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Pinto, Y.; de Haan, E.H.F.; Lamme, V.A.F.

DOI

[10.1016/j.tics.2017.09.003](https://doi.org/10.1016/j.tics.2017.09.003)

Publication date

2017

Document Version

Final published version

Published in

Trends in Cognitive Sciences

License

Article 25fa Dutch Copyright Act

[Link to publication](#)

Citation for published version (APA):

Pinto, Y., de Haan, E. H. F., & Lamme, V. A. F. (2017). The Split-Brain phenomenon revisited: A single conscious agent with split perception. *Trends in Cognitive Sciences*, 21(11), 835-851. <https://doi.org/10.1016/j.tics.2017.09.003>

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Opinion

The Split-Brain Phenomenon Revisited: A Single Conscious Agent with Split Perception

Yair Pinto,^{1,2,*} Edward H.F. de Haan,^{1,2,3} and Victor A.F. Lamme^{1,2,3}

The split-brain phenomenon is caused by the surgical severing of the corpus callosum, the main route of communication between the cerebral hemispheres. The classical view of this syndrome asserts that conscious unity is abolished. The left hemisphere consciously experiences and functions independently of the right hemisphere. This view is a cornerstone of current consciousness research. In this review, we first discuss the evidence for the classical view. We then propose an alternative, the ‘conscious unity, split perception’ model. This model asserts that a split brain produces one conscious agent who experiences two parallel, unintegrated streams of information. In addition to changing our view of the split-brain phenomenon, this new model also poses a serious challenge for current dominant theories of consciousness.

The Five Hallmarks of the Split-Brain Syndrome

In humans, nearly all communication between the cerebral hemispheres occurs via the corpus callosum [1–3]. In **split-brain patients** (**callosotomized**; see Glossary), the corpus callosum is surgically severed, normally at an adult age, to alleviate otherwise intractable seizures (Box 1). Thus, in split-brain patients, communication between the left and the right cerebral hemisphere is almost completely abolished. Although these patients behave normally and report to feel unchanged after the operation [4–6], research has revealed a multitude of marked, and sometimes dramatic, changes (Figure 1, Key Figure; see **callosal agenesis** for comparison).

One task has been particularly useful in documenting the cognitive changes observed in split-brain patients [6–10]. In this task, a visual stimulus is either presented to the left **visual field** or the right visual field. This is ensured by monitoring eye fixations and movements, and by presenting stimuli for less than 0.15 s (the minimum amount of time needed to initiate and execute an eye movement). The reason for this set up is that although both eyes project information to both cerebral hemispheres, all visual information to the left of fixation (i.e., the left visual field) is exclusively processed by the right cerebral hemisphere, while all visual information to the right of fixation (the right visual field) is processed solely by the left hemisphere. Another key aspect of this task is the response type. The patient either reacts with the left hand, the right hand, or verbally. The idea behind this is that the right hemisphere controls the left side of the body, including the left hand, and the left hemisphere controls the right hand and verbal responses. Thus, this task controls both which hemisphere receives input and which hemisphere produces output.

The prototypical split-brain patient shows five related phenomena on variations of this task. Arguably, these five aspects encompass the main differences between split-brain patients and

Trends

Five hallmarks characterize the split-brain syndrome: a response × visual field interaction, strong hemispheric specialization, confabulations after left-hand actions, split attention, and the inability to compare stimuli across the midline.

These hallmarks underlie the classical notion that split brain implies split consciousness. This notion suggests that massive interhemispheric communication is necessary for conscious unity.

Closer examination challenges the classical notion. Either the hallmark also occurs in healthy adults or the hallmark does not hold up for all split-brain patients.

A re-evaluation of the split-brain data suggests a new model that might better account for the data. This model asserts that a split-brain patient is one conscious agent with unintegrated visual perception.

This new model challenges prominent theories of consciousness, since it implies that massive communication is not needed for conscious unity.

¹Department of Psychology, University of Amsterdam, Amsterdam, The Netherlands

²Amsterdam Brain & Cognition (ABC) Center, University of Amsterdam, Amsterdam, The Netherlands

³These authors contributed equally to this manuscript

*Correspondence: y.pinto@uva.nl (Y. Pinto).

Box 1. Midline Connections

In split-brain patients, the corpus callosum is surgically removed after age 12. The corpus callosum is by far the largest of the commissures – white matter tracts that connect homologous structures on both sides of the central nervous system – and possesses a complex architecture (e.g., [117,118]). A large part of the corpus callosum, extending from the genu to the posterior part, connects the prefrontal cortices. Fibers from the parietal lobes cross mainly in dorsal areas of the splenium and isthmus, while the temporal lobes are largely connected via the posterior and ventral regions of the corpus callosum. The medial cortical surface is largely connected via the dorsal corpus callosum, while the fibers from the ventral regions of the brain cross ventrally (e.g., [119,120]). The visual cortices are mainly connected via the splenium [121]. With respect to subcortical structures, there is evidence that the claustrum connects to the contralateral prefrontal cortex, precentral gyrus, and postcentral gyrus and claustrum via the body of the corpus callosum [122].

The anterior commissure entails connections between the orbitofrontal, temporal, parietal, and occipital lobes [123], and even the insular cortices. In terms of subcortical structures, the anterior commissure connects the olfactory bulbs, the septal area, the amygdalae, and the overlying entorhinal cortices [124]. In addition, a small number of fibers connecting both claustra pass through the anterior commissure [122]. In some split-brain patients this commissure is removed as well.

The posterior commissure connects the precentral and postcentral gyri, the superior parietal region in the left hemisphere to the temporal region, and lateral occipital and superior parietal regions of the right hemisphere [119]. The subcortical connections that run through the posterior commissure originate in the thalamic, superior colliculus and the habenular nuclei.

Other smaller commissures include the hippocampal commissure (connecting the subicular and parahippocampal cortices [124]), the commissure of Probst (connecting the dorsal nucleus of the lateral lemniscus and the inferior colliculus), the commissure of the inferior colliculi (connecting the two inferior colliculi), the commissure of the superior colliculi (connecting the two superior colliculi), the habenular commissure (which connects the habenular nuclei), the middle commissure (connecting the thalamus), and the anterior and posterior cerebellar commissures (connecting the two cerebellar hemispheres). Finally, many fibers decussate in lower brain structures, such as the pons. Examples are the white matter tracts from the two hemispheres of the cerebellum to the cortical hemispheres (e.g., [125]). In general, the smaller commissures and decussations are intact in split-brain patients.

healthy adults. The first, and most salient, observation in split-brain patients is the **response × visual field interaction** [1,5,6,8,9,11]. When a stimulus is presented to the left visual field, the patient can only respond adequately with his/her left hand, and vice versa for the right field and hand. The second aspect concerns the hemispheric specialization, with each of the two hemispheres being better at certain tasks [8,10,12–14]. The third aspect focusses on *post hoc* confabulations after actions with the left hand [1,15]. The fourth characteristic concerns the observation that each hemisphere may have its own independent focus of attention [16–19]. Finally, there is abundant evidence that shows that split-brain patients are incapable of comparing stimuli across the visual midline [10,20–23].

Altogether these five observations have led to what we dub the classical models of split-brain patients. There are two primary classical models. The first model revolves around the notion that only the left hemisphere gives rise to consciousness, while the right hemisphere only processes information in an unconscious manner. The right hemisphere may prime the left hemisphere toward certain behavior, but this will only affect consciousness after it has been molded and interpreted by the left hemisphere. This is the so-called partial consciousness model [1,11]. The second classical model posits that in a split-brain patient each hemisphere has its own consciousness, independent of the other hemisphere [5,6,24]. Thus, according to this ‘**split consciousness**’ model, a split-brain patient houses two independent conscious agents. This model has been concisely argued by Sperry [24] who wrote that the two hemispheres acted as if they were ‘two separate conscious entities or minds running in parallel in the same cranium, each with its own sensations, perceptions, cognitive processes’ (p. 318).

By contrast, we will argue that despite their prominence, these classical models face serious challenges. This is because three of the five hallmarks (hemispheric specialization, *post hoc*

Glossary

Callosal agenesis: person born without a corpus callosum. These subjects show few of the characteristics of the split-brain syndrome.

Callosotomized: another term to describe a split-brain patient.

Gaze contingent presentation: in this procedure, gaze fixation is determined through eye tracking. Based on this, the visual stimulus is presented relative to fixation (e.g., 3 visual degrees to the left or the right of fixation). Subsequently, the presentation time is either kept too short for the subject to move his/her eyes to the stimulus, or the stimulus moves in sync with the gaze of the subject.

Response × visual field

interaction: there are three different response types (left hand, right hand, and verbally) and two visual fields (left and right). If a subject is more accurate in responding to the left visual field with the left hand than with the right hand/verbally or more accurate in responding to the right visual field with the right hand/verbally than with the left hand, then a response × visual field interaction exists. However, if accuracy does not depend on a combination of response type and visual field, then this interaction is absent. If, for instance, a subject is better at responding with the left hand, but irrespective of whether stimuli appear in the left or the right visual field, then this interaction is absent. Similarly, if performance is superior for stimuli in the right visual field, but irrespective of response type, then the interaction is also absent.

Split and unified consciousness:

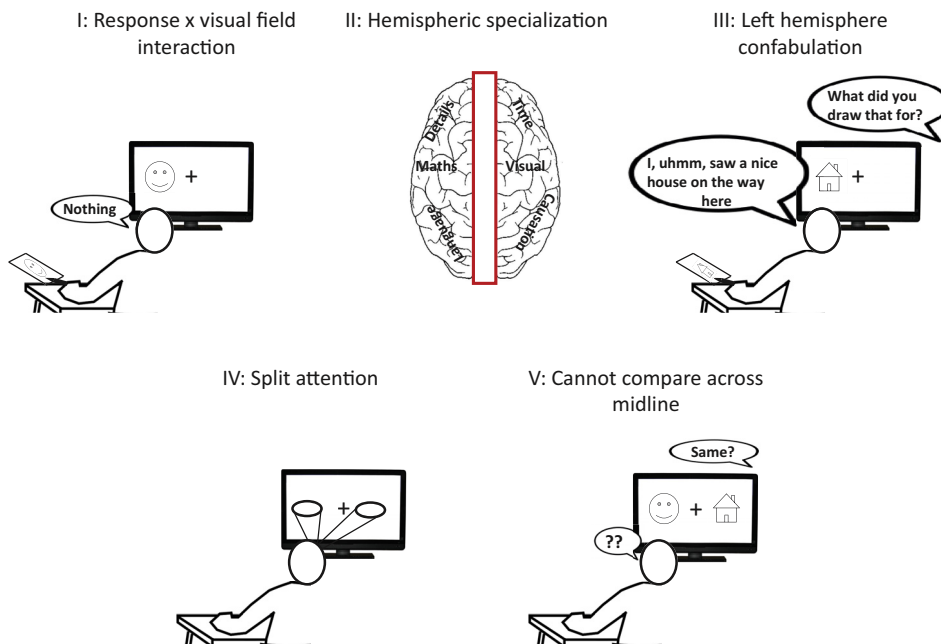
split consciousness indicates the existence of two independent conscious agents, whereas unified consciousness (or conscious unity) implies the existence of only one conscious agent.

Split-brain patient: patients in whom the corpus callosum is surgically removed. This is generally done to alleviate otherwise intractable seizures.

Visual field: all stimuli appearing to the left of where a subject fixates are considered to be part of the left visual field. Everything to the right of where the subject fixates is part of the right visual field.

Key Figure

The Five Hallmarks of the Split-Brain Syndrome



Trends in Cognitive Sciences

Figure 1. The classical view of split-brain patients asserts that conscious unity is disrupted in this syndrome. The evidence for this view comes from five hallmarks. First, a marked response type \times visual field interaction occurs in split-brain patients [1,5,6,8,9,11]. They can only respond accurately to stimuli in the right visual field with the right hand or verbally, and to stimuli in the left visual field with the left hand. Therefore, when a stimulus appears in the left visual field, the patient verbally reports that he/she saw nothing, yet draws the image with his/her left hand. This supports the notion that each hemisphere controls half the body, and consciously perceives half the visual field. The second hallmark is extreme hemispheric specialization [8,10,12–14,36–45]. The left hemisphere is, among other things, better at language, maths, and detailed processing. The right hemisphere is better at visuospatial tasks, time perception, and causal inferencing. This again suggests that each hemisphere operates independently of the other, and thereby creates consciousness autonomously. The third striking phenomenon is that split-brain patients confabulate wildly when asked to explain actions of their left hand (controlled by the mute right hemisphere) [1,15]. The notion here is that the left hemisphere creates an independent conscious agent, who is unaware of why the right hemisphere chooses its actions. Therefore, this agent resorts to *ad hoc* confabulations. Fourth, in split-brain patients, each hemisphere seems to have its own focus of attention [16–19]. Since attention and consciousness are thought to be tightly linked [64–67], this again supports the classical notion that consciousness is not unified in split-brain patients. Fifth, split-brain patients cannot compare stimuli across the midline [10,20–23,85–87]. This makes sense if two independent conscious agents each view half of the visual field, and cannot communicate their perceptions to each other.

confabulations, and split attention) also exist in healthy adults with **unified consciousness**. Thus, these hallmarks cannot constitute proof for disturbances in conscious unity. Moreover, one hallmark (inability to compare across the midline) also fits the more modest explanation that visual processing is unintegrated. In general, a more extreme explanation (destroyed conscious unity) should only be preferred if simpler explanations do not suffice. Finally, the strongest proof for a breakdown of unified consciousness, the response \times visual field interaction, does not hold for all split-brain patients. We posit a new model of the split-brain syndrome, which claims that both hemispheres give rise to a single conscious agent, and discuss its wider implications.

Hallmark 1: Response \times Visual Field Interaction

The most striking effect of a severed corpus callosum is a remarkable response type \times visual field interaction. When a stimulus is presented to the right visual field, the patient responds essentially in a normal manner. However, when a stimulus is presented to the left visual field, the patient verbally indicates that he/she saw nothing, yet with his/her left hand he/she indicates that he/she did see the stimulus. When probed, the patient cannot explain the action of his/her left hand [1,5,6,8,9,11,15]. This is a key data point for the classical models, since it dramatically shows that normal consciousness and control are disrupted. In healthy adults, where both hemispheres give rise to one conscious agent, a response type \times visual field interaction is completely absent. Therefore, this finding is perhaps the most well-known split-brain finding, and is highlighted in textbooks and reviews [25–27]. Both classical models explain this finding along the same lines. Concordant with human anatomy, the right visual field is solely processed by the left hemisphere, which controls language and the right hand [28–33]. Thus, when a stimulus appears in the right visual field, the patient will produce a normal verbal response. However, when stimuli are presented to the left visual field, they are processed by the mute right hemisphere, which controls the left hand. Thus, in such a case, the left hemisphere will verbally, and truthfully, indicate that it saw nothing. Yet, the right hemisphere will indicate that it ‘did’ see a stimulus, and will make this clear by its control of the left hand. However, the models disagree on whether the action initiated by the right hemisphere is based on an automatic response (the partial consciousness model) or on conscious control (the split consciousness model).

On closer examination, the response \times visual field interaction appears less than beyond dispute. First, Sperry [6] himself, when describing the response \times visual field interaction, notes in the last paragraph that ‘Although the general picture has continued to hold up in the main as described . . . striking modifications and even outright exceptions can be found among the small group of patients examined to date’ (p 733), suggesting that the response \times visual field interaction may be less absolute than commonly assumed. Similarly, other studies [7,16] also cast doubt on the generality of a response \times visual field interaction in split-brain patients. In one study [7] split-brain patients viewed chimeric faces, with one half of the face presented to the left visual field, and the other to the right visual field. The patients then either indicated the name of the face they had just seen (when they responded verbally), or pointed to one of three possible faces (when they responded manually). When responding verbally, they overwhelmingly named the face that had appeared in the right visual field. However, when they selected a face by pointing, they overwhelmingly selected the face presented to the left visual field. Crucially, this was even the case when they responded with the right hand. Another study [16] investigated attention in split-brain patients, and controlled for the role of response type (left hand or right hand). Interestingly, although they found an effect of visual field, response type did not play a significant role.

More recently, we [10] performed a quantitative study into the interaction, using sophisticated fixation control with an eye tracker, a substantial number of trials in each condition, forced-choice responding, and a large number of different stimuli. The response type (left hand, right hand, or verbally) was varied systematically. We found, in two split-brain patients, that although visual field played a large role in most tasks, a response type \times visual field interaction was never observed. This result held across all tasks (detection, localization, orientation determination, labeling, and visual matching), and all tested types of stimuli (isoluminant dots, simple shapes, oriented rectangles, objects). For instance, when the subject indicated changes in orientation of a stimulus, performance was superior for stimuli in the left visual field, even when he/she responded verbally, or with the right hand. The result also held for high confidence trials, suggesting that the lack of interaction cannot be explained by implicit processing [34,35]. Thus, although the textbook claim of an absolute response \times visual field

interaction would be strong evidence for the classical models, closer examination reveals that, at least in some patients, this interaction is absent. Consequently, this hallmark cannot be taken as evidence that conscious unity necessarily breaks down when the corpus callosum is removed.

Why are the results we obtained so different from the results obtained in some earlier research? One possibility is that split-brain patients show strong individual differences [6]. Another intriguing possibility is that the difference is due to a change in methodology. Note that the earlier claims of a strong response \times visual field interaction are almost solely based on qualitative reports (Table 1, Key Table). In our recent research, we not only ensured a quantitative approach, but also ensured complete clarity of the task. For instance, when the patient verbally labeled objects, he/she initially tended to indicate that 'he/she saw nothing', when an image was presented to the left visual field. However, after clarifying the instructions and adding catch trials where nothing was presented, these responses entirely disappeared. Rather, now the patient only indicated that he/she saw nothing on the catch trials, and (sometimes) reported an inability to name stimuli when they appeared in the left visual field. Thus, it is also possible that with our new, rigorous methodology virtually no split-brain patients would show a response \times visual field interaction on accuracy.

Hallmark 2: Hemispheric Specialization

Another key hallmark is that split-brain patients show pronounced hemispheric specialization. This is in line with the notion that each hemisphere operates largely independently of the other, and thus that conscious unity is disturbed. The general procedure for determining hemispheric differences in split-brain patients is by presenting an image/task either to the left visual field (which is processed by the right hemisphere) or to the right visual field (processed by the left hemisphere). Therefore, when a patient is better at naming objects when they are presented to the right visual field, this leads to the conclusion that the left hemisphere is better at naming. This methodology has revealed an abundance of hemispheric specialization in split-brain patients. For instance, the left hemisphere is superior in language production and verbal labeling of images [8,10,12–14], solving mathematical problems [36], recognizing local details [37], and self-recognition [38]. The right hemisphere is better at visual-spatial tasks [10,39], causal inference [40], temporal discrimination [41], object-recognition based on fragments [42–44], and detecting statistical regularities in visual scenes [45].

Although the data here are unequivocal, they also do not provide conclusive evidence for the classical models, since hemispheric specialization is also observed in healthy adults. Using a similar procedure as in split-brain patients, the left hemisphere has been found to be superior in abstract category processing [46,47], recognizing words [48], processing high spatial frequency [49–52], local processing [53,54], and recognizing positive emotions [55,56]. The right hemisphere shows superior performance for stimulus-specific visual processing [46,47], recognizing faces [48], processing low spatial frequency [49–52], global processing [53,54], and recognizing negative emotions [55,56]. Thus, also in a healthy adult human brain it seems that different types of processes run in parallel in the different cerebral hemispheres, without apparently disturbing conscious unity.

Hallmark 3: *Post Hoc* Confabulation

An intriguing split-brain phenomenon is the observed *post hoc* confabulations to explain one's own behavior [1,15]. In one example [15], a split-brain patient was shown a picture of a bell tower in his left visual field. He then indicated which picture he had just seen, by pointing to one of four pictures with his left hand. When asked why he chose the picture, the patient indicated that he 'must have heard a bell ringing on [his] way into the lab'.

Key Table

Table 1. Overview of the Best Known Split-Brain Patients on the Hallmarks of the Split-Brain Syndrome^a

Initials ^b	Patient info	R × VF, QL ^c	R × VF, QN ^d	Cannot compare, V1 ^e	Can compare, V2 ^f	Cannot compare, T ^g	Split attention
W.J.	Age of operation: 48 Extent: corpus callosum [8]	Yes [8]	Yes [23]	Yes [8]		Yes [8]	
L.B.	Age of operation: 13, corpus callosum [126,127]	Yes [6]	No [7,128–130] Mixed [131,132]	Yes [86]	Yes [87,88,133] Mixed [132]		Yes, visual search [18,19] No, negative priming [134]
N.G.	Age of operation: 30 Extent: corpus callosum [126,127]	Yes [6] Mixed [23]	No [7,128–130]	No [86]	Yes [88]	No [23]	Yes [18] No, negative priming [134]
A.A.	Age of operation: 13 Extent: corpus callosum [126,127]	Yes [6]	No [7,128,135]	Yes [86]	Yes [88]		
R.Y.	Age of operation: 43, corpus callosum [126,127]	Yes [6]	Yes [128]	Yes [86]			
C.C.	Age of operation: 13 Extent: corpus callosum [126,127]	Yes [6]	Mixed [7,128]				
M.E.	Age: 19 Extent: corpus callosum [136]		No [136]				
J.W.	Age: 26 Extent: corpus callosum [137]	Yes [1]	No [16,138,139] Mixed [132]	Yes [140] No [141]	Mixed [132] No [142]		Yes, visual search [18,19] Yes, object-based attention [16,17] Yes, guided search [143] Yes, object-based inhibition [144] No, attentional blink [81] No, spatial cueing [83,84] No, object-based facilitation [144]
D.D.C.	Age: 19 Extent: corpus callosum, most of the anterior commissure [145,146]		No [10,147]	Yes [10]	Yes [89] (Y. Pinto <i>et al.</i> , unpublished)	No [148]	
D.D.V.	Age: 22 Extent: corpus callosum [145,146]		No [10]		Yes [142]	Mixed [148]	

^aHemispheric specialization is not listed, since all patients show this strongly. Confabulation is not listed, since there are almost no studies into this topic.

^bPatient V.P. is not listed, because her callosotomy turned out to be incomplete.

^cR × VF, QL: response × visual field interaction, but only qualitative report.

^dR × VF, QN: response × visual field interaction, but (also) quantitative report. Interaction only refers to the ability to accurately respond to stimuli in left visual field, verbally and with the right hand, and to stimuli in right visual field with the left hand, not to reaction time differences for incongruent responses (since these also occur for healthy subjects).

^eV1 refers to cross hemifield comparisons that are generally thought to be impossible for split-brain patients (numbers, orientation, shapes, etc.).

^fV2 refers to cross hemifield comparisons that should be possible (apparent motion, gestalt/gist perception).

^gT refers to interhemispheric comparisons based on tactile information.

Both the classical models ascribe the *post hoc* confabulations to the breakdown of conscious unity. The initial information is projected to the right hemisphere, which controls the left hand. However, the verbal explanation is provided by the left hemisphere. Thus, the explanation is given by a conscious agent who did not initiate or execute the action. Therefore, the left hemisphere confabulates an answer. The classical models only differ on whether the actions by the right hemisphere are automatic (partial consciousness model) or consciously controlled (split consciousness model).

Crucially, like hemispheric specialization, *post hoc* confabulation is not unique to split-brain patients. First, also in healthy adults, behavior can often be caused by factors that the subject is unaware of. For instance, when people communicate they seem to engage in automatic mimicry [57,58], where they mirror the behavior of the other without being aware of doing so. A more dramatic example is that when people are shopping for wine, the background music seems to affect their choices (when listening to French music, people are more inclined to buy French wine [59,60]). Second, when probed about the reasons for their choices, even when these choices were consciously made, subjects are not immune to wild confabulations. The phenomenon of ‘choice blindness’ clearly illustrates this [61–63]. In choice blindness, subjects are asked to choose from two options, for instance, which of two people they find most attractive. After the subject has made his/her choice, the experimenter, on some trials, swaps the choice outcome, and now presents the rejected option to the subject as the one that was chosen. If the subject is subsequently asked why he/she had chosen this option (the one he/she actually rejected) over the other (the option he/she actually chose), the most frequent response is an impromptu confabulation. This has also been found for gustatory, aesthetic, and moral choices. Thus, also in healthy adults (with unified consciousness) behavior can be elicited by factors unknown to the subject. Moreover, healthy subjects may confabulate to explain their own behavior.

Hallmark 4: Split Attention

It is often argued that attention and consciousness are closely related ([64–67], but see also [68–71]). Therefore, key support for the classical models has been drawn from studies that suggest that attention is split in split-brain patients (Figure 2). Several studies suggest that, in split-brain patients, object-based and space-based attention are situated in different hemispheres [16,17], implying independent attentional centers. Moreover, when split-brain patients search for a target among distractors, search efficiency doubles when the distractors are distributed across two, rather than one, visual hemifields [18,19]. This suggests that each hemisphere autonomously scans half of the visual field.

However, these findings do not conclusively show a disturbance of conscious unity for two reasons. First, again similar phenomena are observed in healthy adults. In multiple object tracking [72–75] subjects attentively follow a subset of dots. When the dots are presented to both visual fields, subjects are able to track two times as many dots as when all stimuli are presented to one visual field [76,77], suggesting that each hemisphere has a fixed capacity and tracks the moving dots independently of the other. Moreover, when a tracked dot crosses the midline, and thus passes from one visual field to the other, the electroencephalogram signal indicates that one hemisphere passes the relevant information of the moving dot to the other hemisphere [78]. This confirms the notion that each hemisphere tracks information independently of the other, and only shares information when necessary.

Second, in addition to ‘split attention’ occurring in healthy subjects, attention can also be unified in split-brain patients (Figure 2). Normally, when subjects have to detect two targets in a rapid serial visual presentation, for instance, two letters in a stream of numbers, performance is lowest when the time between the first and the second target is 200–500 ms. This is called the

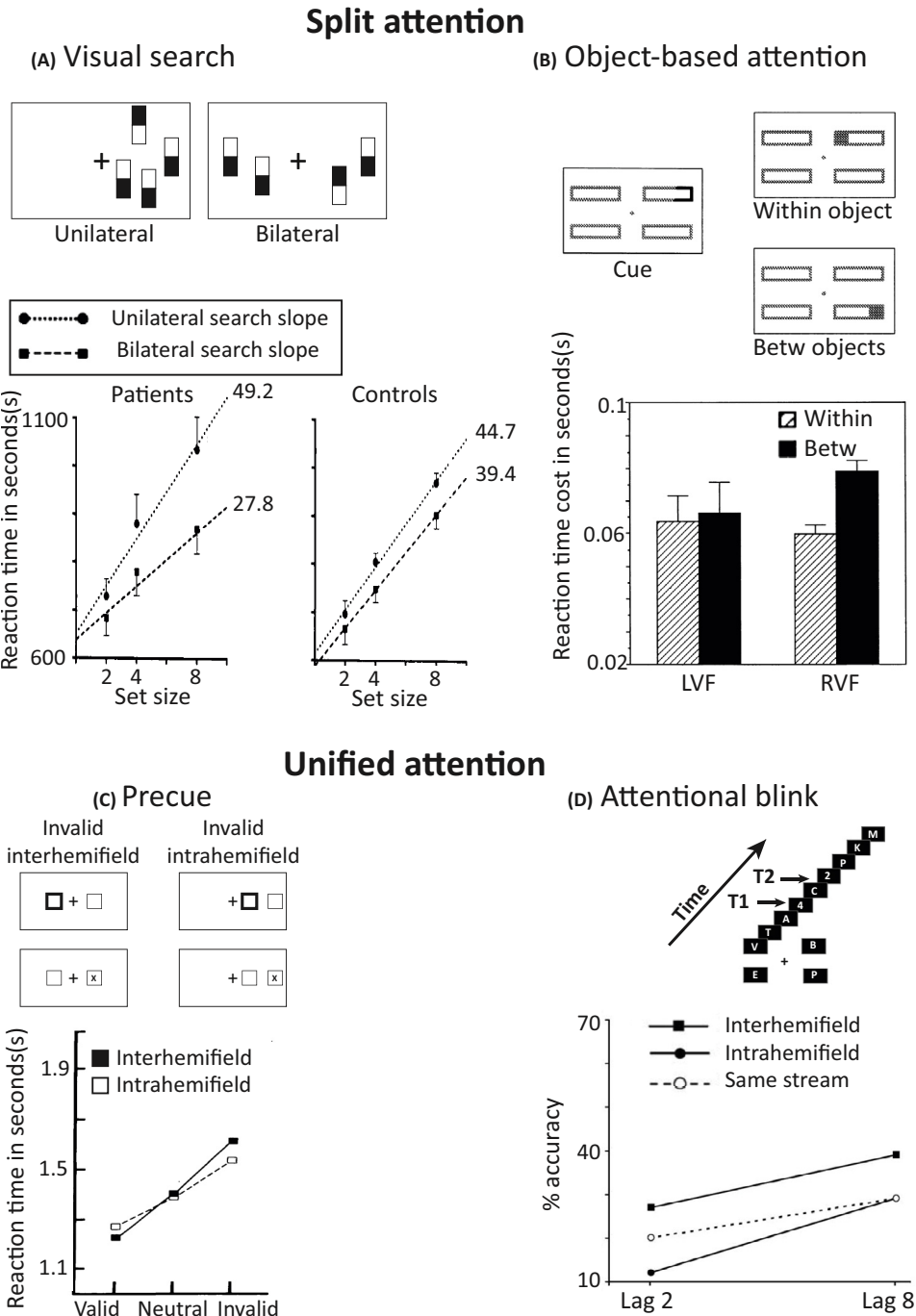


Figure 2. Split and Unified Attention in Split-Brain Patients. Evidence has been found both for and against split attention in split-brain patients. When split-brain patients search through a bilateral display (A) they are two times as efficient as searching through a unilateral display [18,19]. This effect is not observed in controls, who are equally efficient in both cases. This suggests that in split-brain patients each hemisphere autonomously scans half of the visual field. Moreover, in split-brain patients, reaction time costs for invalidly cued items (B) are higher when the invalidly cued location is on a different object. However, this is only the case for objects appearing in the right visual field, suggesting that only the attentional center in the left hemisphere employs object-based attention [16]. By contrast, behavior of split-brain patients in a Posner-cueing [116] paradigm (C) reveals evidence for unified attention [83]. A valid attentional precue accelerates reaction times, while an invalid one slows them. This pattern holds both within and across hemispheres, suggesting that

(Figure legend continued on the bottom of the next page.)

attentional blink [79,80]. Moreover, when there are multiple rapid serial visual presentation streams, this attentional blink transfers between streams. Therefore, if the first target appears in stream 1, and the second target in stream 2, detection of the second target is still lowest when time between the first and second target is between 200 and 500 ms. Crucially, split-brain patients show a similar transfer of attentional blink [81,82]. When the first target is presented in one visual field, split-brain patients still show a normal attentional blink for the second target, even if it appears in the other visual field. Thus, when it comes to the attentional blink (unlike in visual search) attention is unified. Moreover, attentional unity in split-brain patients also seems preserved for attentional precueing. When a precue highlights a location in the other visual field, split-brain patients still benefit from it [83]. In addition, when a target can appear in two locations, one in each visual field, a singular precue is effective, regardless of whether the precue appears in the same or the other visual field. However, two simultaneous precues, one per visual field, are ineffective [84].

Hallmark 5: Inability to Compare Stimuli across the Midline

Split-brain patients seem incapable of comparing stimuli across the midline, irrespective of the type of stimulus (digits, simple shapes, rectangles, or images) [10,20–23,85–87] (see Figure 3). In other words, when one stimulus is presented to the left visual field and the other to the right visual field, the patient cannot accurately indicate whether both stimuli are the same, although he/she can do so when both stimuli are presented within one visual field. This is consistent with the notion that each hemisphere independently perceives the contralateral visual field (the right hemisphere possibly perceiving the left visual field unconsciously).

Again, the data are more mixed than generally thought. Although there are indeed many examples of split-brain patients who are incapable of comparing stimuli across the midline, prominent examples can also be found of patients who can compare stimuli across the midline. For instance, one study found that although some split-brain patients could not compare stimuli across the midline, others could do so well above chance [86] (Figure 3). Moreover, under certain circumstances nearly all tested split-brain patients seem able to compare stimuli across visual fields. For instance, in one experiment two tilted lines were presented with a gap in between them. The lines were positioned in such a way that extending them across the gap would either cause the lines to coincide or to run in parallel. When split-brain patients had to indicate which was the case, they could do so highly accurately, even when both line segments were located in different visual fields [87] (Y. Pinto *et al.*, unpublished). In addition, when a split-brain patient viewed a visual field consisting of many circles, he/she could accurately indicate on which side the circle with the largest average radius appeared (Y. Pinto *et al.*, unpublished). A final example of visual integration across the midline involves apparent motion. When two dots were presented in succession at a short distance (2 to 14 visual degrees; see **gaze contingent presentation**), split-brain patients were able to accurately indicate whether the dots created apparent motion, or that they were presented simultaneously or with delays too long to create apparent motion. Critically, they were able to do so even when one dot appeared in the left visual field, and the other in the right visual field [87–89]. Note that although this capability is found in nearly all tested patients, individual differences may play a role here, since one split-brain patient was not able to perceive apparent motion across the midline [90]. Thus, although split-brain patients generally cannot compare stimuli across the midline, they may be able to do so in some special cases, perhaps involving gestalt principles [91] or statistical/gist processing [92–94].

unified attentional resources are employed. The attentional blink of split-brain patients also suggests unified attention (D). When controls view multiple streams consisting of items presented in rapid succession, they have a 'universal' attentional blink. That is, when the first target (in this example a number among letters) is detected, the second target is less well detected at lag 2 in all other streams. Split-brain patients also show a universal attentional blink, even when the first and the second target appear in different visual fields [81,82]. Abbreviation: Betw., between.

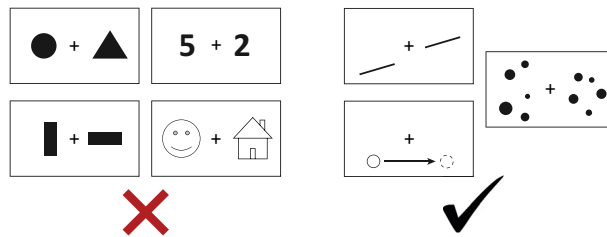


Figure 3. Visual Integration across Hemispheres without a Corpus Callosum. Investigations into visual integration in split-brain patients reveal an equivocal picture. Most patients cannot perform simple comparisons across the midline, such as comparing simple shapes, numbers, orientation, or pictures [10,20–23,85–87]. Yet, other types of visual integration do seem possible. Split-brain patients can generally indicate whether two interrupted lines would or would not coincide across the midline [87] (Y. Pinto *et al.*, unpublished), whether an object produces apparent motion across the midline [87–89], and which visual field contains the largest circle (Y. Pinto *et al.*, unpublished).

A New Model: One Conscious Agent with Unintegrated Visual Perception

Critically considering all five characteristics of the split-brain phenomenon, our first conclusion is that none of the data provide compelling proof for the central tenet of the classical models, that is, consciousness is split in split-brain patients. Hemispheric dominance and *post hoc* confabulations cannot be proof for split consciousness, since they also occur in healthy adults with unified consciousness. Split attention cannot be proof, since this also sometimes occurs in healthy adults, and moreover attention is sometimes unified in split-brain patients. A response \times visual field interaction would be a very strong proof, since it never occurs in healthy adults, and is exactly what you would expect to observe if consciousness is split. However, this characteristic is not universally true for split-brain patients.

Moreover, not only is conclusive evidence for disturbances in conscious unity lacking, there is also positive evidence for preserved conscious unity in split-brain patients. First, a breakdown of conscious unity seems incompatible with the observation that split-brain patients often behave and feel normally [4–6,10]. It seems implausible that both the patient himself/herself and the people in close contact with the patient fail to observe that after the surgical removal of the corpus callosum the original agent only perceives half the visual field and controls only half the body. Even when probed explicitly, the patient still insists that he/she controls his/her entire body and can see perfectly fine at both sides of fixation [10].

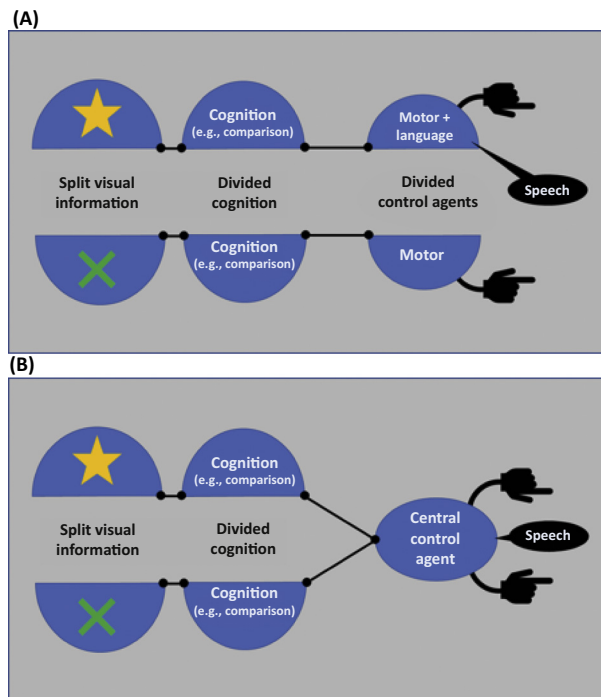
Second, controlled laboratory tests confirm this self-assessment. The absence of a response type \times visual field interaction in (some) split-brain patients seems incompatible with split consciousness. Imagine one conscious agent controlling language and the right hand (the left hemisphere) and another (conscious or unconscious) agent controlling the left hand. Furthermore, the former agent only perceives the right visual field, and the latter the left visual field. This model seems to logically imply a response type \times visual field interaction, where performance for the left visual field is better when the patient responds with the left hand than with the right hand/verbally (and vice versa).

Thus, our new model asserts that consciousness is unified in split-brain patients. This can explain why these patients feel normal and behave normally. They have not become half blind and half paralyzed after the surgery (and forced to share their brain with another conscious being). Rather, they are still one conscious agent in control of their entire body, and thus feel mostly unchanged. This one agent experiences the entire visual field, and controls his/her entire body. Therefore, it is trivially easy for this agent to respond to stimuli anywhere in the visual field, with any response type, even with the left hand to stimuli in the right visual field and vice versa. In other words, the

preserved conscious unity that our model hypothesizes for split-brain patients can explain why they are mostly normal in their behavior and show no response \times visual field interaction.

However, this cannot be the whole story, since split-brain patients do show marked differences from healthy adults. Many comparisons across the midline that are trivially easy for healthy adults prove impossible for split-brain patients. Moreover, hemispheric specialization is much more pronounced in these patients than in healthy adults. We argue that these differences can be explained by something less extreme than split consciousness, namely, by unintegrated perception. That is, we posit that in split-brain patients visual perception is (largely) unintegrated across visual fields. Therefore, they cannot make comparisons across the midline. Moreover, this unintegrated perception can also explain the increased hemispheric specialization. In healthy adults, hemispheric specialization occurs if the contralateral hemisphere contributes more to visual processing than the ipsilateral one. In split-brain patients, we posit that visual information is not shared, and thus that the contralateral hemisphere does all the visual processing, leading to maximal hemispheric specialization.

In short, the ‘conscious unity, split perception’ model (Figure 4) asserts that the split-brain patient is one conscious agent, in whom visual perception remains unintegrated across hemifields. What could this be like from a first-person perspective? We speculate that this can be thought of as watching an ‘out-of-sync’ movie. When you watch such a movie, your conscious unity is preserved, in the sense that you are still one conscious agent. Yet, your



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Figure 4. Different Models of the Split-Brain Syndrome. The classic and alternative ways to explain the set of split-brain findings discussed in this paper. Classically (A), split-brain patients are considered to have their visual information, cognition (e.g., the ability to compare objects), and their output control mechanisms split, each sitting in separate hemispheres, with language predominantly processed and produced by the left hemisphere. Alternatively (B), and better fitting the findings on hemifield \times response type interaction, both visual information and cognition might indeed be split across the midline (so that objects cannot be compared across the midline). Yet each visual half field and cognition module can be monitored by a single central agent, which simultaneously controls both hands and speech (as in normal subjects).

perception is split, since you experience a visual and an auditory stream, and you are unable to integrate these two streams. The strength of our new model is that it can explain both the normalities (because consciousness is unified) and the abnormalities (because perception is split) of the split-brain syndrome. Notice that this model makes a surprising prediction. Although the split-brain patient is not able to compare visual stimuli across the midline when they are presented simultaneously (because there is no automatic integration of information), he/she should be able to do so when the stimuli are presented with a considerable delay in between them. Since the patient experiences all the relevant information, he/she should be able to use a conscious strategy to resolve the task. Thus, whereas for normal people simultaneous comparisons are easier than sequential ones, this should be reversed for split-brain patients.

Implications for Leading Theories of Consciousness

The classical models of the split-brain syndrome have had an enormous impact on our view of consciousness. These models assert that without a corpus callosum, and thus without massive communication between both cerebral hemispheres, conscious unity is destroyed. The idea that unified consciousness requires massive, direct communication has served as a cornerstone in consciousness research. Thus, our new model, which suggests that unified consciousness may arise without massive communication, challenges currently leading theories on consciousness, such as the integrated information theory (IIT [95–97]), the global workspace (GW) theory [64,98,99], and the recurrent processing (RP) theory [100–102]. According to IIT, consciousness arises when a system has a rich representation repertoire and its subsystems are strongly interconnected. However, when the integration within a subsystem is larger than the connection between subsystems, consciousness will arise as a function of the subsystem rather than of the system as a whole. In split-brain patients, intrahemispheric connectivity exceeds interhemispheric connectivity, and thus each hemisphere should give rise to an independent conscious agent [96].

GW theory makes a similar prediction as IIT. According to this theory, the cerebral hemispheres house a ‘global workspace’ [64,98,99]. This GW can be thought of as the ‘headquarters’ of the cortex, which receives information from and projects to many cortical modules. Only information processed by the GW reaches consciousness. Crucially, when the two cerebral hemispheres are prevented from exchanging information, they can no longer give rise to one integrated GW [98]. Consequently, either only one hemisphere has a GW or both hemispheres create their own GW. Thus, GW theory implies that in split-brain patients partial or split consciousness arises.

RP theory asserts that consciousness can arise through local RP between cortical modules, even in the absence of global or integrative cortical processes [100–102]. However, such local processing only leads to phenomenal consciousness that is otherwise inaccessible, and unreportable. Thus, for unified ‘reportable’ consciousness, strong integration between the hemispheres is still needed. Yet, RP theory could be more compatible with our new model than IIT and GW theory. It could also be argued that, according to RP theory, a more basic, nonverbalizable type of consciousness is not dependent on interhemispheric integration [101]. Thus, whether the newly proposed model supports or challenges RP theory depends on the specifics. If consciousness is unified in all respects, including reporting capacities, then it does challenge. However, if a split-brain patient is one conscious agent, but with split reporting capacities, then it may be compatible with RP theory.

Subcortical or Functional Unity as the Basis of Unified Consciousness

Interestingly, two less prominent notions within consciousness research may be able to explain preserved conscious unity in split-brain patients. First, subcortical areas are still unified in split-brain patients (Box 1). Thus, if consciousness is critically linked to subcortical processing, such

as thalamic processing [103,104], then conscious unity may be unaffected in the split-brain syndrome. For instance, if corticothalamic loops drive consciousness [104], then it is possible that the specific contents of consciousness depend on cortical activity, but that the unity of consciousness is rooted in the thalamic structures involved in these loops.

Second, it is possible that conscious unity is strongly related to functional unity [66,105]. Functional unity means that different parts of a system operate mostly in conjunction, rather than independently. Note that functional unity can arise when subsystems are connected to a common source, even when they are not directly linked. For instance, according to the sensorimotor account of consciousness [66], conscious experiences are driven by the functional structure of processed information, rather than by the specific cortical implementation. Moreover, if the different cortical systems in a split-brain patient are driven by common input and produce conjoined output, then functional unity could still arise in the cortex, even without direct links between both cerebral hemispheres. Supporting the idea that functional unity is preserved in split-brain patients is the finding that interhemispheric neural activity in resting state is highly synchronized in split-brain patients, even as synchronized as resting state activity in healthy subjects [106]. If consciousness is indeed mostly dependent on functional structure, then preserved functional unity could underlie conscious unity in the split-brain syndrome.

Now, what about the neuroanatomical underpinning of this central agent? Broadly speaking, two explanations seem most likely. One possibility, in line with the subcortical theory of consciousness, is that the unification of consciousness relies on certain key hardware requirements. Perhaps unified consciousness remains intact when a minimal number of axonal connections between subcortical structures exist, or certain key parts are directly connected. Another possibility is more in line with the functional notion of consciousness. According to this explanation, consciousness remains unified if a minimal amount of synchronization between subsystems is preserved, regardless of whether this synchrony is driven by direct or indirect connections. The former explanation suggests that consciousness will split if more (subcortical) connections between the hemispheres are cut, even if synchrony between the hemispheres is preserved. The latter account predicts that even without any direct connections, consciousness can remain unified if synchrony remains intact.

Concluding Remarks and Future Perspectives

The status of conscious unity in the split-brain syndrome is crucial for our broader understanding of consciousness. The classical view of the syndrome, which asserts that unified consciousness is destroyed, supports the currently leading theories of consciousness. However, if conscious unity is preserved, then subcortical or functionally unifying processes likely play an important role in consciousness. The classical view is based on five defining features of the split-brain syndrome. Split-brain patients show strongly pronounced hemispheric specialization, cannot verbally explain their left-hand movements, have independent centers of attention, cannot compare stimuli across the midline and, most importantly, can only respond accurately to stimuli in the left visual field with the left hand, and to stimuli in the right visual field with the right hand/verbally (the response \times visual field interaction).

We argue that the classical view may not hold for several reasons. First, some of the defining features also occur in healthy adults with unified consciousness (hemispheric specialization, inability to explain own actions, and split attention). Second, the most convincing argument against unified consciousness in split-brain patients (the response \times visual field interaction) does not hold for all split-brain patients. Third, in the absence of any convincing proof against split consciousness, unified consciousness should be the default position. Both the patients and the people nearest to them claim that consciousness is still unified in the patient. Moreover, their everyday behavior confirms this. Thus, the claim of destroyed conscious unity is

extraordinary, and requires extraordinary evidence. Past research seemed to provide this extraordinary proof through the response \times visual field interaction, but recent research has invalidated this proof.

Further progress on the issue of unified consciousness with a split brain could come not only from studies with split-brain patients, but also through studying ‘temporary split brain’ (a temporary suspension of communication between neural modules in a healthy subject), so one can experience the syndrome from a first-person perspective. Different manipulations of attention may result in a temporary split brain. As mentioned, in multiple object tracking each hemisphere seems to track dots independently. If further behavioral and neural research confirms this, then multiple object tracking or multiple identity tracking [73,74,107] tasks may provide a tool for creating a transient split-brain state. Moreover, during inattentive blindness [108–110], unattended information seems to be processed only locally [111,112]. Thus, strongly focusing attention may also create a temporary split brain, where attended and unattended information is processed independently. A window into the consciousness of the unattended information is available during a short time frame after disappearance of the stimuli, during the so-called fragile memory stage [113–115]. Recent work [68] suggests that unattended information in fragile memory elicits normal consciousness. Only after information is transferred from fragile to working memory (a different stage of visual short-term memory [68,114,115]) does unattended information become unconscious [68]. Future research may unveil whether this unattended information indeed gives rise to normal conscious experiences while eliciting only local neural processing, virtually insulated from other cortical processing. Several other questions are currently unanswered (see Outstanding Questions). For instance, if a split-brain patient is really one conscious agent, can the individual overcome the lack of visual integration by conscious effort? Why are some forms of visual integration possible, and others not? What are the neural mechanisms underlying unified control in split-brain patients?

Acknowledgments

This work was supported by ERC Advanced grant FAB4V (#339374), and an ERC Advanced grant to V.A.F.L.

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Outstanding Questions

Can a split-brain patient overcome his/her inability to compare stimuli across visual fields? In general, a split-brain patient cannot compare visual information across the midline. However, if the patient is really one conscious agent, who is aware of two independent streams of information, can the comparison be made through conscious effort? For instance, if stimuli are presented across the midline sequentially, with a long delay in between, can the patient develop an effortful strategy to accomplish accurate comparisons?

Where does the ability to integrate visual information across the midline fall apart? The patient is able to accurately indicate whether two lines would coincide or run in parallel if they would be extended across the midline. However, he/she cannot determine whether two bars, appearing in two visual fields, have the same orientation. Can he/she only visually integrate lines, or can bars also be integrated? Do the stimuli need to have the same degree of rotation? Are the differences in ability driven by task requirements (indicate similarity or indicate continuity) rather than differences in low-level properties?

What are the neural principles underlying unified control in a split-brain patient? When the patient responds with the left hand to stimuli in the right visual field, is this movement controlled by the ipsilateral or the contralateral cerebral hemisphere? If the patient responds by performing a mental action (e.g., think of swimming when the answer is A, think of arithmetics when the answer is B), can the correct response then be decoded from both hemispheres, or only from the contralateral hemisphere?

What would it be like to be a split-brain patient? Third-person observations can only tell us so much about unified consciousness in others; the ultimate test would come from a first-person perspective. Is it possible to create a temporary split brain through attentional, or other, manipulations?

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