.W. was referring to the bells that ring regularly from the Dartmouth library. (D) Patient V.P., who can make single-word utterances out of her right hemisphere as well as speak out of her left. When a picture is shown to her left hemisphere she describes it at length and accurately. For example, when shown a picture of a hurdler she says, 'I don't know if he's an athlete or not, but he is a man running over hurdles. He's got gym shorts on and I don't know for sure if he had a shirt on. I think he did and tennis shoes, jogger's shoes'. At a later time the same picture is shown to the right hemisphere and she utters a one-word description which is heard by the left brain. From that point the left tries to describe something it didn't in fact see. Patient V.P. says, 'An athlete—a basketball guy? Had a uniform. His back was facing me, and he was on an angle. He looked like he had been walking, and he was gonna take another step because one foot was like more out'.

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.

The difference in the way the two hemispheres approach the world can be seen as adaptive. It might also provide some clues about the nature of human consciousness. In the media, split-brain patients have been described as having two brains. The patients themselves, however, claim that they do not feel any different after the surgery than they did before. They do not have any sense of the dual consciousness implied by the notion of having two brains. How is it that two isolated hemispheres give rise to a single consciousness? The left hemisphere interpreter may be the answer. The interpreter is driven to generate explanations and hypotheses regardless of circumstances. The left hemisphere of split-brain patients does not hesitate to offer explanations for behaviours which are generated by the right hemisphere. In neurologically intact individuals, the interpreter does not hesitate to generate spurious explanations for sympathetic nervous system arousal. In these ways, the left hemisphere interpreter may generate a feeling in all of us that we are integrated and unified.

Implications for understanding some neurological syndromes

Clinical neurologists have described a variety of peculiar syndromes, such as anosognosia, that affect the perceptual and cognitive systems (Prigatano and Schacter, 1991). Patients with anosognosia claim that the left half of their body is not theirs. They see their paralysed left hand and yet maintain that it has nothing to do with them. Although the region of brain damage associated with this syndrome is known, it is still difficult to understand why damage to the parietal lobe causes such bizarre behaviour in the patient. Other types of neurological damage can cause equally extraordinary symptoms. The concept of the interpreter, derived from split-brain research, may provide a way of understanding the more extraordinary results of cortical damage.

Consider what may happen as a result of a lesion in a person's optic tract. If the lesion is in the nerve that carries information about vision to the visual cortex, the damaged nerve ceases to carry that information; the patient complains that he is blind in the relevant part of his visual field. For example, such a patient might have a huge blind spot to the left of the centre of his visual field. He rightly complains.

If another patient has a lesion not in the optic tract but in the visual cortex, creating a blind spot of the same size and in the same place, he does not complain at all. The reason is that the cortical lesion is in the place in his brain which represents an exact part of the visual world, the place

that ordinarily asks, 'What is going on to the left of visual centre?' With a lesion on the optic nerve, this brain area was functioning; when it could not get any information from the nerve, it put up a squawk—something is wrong. When that same brain area is itself lesioned, the patient's brain no longer cares about what is going on in that part of the visual field; there is no squawk at all. The patient with the central lesion does not have a complaint because the part of the brain that might complain has been incapacitated, and no other can take over.

As we move farther into the brain's processing centres, we see the same pattern, but now the problem is with the interpretive function. The parietal cortex that is constantly seeking information on the arm's position in three-dimensional space also monitors the arm's existence in relation to everything else. If there is a lesion in sensory nerves that bring information to the brain about where the arm is, what is in its hand, or whether it is in pain or feels hot or cold, the brain communicates that something is wrong: 'I am not getting input'. But if the lesion is in the parietal cortex, that monitoring function is gone with no squawk raised, because the squawker is damaged.

Consider our case of anosognosia and the disowned left hand. A patient with a right parietal lesion suffers damage to the area that represents the body's left half. The brain area cannot feel the state of the left hand. When a neurologist holds a patient's left hand up to the patient's face, the patient gives a reasonable response: 'That's not my hand'. The interpreter, which is intact and working, cannot get news from the parietal lobe, since the flow of information has been disrupted by the lesion. For the interpreter, the left hand simply does not exist any more, just as seeing behind the head is not something the interpreter is supposed to worry about. It is true, then, that the hand held in front of him cannot be his. In this light, the claims of the patient are more reasonable.

An even more fascinating syndrome is called 'reduplicative paramnesia' (Ramachandran 1996; Murai *et al.*, 1997). In one patient I had, the patient was a woman who, although she was being examined in my office at New York Hospital, claimed we were in her home in Freeport, Maine. The standard interpretation of this syndrome is that she made a duplicate copy of a place (or person) and insisted that there are two.

This woman was intelligent; before the interview she was bidding her time reading the New York Times. I started with the 'So, where are you?' question. 'I am in Freeport, Maine. I know you don't believe it. Dr Posner told me this morning when he came to see me that I was in Memorial Sloan-Kettering Hospital and that when the residents come on rounds to say that to them. Well, that is fine, but I know I am in my house on Main Street in Freeport, Maine!' I asked, 'Well, if you are in Freeport and in your house, how come there are elevators outside the door here?' The grand lady peered at me and calmly responded, 'Doctor, do you know how much it cost me to have those put in?'

This patient's interpreter tries to make sense of what she knows and feels and does. Because of her lesion the part of the brain that represents locality is overactive and sending out an erroneous message about her location. The interpreter is only as good as the information it receives, and in this instance it is getting a wacky piece of information. Yet the interpreter still has to field questions and make sense of other incoming information—information that to the interpreter is self-evident. The result? A lot of imaginative stories.

Creating our autobiography and personal conscious experience

The interpreter's activities can be viewed on a larger canvas. Most neuroscientists want an understanding of consciousness but also a neuroscience of human consciousness. When considering the problem of consciousness, it is important to consider the possibility that consciousness is an instinct—a built-in property of brains. Like all instincts, it is just there. One does not learn to be conscious and one cannot unlearn the reality of conscious experience. Some day a more mechanistic understanding of its operation will be to hand, but it will probably not be a personally fulfilling one.

We should abandon our expectations that a scientific understanding of consciousness will sweep away our sense of strangeness about its nature. Consider our reproductive instinct. Does it help our sense of desire to understand the role of testosterone when we see a shapely figure across the room? Or take the human instinct for language. Does it help us to enjoy language more when we understand that grammar is a universal built-in reflex but that our lexicon is learned? It would seem that something wonderfully new and complex happens as the brain enlarges to its full human form. Whatever happens, it triggers our capacity for self-reflection and all that goes with it. How do we account for this?

When the foregoing research is taken together, rather simple suggestions are appropriate. First, focus on what is meant by 'conscious experience'. The concept refers to the awareness human beings have of their capacities as a species—awareness not of the capacities themselves but of our experience of exercising them and our feelings about them. The brain is not a general-purpose computing device; it is a collection of circuits devoted to these capacities. This is true for all brains, but what is amazing about the human brain is the sheer number of its capacities. The human has more than the chimp, which has more than the monkey, which has more than the cat, which runs circles around the rat. Step one is to recognize that the human mind is a collection of adaptive brain systems and, further, to recognize that each species' capacities affect its experience of the world.

Now consider step two. Can there be any doubt that a rat at the moment of copulation is as sensorially fulfilled as a human being? A cat surely enjoys a good piece of cod. And a monkey must enjoy a spectacular swing. Each species is aware of its special capacities. So what is human

consciousness? It is awareness of the very same kind, except that we humans are aware of so much more, so many wonderful things.

Think of the variations in capacity within our own species; they are not unlike the vast differences between species. Years of split-brain research have shown that the left hemisphere has many more mental capacities than does the right. The left is capable of logical feats that the right cannot manage. Even with both our hemispheres, though, the limits of human capacity are everywhere in the population. No one need be offended to realize that some people with normal intelligence can understand Ohm's law, while others, such as this author, are clueless about hundreds of mathematical concepts.

When we realize that specialized brain circuits arose through natural selection, it becomes evident that the brain is not a unified neural net that supports a problem-solving device. If this view is accepted it becomes equally clear that smaller, more manageable circuits produce awareness of a species' capacities. By contrast, holding fast to the notion of a unified neural net forces us to try to understand human consciousness by figuring out the interactions of billions of neurons. That task is hopeless; this scheme is not.

Hence step three. The same split-brain research that exposed startling differences between the two hemispheres revealed that the human left hemisphere harbours our interpreter. Its job is to interpret our responses—cognitive or emotional—to what we encounter in our environment. The interpreter sustains a running narrative of our actions, emotions, thoughts, and dreams. The interpreter is the glue that keeps our story unified and creates our sense of being a coherent, rational agent. To our bag of individual instincts it brings theories about our life. These narratives of our past behaviour seep into our awareness and give us an autobiography.

Insertion of an interpreter into an otherwise functioning brain creates many by-products. A device that begins by asking how one thing relates to another, a device that asks about an infinite number of things, in fact, and that can get productive answers to its questions, cannot help but give birth to the concept of self. Surely one question the device would ask is, 'Who is solving all these problems? Let's call it *me*'—and away it goes! A device with rules for figuring out how one thing relates to another will quickly be reinforced for having that capacity, just as an ant's solving where to have its evening meal reinforces the ant's food-seeking devices. Once mutational events in the history of our species brought the interpreter into existence, there was no getting rid of it.

Our brains are automatic because physical tissue carries out what we do. How could it be otherwise? Our brains are operating before our conceptual self knows it. But the conceptual self emerges and grows until it can find interesting—but not disheartening—the biological fact that our brain does things before we are consciously aware of them. The interpretation of things that we encounter has liberated us from a sense of being determined by our

environment; it has created the wonderful sense that our self is in charge of our destiny. All of our everyday success at reasoning through life's data convinces us of this. And because of the interpreter within us, we can drive our automatic brains to greater accomplishment and enjoyment of life.

Acknowledgements

I am deeply in debt to my colleagues who have helped review this current report. They include Steven Hillyard, Steve Luck, Paul Corballis, Michael Corballis, Margaret Funnell, Kathleen Baynes, G. R. Mangun, Alan Kingstone, Robert Fendrich, James Eliassen, Scott Johnson, Michael B. Miller, Richard Ivry and Charlotte Smylie. In addition I wish to acknowledge the generous support of the McDonnell-Pew Program in Cognitive Neuroscience and the NINDS and NIMH. All of these organizations have provided support over the years.

References

- Aglioti S, Berlucchi G, Pallini R, Rossi GF, Tassinari G. Hemispheric control of unilateral and bilateral responses to lateralized light stimuli after callosotomy and in callosal agenesis. *Exp Brain Res* 1993; 95: 151–65.
- Allman JM. *Evolving brains*. Scientific American Library Series, No. 68. New York: Scientific American Library; 1999.
- Baron-Cohen S. *Mindblindness. An essay on autism and theory of mind*. Learning, development, and conceptual change. Cambridge (MA): MIT Press; 1995.
- Baynes K. Language and reading in the right hemisphere: highways or byways of the brain? *J Cogn Neurosci* 1990; 2: 159–79.
- Baynes K, Eliassen JC. The visual lexicon: its access and organization in commissurotomy patients. In: Beeman M, Chiarello C, editors. *Right hemisphere language comprehension: perspectives from cognitive neuroscience*. Hillsdale (NJ): Lawrence Erlbaum; 1998. p. 79–104.
- Baynes K, Gazzaniga MS. Right hemisphere language: insights into normal language mechanisms? In: Plum F, editor. *Language, communication, and the brain*. New York: Raven Press; 1988. p. 117–26.
- Baynes K, Tramo MJ, Gazzaniga MS. Reading with a limited lexicon in the right hemisphere of a callosotomy patient. *Neuropsychologia* 1992; 30: 187–200.
- Baynes K, Funnell MG, Fowler CA. Hemispheric contributions to the integration of visual and auditory information in speech perception. *Percept Psychophys* 1994; 55: 633–41.
- Baynes K, Wessinger CM, Fendrich R, Gazzaniga MS. The emergence of the capacity to name left visual field stimuli in a callosotomy patient: implications for functional plasticity. *Neuropsychologia* 1995; 33: 1225–42.
- Baynes K, Kroll N, Dronkers N. Contributions of the corpus callosum to semantic facilitation [abstract]. *J Int Neuropsychol Soc* 1997a; 3: 9.
- Baynes K, Tramo MJ, Reeves AG, Gazzaniga MS. Isolation of a right hemisphere cognitive system in a patient with anarchic (alien) hand sign. *Neuropsychologia* 1997b; 35: 1159–73.
- Baynes K, Eliassen JC, Lutsep HL, Gazzaniga MS. Modular organization of cognitive systems masked by interhemispheric integration. *Science* 1998; 280: 902–5.
- Berlucchi G, Mangun GR, Gazzaniga MS. Visuospatial attention and the split brain. *News Physiol Sci* 1997; 12: 226–31.
- Black P, Myers RE. Visual function of the forebrain commissures in the chimpanzee. *Science* 1964; 146: 799–800.
- Bogen JE, Gazzaniga MS. Cerebral commissurotomy in man: minor hemisphere dominance for certain visuospatial functions. *J Neurosurg* 1965; 23: 394–9.
- Bogen JE, Fisher ED, Vogel PJ. Cerebral commissurotomy: a second case report. *JAMA* 1965; 194: 1328–9.
- Bogen JE, Schultz DH, Vogel PJ. Completeness of callosotomy shown by magnetic resonance imaging in the long term. *Arch Neurol* 1988; 45: 1203–5.
- Bruce CJ, Goldberg ME. Physiology of the frontal eye fields. *Trends Neurosci* 1984; 7: 436–41.
- Buckner RL, Koutstaal W. Functional neuroimaging studies of encoding, priming, and explicit memory retrieval. [Review]. *Proc Natl Acad Sci USA* 1998; 95: 891–8.
- Bunt AH, Minckler DS. Foveal sparing: new anatomical evidence for bilateral representation of the central retina. *Arch Ophthalmol* 1977; 95: 1445–7.
- Cabeza R, Kapur S, Craik FIM, McIntosh AR, Houle S, Tulving E. Functional neuroanatomy of recall and recognition: a PET study of episodic memory. *J Cogn Neurosci* 1997; 9: 254–6.
- Cherniak C. Component placement optimization in the brain. *J Neurosci* 1994; 14: 2418–27.
- Corballis MC. Can commissurotomized subjects compare digits between the visual fields? *Neuropsychologia* 1994; 32: 1475–86.
- Corballis MC. Visual integration in the split brain. [Review]. *Neuropsychologia* 1995; 33: 937–59.
- Corballis MC. Hemispheric interactions in temporal judgments about spatially separated stimuli. *Neuropsychology* 1996; 10: 42–50.
- Corballis MC, Trudel CI. Role of the forebrain commissures in interhemispheric integration. *Neuropsychology* 1993; 7: 306–24.
- Corballis PM, Funnell MG, Gazzaniga MS. A dissociation between spatial and identity matching in callosotomy patients. *Neuroreport* 1999; 10: 2183–7.
- Corballis PM, Funnell M, Gazzaniga MS. An evolutionary perspective on hemispheric asymmetry. *Brain Cognition*. In press 2000.
- Cronin-Golomb A. Subcortical transfer of cognitive information in subjects with complete forebrain commissurotomy. *Cortex* 1986; 22: 499–519.

- Demb JB, Desmond JE, Wagner AD, Vaidya CJ, Glover GH, Gabrieli JD. Semantic encoding and retrieval in the left inferior prefrontal cortex: a functional MRI study of task difficulty and process specificity. *J Neurosci* 1995; 15: 5870–8.
- De Renzi E, Spinnler H. Visual recognition in patients with unilateral cerebral disease. *J Nerv Ment Dis* 1966; 142: 515–24.
- De Renzi E, Liotti M, Nichelli P. Semantic amnesia with preservation of autobiographic memory: a case report. *Cortex* 1987; 23: 575–97.
- Dolan RJ, Fletcher PC. Dissociating prefrontal and hippocampal function in episodic memory encoding. *Nature* 1997; 388: 582–5.
- Eliassen JC, Baynes K, Gazzaniga MS. Direction information coordinated via the posterior third of the corpus callosum during bimanual movements. *Exp Brain Res* 1999; 128: 573–7.
- Eliassen JC, Baynes K, Gazzaniga MS. Anterior and posterior callosal contributions to manual movements of the fingers, hands and arms. *Brain* 2000. In press.
- Enns JT, Kingstone A. Hemispheric cooperation in visual search: evidence from normal and split-brain observers. In: Christman S, editor. *Cerebral asymmetries in sensory and perceptual processes*. Amsterdam: North-Holland; 1997. p. 197–231.
- Fendrich R, Gazzaniga MS. Evidence of foveal splitting in a commissurotomy patient. *Neuropsychologia* 1989; 27: 273–81.
- Fendrich R, Reuter-Lorenz P, Hughes H, Gazzaniga MS. Bidirectional pursuit of lateralized targets in a callosotomy patient [abstract]. *Soc Neurosci Abstr* 1990; 16: 900.
- Fendrich R, Wessinger CM, Gazzaniga MS. Processing profiles at the retinal vertical midline of a callosotomy patient [abstract]. *Soc Neurosci Abstr* 1994; 20: 1579.
- Fendrich R, Wessinger CM, Gazzaniga MS. Hemispheric equivalence in anorthoscopic perception. *Cogn Neurosci Abstr* 1996; 3: 113.
- Fendrich R, Corballis PM, Gazzaniga M. Position constancy in a callosotomy patient [abstract]. *Soc Neurosci Abstr* 1998; 24: 1144.
- Forster B, Corballis PM, Corballis MC. The perception of sequentiality following callosotomy. *Neuropsychologia*. In press 2000.
- Franz E, Ivry R, Gazzaniga MS. Dissociation of spatial and temporal coupling in the bimanual movements of callosotomy patients. *Psychol Sci* 1996; 7: 306–10.
- Funnell MG, Corballis PM, Gazzaniga MS. A deficit in perceptual matching in the left hemisphere of a callosotomy patient. *Neuropsychologia* 1999; 37: 1143–54.
- Funnell MG, Gazzaniga MS. Right hemisphere deficits in reasoning processes. *Cogn Neurosci Soc Abstr Suppl* 2000; 12: 110.
- Funnell MG, Corballis PM, Gazzaniga MS. Cortical and subcortical interhemispheric interactions following partial and complete callosotomy. *Arch Neurol* 2000a; 57: 185–9.
- Funnell MG, Corballis PM, Gazzaniga MS. Insights into functional specificity of the human corpus callosum. *Brain* 2000b; 123: 920–6.
- Gazzaniga MS. Interhemispheric communication of visual learning. *Neuropsychologia* 1966; 4: 183–9.
- Gazzaniga MS. The bisected brain. New York: Appleton-Century-Crofts; 1970.
- Gazzaniga MS. Right hemisphere language following brain bisection: a 20-year perspective. [Review]. *Am Psychol* 1983; 38: 525–37.
- Gazzaniga MS. Organization of the human brain. [Review]. *Science* 1989; 245: 947–52.
- Gazzaniga MS. On neural circuits and cognition. [Review]. *Neural Comput* 1995; 7: 1–12.
- Gazzaniga MS. The mind's past. Berkeley (CA): University of California Press; 1998.
- Gazzaniga MS, Miller GA. The recognition of antonymy by a language enriched right hemisphere. *J Cogn Neurosci* 1989; 1: 187–93.
- Gazzaniga MS, Sperry RW. Language after section of the cerebral commissures. *Brain* 1967; 90: 131–48.
- Gazzaniga MS, Smylie CS. Facial recognition and brain asymmetries: clues to underlying mechanisms. *Ann Neurology* 1983; 13: 536–40.
- Gazzaniga MS, Smylie CS. Dissociation of language and cognition. *Brain* 1984; 107: 145–53.
- Gazzaniga MS, Smylie CS. Hemispheric mechanisms controlling voluntary and spontaneous facial expressions. *J Cogn Neurosci* 1990; 2: 239–45.
- Gazzaniga MS, Bogen JE, Sperry RW. Some functional effects of sectioning the cerebral commissures in man. *Proc Natl Acad Sci USA* 1962; 48: 1765–9.
- Gazzaniga MS, Bogen JE, Sperry RW. Laterality effects in somesthesia following cerebral commissurotomy in man. *Neuropsychologia* 1963; 1: 209–15.
- Gazzaniga MS, Bogen JE, Sperry RW. Observations on visual perception after disconnection of the cerebral hemispheres in man. *Brain* 1965; 88: 221–36.
- Gazzaniga MS, Bogen JE, Sperry RW. Dyspraxia following division of the cerebral commissures. *Arch Neurol* 1967; 16: 606–12.
- Gazzaniga MS, Volpe BT, Smylie CS, LeDoux JE, Wilson DH. Plasticity in speech organization following commissurotomy. *Brain* 1979; 102: 805–15.
- Gazzaniga MS, Nass R, Reeves A, Roberts D. Neurologic perspectives on right hemisphere language following surgical section of the corpus callosum. *Semin Neurol* 1984; 4: 126–35.
- Gazzaniga MS, Kutas M, Van Petten C, Fendrich R. Human callosal function: MRI-verified neuropsychological functions. *Neurology* 1989; 39: 942–6.
- Gazzaniga MS, Eliassen JC, Nisenson L, Wessinger CM, Fendrich R, Baynes K. Collaboration between the hemispheres of a callosotomy patient: emerging right hemisphere speech and the left hemisphere interpreter. *Brain* 1996; 119: 1255–62.
- Geschwind N. Disconnection syndromes in animals and man. I. [Review]. *Brain* 1965a; 88: 237–94.

- Geschwind N. Disconnexion syndromes in animals and man. II. [Review]. *Brain* 1965; 88: 585–644.
- Hamilton CR. Mechanisms of interocular equivalence. In: Ingle DJ, Goodale MM, Mayfield RJW, editors. *Analysis of visual behavior*. Cambridge (MA): MIT Press; 1982. p. 693–718.
- Hamilton CR, Vermeire BA. Complementary hemisphere specialization in monkeys. *Science* 1988; 242: 1691–4.
- Hamilton CR, Vermeire BA. Functional lateralization in monkeys. In: Kitterle FL, editor. *Cerebral laterality: theory and research: the Toledo symposium*. Hillsdale (NJ): Lawrence Erlbaum; 1991. p. 19–34.
- Harvey LO Jr. Single representation of the visual midline in humans. *Neuropsychologia* 1978; 16: 601–10.
- Hauser M, Carey S. Building a cognitive creature from a set of primitives: evolutionary and developmental insights. In: Cummins Dellarosa D, Allen C, editors. *The evolution of the mind*. New York: Oxford University Press; 1998. p. 51–106.
- Hirsch J, DeLaPaz RL, Relkin NR, Victor J, Kim K, Li T, et al. Illusory contours activate specific regions in human visual cortex: evidence from functional magnetic resonance imaging. *Proc Natl Acad Sci USA* 1995; 92: 6469–73.
- Holtzman JD. Interactions between cortical and subcortical visual areas: evidence from human commissurotomy patients. *Vision Res* 1984; 24: 801–13.
- Holtzman JD, Gazzaniga MS. Dual task interactions due exclusively to limits in processing resources. *Science* 1982; 218: 1325–7.
- Holtzman JD, Gazzaniga MS. Enhanced dual task performance following corpus commissurotomy in humans. *Neuropsychologia* 1985; 23: 315–21.
- Holtzman JD, Sidtis JJ, Volpe BT, Wilson DH, Gazzaniga MS. Dissociation of spatial information for stimulus localization and the control of attention. *Brain* 1981; 104: 861–72.
- Holtzman JD, Volpe BT, Gazzaniga MS. Spatial orientation following commissural section. In: Parasuraman R, Davies DR, editors. *Varieties of attention*. Orlando (FL): Academic Press; 1984. p. 375–94.
- Hughes HC, Reuter-Lorenz PA, Fendrich R, Gazzaniga MS. Bidirectional control of saccadic eye movements by the disconnected cerebral hemispheres. *Exp Brain Res* 1992; 91: 335–9.
- Ivry RB, Hazeltine E. Subcortical locus of temporal coupling in the bimanual movements of a callosotomy patient. *Hum Move Sci* 1999; 18: 345–75.
- Ivry RB, Franz EA, Kingstone A, Johnston JC. The psychological refractory period effect following callosotomy: uncoupling of lateralized response codes. *J Exp Psychol Hum Percept Perform* 1998; 24: 463–80.
- Jeannerod M. Specialized channels for cognitive responses. *Cognition* 1981; 10: 135–7.
- Jeeves MA, Silver PH. Interhemispheric transfer of spatial tactile information in callosal agenesis and partial commissurotomy. *Cortex* 1988; 24: 601–4.
- Johnson SH. Cerebral organization of motor imagery: contralateral control of grip selection in mentally represented prehension. *Psychol Sci* 1998; 9: 219–22.
- Johnson SH, Corballis PM, Gazzaniga MS. Roles of the cerebral hemispheres in planning prehension: accuracy of movement selection following callosotomy. *J Cogn Neurosci* 1999; 11Suppl: 85.
- Jouandet ML, Gazzaniga MS. Cortical field of origin of the anterior commissure of the rhesus monkey. *Exp Neurol* 1979; 66: 381–97.
- Kanizsa G. Subjective contours. *Sci Am* 1976; 234: 48–52.
- Kanizsa G. *Organization in vision: essays on Gestalt perception*. New York: Praeger; 1979.
- Kanizsa G, Renzi P, Conte S, Compostela C, Guerani L. Amodal completion in mouse vision. *Perception* 1993; 22: 713–21.
- Kapur S, Craik FI, Tulving E, Wilson AA, Houle S, Brown GM. Neuroanatomical correlates of encoding in episodic memory: levels of processing effect. *Proc Natl Acad Sci USA* 1994; 91: 2008–11.
- Kapur S, Tulving E, Cabeza R, McIntosh AR, Houle S, Craik FI. The neural correlates of intentional learning of verbal materials: a PET study in humans. *Brain Res Cogn Brain Res* 1996; 4: 243–9.
- Kelley WM, Miezin FM, McDermott KB, Buckner RL, Raichle ME, Cohen NJ, et al. Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron* 1998; 20: 927–36.
- Kellman PJ, Loukides MG. An object perception approach to static and kinetic subjective contours. In: Petry S, Meyer GE, editors. *The perception of illusory contours*. New York: Springer; 1987. p. 151–64.
- Kellman PJ, Shipley TF. A theory of visual interpolation in object perception. [Review]. *Cognit Psychol* 1991; 23: 141–221.
- Kingstone A, Gazzaniga MS. Subcortical transfer of higher order information: more illusory than real? *Neuropsychology* 1995; 9: 321–8.
- Kingstone A, Enns J, Mangun GR, Gazzaniga MS. Guided visual search is a left hemisphere process in split-brain patients. *Psychol Sci* 1995; 6: 118–21.
- Kingstone A, Grabowecky M, Mangun GR, Valsangkar MA, Gazzaniga MS. Paying attention to the brain. The study of selective visual attention in cognitive neuroscience. In: Burak J, Enns JT, editors. *Attention, development, and psychopathology*. New York: Guilford Press; 1997. p. 263–87.
- Kingstone A, Friesen CK, Gazzaniga MS. Reflexive joint attention depends on lateralized cortical connections. *Psychol Sci* 2000; 11: 159–66.
- Kitchener EG, Hodges JR, McCarthy R. Acquisition of post-morbid vocabulary and semantic facts in the absence of episodic memory. *Brain* 1998; 121: 1313–27.
- Koffka K. *The growth of the mind: an introduction to child-psychology*. New York: Harcourt, Brace; 1924.
- Kolers PA. *Aspects of motion perception*. Oxford: Pergamon Press; 1972.
- Kosslyn SM, Koenig O, Barrett A, Cave CB, Tang J, Gabrieli JDE. Evidence for two types of spatial representations: hemispheric

- specialization for categorical and coordinate relations. *J Exp Psychol Hum Percept Perform* 1989; 15: 723–35.
- Kutas M, Hillyard SA, Gazzaniga MS. Processing of semantic anomaly by right and left hemispheres of commissurotomy patients: evidence from event-related brain potentials. *Brain* 1988; 111: 553–76.
- Kutas M, Hillyard SA, Volpe BT, Gazzaniga MS. Late positive event-related potentials after commissural section in humans. *J Cogn Neurosci* 1990; 2: 258–71.
- Lamb MR, Robertson LC, Knight RT. Attention and interference in the processing of global and local information: effects of unilateral temporal-parietal junction lesions. *Neuropsychologia* 1989; 27: 471–83.
- Lassonde M, Sauerwein HC, Lepore E. Extent and limits of callosal plasticity: presence of disconnection symptoms in callosal agenesis. *Neuropsychologia* 1995; 33: 989–1007.
- LeDoux JE, Risse GL, Springer SP, Wilson DH, Gazzaniga MS. Cognition and commissurotomy. *Brain* 1977a; 100: 87–104.
- LeDoux JE, Wilson DH, Gazzaniga MS. Manipulo-spatial aspects of cerebral lateralization: clues to the origin of lateralization. *Neuropsychologia* 1977b; 15: 743–50.
- LeDoux JE, Wilson DH, Gazzaniga MS. A divided mind: observations on the conscious properties of the separated hemispheres. *Ann Neurol* 1977c; 2: 417–21.
- Lenneberg EH. *Biological foundations of language*. London: Wiley; 1967.
- Leventhal AG, Ault SJ, Vitek DJ. The nasotemporal division in primate retina: the neural bases of macular sparing and splitting. *Science* 1988; 240: 66–7.
- Levy J, Trevarthen C, Sperry RW. Reception of bilateral chimeric figures following hemispheric deconnection. *Brain* 1972; 95: 61–78.
- Lewine JD, Doty RW, Astur RS, Provencal SL. Role of the forebrain commissures in bihemispheric mnemonic integration in macaques. *J Neurosci* 1994; 14: 2515–30.
- Lines CR, Milner AD. Nasotemporal overlap in the human retina investigated by means of simple reaction time to lateralized light flash. *Exp Brain Res* 1983; 50: 166–72.
- Luck SJ, Hillyard SA, Mangun GR, Gazzaniga MS. Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature* 1989; 342: 543–5.
- Luck SJ, Hillyard SA, Mangun GR, Gazzaniga MS. Independent attentional scanning in the separated hemispheres of split-brain patients. *J Cogn Neurosci* 1994; 6: 84–91.
- Luck SJ, Hillyard SA. The operation of selective attention at multiple stages of processing: evidence from human and monkey electrophysiology. In: Gazzaniga MS, editor. *The cognitive neurosciences*. 2nd ed. Cambridge: MIT Press; 2000.
- Lutsep HL, Wessinger CM, Gazzaniga MS. Cerebral and callosal organisation in a right-hemisphere-dominant 'split brain' patient. *J Neurol Neurosurg Psychiatry* 1995; 59: 50–4.
- Mangun GR, Luck SJ, Gazzaniga MS, Hillyard SA. Electrophysiological measures of interhemispheric transfer of visual information: studies in split-brain patients [abstract]. *Soc Neurosci Abstr* 1991; 17: 866.
- Mangun GR, Luck SJ, Plager R, Loftus W, Hillyard SA, Clark VP, et al. Monitoring the visual world: hemispheric asymmetries and subcortical processes in attention. *J Cogn Neurosci* 1994; 6: 267–75.
- McKeever WF, Sullivan KF, Ferguson SM, Rayport M. Typical cerebral hemisphere disconnection deficits following corpus callosum section despite sparing of the anterior commissure. *Neuropsychologia* 1981; 19: 745–55.
- Metcalfe J, Funnell M, Gazzaniga MS. Right-hemisphere memory superiority: studies of a split-brain patient. *Psychol Sci* 1995; 6(3): 157–164.
- Michotte A, Thines G, Crabbe G. Les complements amodaux des structures perceptives. In: *Studia psychologica*. Louvain: Institut de Psychologie de l'Université de Louvain; 1964.
- Miller MB, Kingstone A, Gazzaniga MS. HERA and the split-brain [abstract]. *Soc Neurosci Abstr* 1997; 23: 1579.
- Miller, MB, Wolford GL, Knight R, Gazzaniga MS. Memory distortions in the frontal lobes: a patient study [abstract]. *Soc Neurosci Abstr* 1998; 24: 2114.
- Milner B, Kolb B. Performance of complex arm movements and facial-movement sequences after cerebral commissurotomy. *Neuropsychologia* 1985; 23: 791–9.
- Milner B, Taylor L. Right-hemisphere superiority in tactile pattern-recognition after cerebral commissurotomy: evidence for nonverbal memory. *Neuropsychologia* 1972; 10: 1–15.
- Murai T, Toichi M, Sengoku A, Miyoshi K, Morimune S. Reduplicative paramnesia in patients with focal brain damage. *Neuropsychiatry Neuropsychol Behav Neurol* 1997; 10: 190–6.
- Nass RD, Gazzaniga MS. Cerebral lateralization and specialization of human central nervous system. In: Mountcastle VB, Plum F, Geiger SR, editors. *Handbook of physiology*. Sect 1, Vol. 5, Pt. 2. Bethesda (MD): American Physiological Society; 1987. p. 701–61.
- Nyberg L, Cabeza R, Tulving E. PET studies of encoding and retrieval: the HERA model. *Psychonom Bull Rev* 1996; 3: 135–48.
- Parks JR. Prediction and entropy of half-tone pictures. *Behav Sci* 1965; 10: 436–45.
- Parsons LM, Gabrieli JD, Phelps EA, Gazzaniga MS. Cerebrally lateralized mental representations of hand shape and movement. *J Neurosci* 1998; 18: 6539–48.
- Pashler H, Luck SJ, Hillyard SA, Mangun GR, O'Brien S, Gazzaniga MS. Sequential operation of disconnected cerebral hemispheres in split-brain patients. *Neuroreport* 1994; 5: 2381–4.
- Patterson K, Hodges JR. Disorders of semantic memory. In: Baddeley AD, Wilson BA, Watts FN editors. *Handbook of memory disorders*. Chichester (UK): John Wiley; 1995. p. 167–86.
- Petersen SE, Fox PT, Posner MI, Mintun M, Raichle ME. Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* 1988; 331: 585–9.
- Phelps EA, Gazzaniga MS. Hemispheric differences in mnemonic processing: the effects of left hemisphere interpretation. *Neuropsychologia* 1992; 30: 293–7.

- Phelps EA, Hirst W, Gazzaniga MS. Deficits in recall following partial and complete commissurotomy. *Cereb Cortex* 1991; 1: 492–8.
- Pinker S. *The language instinct*. New York: W. Morrow; 1994.
- Posner MI, Snyder CR, Davidson BJ. Attention and the detection of signals. *J Exp Psychol Gen* 1980; 109: 160–74.
- Prigatano GP and Schacter DL, editors. *Awareness of deficit after brain injury*. New York: Oxford University Press; 1991.
- Ramachandran VS. What neurological syndromes can tell us about human nature: some lessons from phantom limbs, Capgras syndrome, and anosognosia. *Cold Spring Harbor Symp Quant Biol* 1996; 61: 115–34.
- Reuter-Lorenz PA, Baynes K. Modes of lexical access in the callosotomized brain. *J Cogn Neurosci* 1992; 4: 155–64.
- Reuter-Lorenz PA, Fendrich R. Orienting attention across the vertical meridian: evidence from callosotomy patients. *J Cogn Neurosci* 1990; 2: 232–8.
- Reuter-Lorenz PA, Jha AP, Rosenquist JN. What is inhibited in inhibition of return? *J Exp Psychol Hum Percept Perform* 1996; 22: 367–78.
- Rilling JK, Insel TR. Differential expansion of neural projection systems in primate brain evolution. *Neuroreport* 1999; 10:1453–9.
- Ringach DL, Shapley R. Spatial and temporal properties of illusory contours and amodal boundary completion. *Vision Res* 1996; 36: 3037–50.
- Rizzolatti G. Mirror neurons. In: Gazzaniga MS, Altman JS, editors. *Brain and mind: evolutionary perspectives*. HFSP workshop reports 5. Strasbourg: Human Frontier Science Program; 1998. p. 102–10.
- Rizzolatti G, Fadiga L, Gallese V, Fogassi L. Premotor cortex and the recognition of motor actions. *Brain Res Cogn Brain Res* 1996; 3: 131–41.
- Rock I. Anorthoscopic perception. *Sci Am* 1981; 244(3): 145–53.
- Rorden C, Mattingley JB, Karnath HO, Driver J. Visual extinction and prior entry: impaired perception of temporal order with intact motion perception after unilateral parietal damage. *Neuropsychologia* 1997; 35: 421–33.
- Schachter S, Singer JE. Cognitive, social, and physiological determinants of emotional state. *Psychol Rev* 1962; 69: 379–99.
- Sergent J. The cerebral balance of power: confrontation or cooperation? *J Exp Psychol Hum Percept Perform* 1982; 8: 253–72.
- Sergent J. Furtive incursions into bicameral minds. *Brain* 1990; 113: 537–68.
- Seymour SA, Reuter-Lorenz PA, Gazzaniga MS. The disconnection syndrome: basic findings reaffirmed. *Brain* 1994; 117: 105–15.
- Sidtis JJ, Volpe BT, Holtzman JD, Wilson DH, Gazzaniga MS. Cognitive interaction after staged callosal section: evidence for transfer of semantic activation. *Science* 1981a; 212: 344–6.
- Sidtis JJ, Volpe BT, Wilson DH, Rayport M, Gazzaniga MS. Variability in right hemisphere language function after callosal section: evidence for a continuum of generative capacity. *J Neurosci* 1981b; 1: 323–31.
- Squire LR, Knowlton BJ. Memory, hippocampus, and brain systems. In: Gazzaniga MS, editor. *The cognitive neurosciences*. Cambridge (MA): MIT Press; 1995. p. 825–37.
- Squire LR, Zola SM. Episodic memory, semantic memory, and amnesia. [Review]. *Hippocampus* 1998; 8: 205–11.
- Stein BE, Price DD, Gazzaniga MS. Pain perception in a man with total corpus callosum transection. *Pain* 1989; 38: 51–6.
- Stone J. The naso-temporal division of the cat's retina. *J Comp Neurol* 1966; 126: 585–600.
- Stone J, Leicester J, Sherman SM. The naso-temporal division of the monkey's retina. *J Comp Neurol* 1973; 150: 333–48.
- Sugishita M, Hamilton CR, Sakuma I, Hemmi I. Hemispheric representation of the central retina of commissurotomy subjects. *Neuropsychologia* 1994; 32: 399–415.
- Sullivan MV, Hamilton CR. Interocular transfer of reversed and nonreversed discrimination via the anterior commissure in monkeys. *Physiol Behav* 1973; 10: 355–9.
- Suzuki K, Yamadori A, Endo K, Fujii T, Ezura M, Takahashi A. Dissociation of letter and picture naming resulting from callosal disconnection. [Review]. *Neurology* 1998; 51: 1390–4.
- Trevarthen CB. Two mechanisms of vision in primates. *Psychol Forsch* 1968; 31: 299–48.
- Trevarthen C, Sperry RW. Perceptual unity of the ambient visual field in human commissurotomy patients. *Brain* 1973; 96: 547–70.
- Tuller B, Kelso JA. Environmentally-specified patterns of movement coordination in normal and split-brain subjects. *Exp Brain Res* 1989; 75: 306–16.
- Tulving E. Episodic and semantic memory: where should we go from here? *Behav Brain Sci* 1986; 9: 573–7.
- Tulving E, Schacter DL, McLachlan DR, Moscovitch M. Priming of semantic autobiographical knowledge: a case study of retrograde amnesia. *Brain Cogn* 1988; 8: 3–20.
- Tulving E, Kapur S, Craik FM, Moscovitch M, Houle S. Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography findings. [Review]. *Proc Natl Acad Sci USA* 1994; 91: 2016–20.
- Vogels R, Saunders RC, Orban GA. Hemispheric lateralization in rhesus monkeys can be task dependent. *Neuropsychologia* 1994; 32: 425–38.
- Warrington EK, Shallice T. Category specific semantic impairments. *Brain* 1984; 107: 829–54.
- Wasserstein J, Zappulla R, Rosen J, Gerstman L, Rock D. In search of closure: subjective contour illusions, Gestalt completion tests, and implications. *Brain Cogn* 1987; 6: 1–14.
- Wilson DH, Reeves A, Gazzaniga M, Culver C. Cerebral commissurotomy for control of intractable seizures. *Neurology* 1977; 27: 708–15.
- Wolford G, Miller MB, Gazzaniga MS. The left hemisphere's role in hypothesis formation. *J Neurosci* 2000; 20: RC64.
- Wurtz RH, Albano JE. Visual-motor function of the primate superior colliculus. [Review]. *Annu Rev Neurosci* 1980; 3: 189–226.

Zaidel, E. Language functions in the two hemispheres following complete cerebral commissurotomy and hemispherectomy. In: Boller F, Grafman J, editors. *Handbook of neuropsychology*, Vol. 4. Amsterdam: Elsevier; 1991. p. 115–50.

Zaidel D, Sperry RW. Memory impairment after commissurotomy in man. *Brain* 1974; 97: 263–72.

Zaidel E, Peters AM. Phonological encoding and ideographic reading by the disconnected right hemisphere: two case studies. *Brain Lang* 1981; 14: 205–34.

Zaidel E, Seibert L. Speech in the disconnected right hemisphere. *Brain Lang* 1997; 60: 188–92.

Zeki SM. Colour coding in rhesus monkey prestriate cortex. *Brain Res* 1973; 53: 422–7.

Received October 6, 1999. Revised January 3, 2000.

Accepted January 27, 2000