Split brain

Divided perception but undivided consciousness

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REPORT

Split brain: divided perception but undivided consciousness

Yair Pinto,1,2 David A. Neville,3 Marte Otten,1,2 Paul M. Corballis,4 Victor A. F. Lamme,1,2 Edward H. F de Haan,1,2 Nicoletta Foschi5 and Mara Fabri6

In extensive studies with two split-brain patients we replicate the standard finding that stimuli cannot be compared across visual half-fields, indicating that each hemisphere processes information independently of the other. Yet, crucially, we show that the canonical textbook findings that a split-brain patient can only respond to stimuli in the left visual half-field with the left hand, and to stimuli in the right visual half-field with the right hand and verbally, are not universally true. Across a wide variety of tasks, split-brain patients with a complete and radiologically confirmed transection of the corpus callosum showed full awareness of presence, and well above chance-level recognition of location, orientation and identity of stimuli throughout the entire visual field, irrespective of response type (left hand, right hand, or verbally). Crucially, we used confidence ratings to assess conscious awareness. This revealed that also on high confidence trials, indicative of conscious perception, response type did not affect performance. These findings suggest that severing the cortical connections between hemispheres splits visual perception, but does not create two independent conscious perceivers within one brain.

1 Department of Psychology, University of Amsterdam, Amsterdam, The Netherlands
2 Amsterdam Brain and Cognition (ABC) Center, University of Amsterdam, The Netherlands
3 Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, The Netherlands
4 School of Psychology, University of Auckland, Auckland, New Zealand
5 Epilepsy Center-Neurological Clinic, Azienda ‘Ospedali Riuniti’, Ancona, Italy
6 Department of Experimental and Clinical Medicine, Marche Politechnical University, Ancona, Italy

Correspondence to: Yair Pinto,
Department of Psychology,
Room 0.07, G building,
Nieuwe Achtergracht 129-B,
1018 WT, Amsterdam,
The Netherlands
E-mail: y.pinto@uva.nl

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Introduction

The corpus callosum is the main route for communication between both cerebral hemispheres (Innocenti, 1986; Gazzaniga, 2000; Wahl et al., 2007). In ‘split-brain’ patients, the corpus callosum has been surgically cut to alleviate intractable, severe epilepsy. One of the Nobel Prize-winning discoveries in neuroscience is that severing the corpus callosum leads to a curious phenomenon (Fig. 1): when an object is presented in the right visual field, the patient responds correctly verbally and with his/her right hand. However, when an object is presented in the left visual field the patient verbally states that he/she saw nothing, and identifies the object accurately with the...
left hand only (Gazzaniga et al., 1962; Gazzaniga, 1967; Sperry, 1968, 1984; Wolman, 2012). This is concordant with the human anatomy; the right hemisphere receives visual input from the left visual field and controls the left hand, and vice versa (Penfield and Boldrey, 1937; Cowey, 1979; Sakata and Taira, 1994). Moreover, the left hemisphere is generally the site of language processing (Ojemann et al., 1989; Cantalupo and Hopkins, 2001; Vigneau et al., 2006). Thus, severing the corpus callosum seems to cause each hemisphere to gain its own consciousness (Sperry, 1984). The left hemisphere is only aware of the right visual half-field and expresses this through its control of the right hand and verbal capacities, while the right hemisphere is only aware of the left visual field, which it expresses through its control of the left hand.

Strikingly, although this clinical observation features in many textbooks (Gazzaniga et al., 1998; Gray, 2002) the reported data are never quantitative. For three reasons it is important to explicitly map out how often ‘blindness’ to the left visual field is indicated by verbal/right hand responses and unawareness to the right visual field is indicated by left hand responses. First, the number of split-brain patients is now rapidly decreasing, and it will soon be impossible to study this phenomenon. Second, there is some doubt about how clear-cut the textbook findings are. In one of the seminal publications on this topic, Sperry (1968) reports that split-brain patients seem blind to the left visual field when responding with the right hand and vice versa. However, in the last paragraph (p. 733), Sperry notes: ‘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’. Moreover, Levy et al. (1972) investigated perception of chimeric faces in five split-brain patients. Although not the focus of their research, they observed that all patients were better at matching a face to a sample when the face was presented in the left visual field, regardless of whether they responded with the left or the right hand (p. 65). Finally, note that there are multiple examples in the literature suggesting some kind of interhemispheric integration of information (Corballis and Trudel, 1993; Corballis, 1995; Corballis and Corballis, 2001; Savazzi and Marzi, 2004; Savazzi et al., 2007). This, like Sperry’s (1968) closing remark, casts doubt on the precise nature of the split-brain phenomenon.

Third, the status of split-brain patients may have important consequences for current dominant theories of consciousness. Congruent with the canonical view of split-brain patients, both the Global Workspace theory (Baars, 1988, 2005; Dehaene and Naccache, 2001) and the Information Integration theory (Tononi, 2004, 2005; Tononi and Koch, 2015) imply that without massive interhemispheric communication two independent conscious systems appear. If the canonical view cannot be quantitatively replicated, and evidence for conscious unity in the split-brain syndrome is found, both theories may require substantial modifications.

In our current studies we reproduced the classic finding that split-brain patients are unable to integrate visual information across the two visual half-fields. However, we also investigated systematically to what extent performance depends on where a stimulus appears. For various tasks and stimuli we studied whether there is a response type x visual

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**Figure 1** A depiction of the traditional view of the split brain syndrome (top) versus what we actually found in two split-brain patients across a wide variety of tasks (bottom). The canonical idea of split-brain patients is that they cannot compare stimuli across visual half-fields (left), because visual processing is not integrated across hemispheres. This is what we found as well. However, another key element of the traditional view is that split-brain patients can only respond accurately to stimuli in the left visual field with their left hand and to stimuli in the right visual field with their right hand and verbally. This is not what we found. Across a wide variety of tasks, we observed that split-brain patients could reliably indicate presence, location, orientation and identity of stimuli throughout the entire visual field regardless of how they responded.
field interaction: can split-brain patients only respond to stimuli in the left visual field with the left hand, and to stimuli in the right visual field with the right hand or verbally?

**Patients and methods**

**Subjects**

Patients were tested across several years, during their routine neurological control visits. For Experiment 1 we tested Patients DDC and DDV, for Experiments 2–5 we tested Patient DDC. Both patients underwent a full callosotomy to relieve epileptic seizures. Crucially, for current purposes, in Patient DDC the complete corpus callosum and most of the anterior commissure was cut, and in Patient DDV the complete corpus callosum was removed. We selected Patient DDC for the extensive follow-up testing since his ‘split’ is the most severe. Note that other than the removal of the corpus callosum, both patients had no brain damage, and fell within the normal IQ range. See Supper material and Pizzini et al. (2010) for detailed descriptions of these patients. In all experiments the patient(s) responded with three response types (response conditions were blocked), verbal, right hand or left hand, except for Experiment 2A, where the patient only responded verbally; and Experiments 2C and 4A where only left and right hand responses and no verbal responses were given. The experimenter (who could not see the test stimuli) mouse-clicked on the response box or location indicated by the patient. In the case of verbal position indication, the mouse was moved by the experimenter (not having seen the stimulus) on the instructions of the patient until the desired position was obtained.

**Procedure**

In Experiment 1 both patients performed a combined detection/localization task. Either nothing appeared (50% of trials) or a red solid circle, on a grey background (see Supplementary material for all stimulus details), appeared for 120 ms anywhere in the visual field. Each trial the patient indicated whether a stimulus had appeared, and if so where.

In Experiment 2A, Patient DDC indicated whether two rectangles had the same orientation, and if not, how large the orientation difference was. In both experiments, after each trial, Patient DDC indicated confidence in his judgement (Experiment 4A on a scale from 1 to 4, Experiment 4B on a scale from 1 to 4). Experiment 5 was similar to Experiment 1, except after each trial Patient DDC indicated confidence in his presence and location judgement (on a scale from 1 to 5). Moreover, stimuli were bright green on a red background, or dim green on a red background. In the latter case stimuli and background were equiluminant (as determined by an objective measurement).

**Results**

Figures 2 to 4 provide an overview of the experiments and results (for a detailed description of the methods and results see the Supplementary material). In all experiments, we measured eye movements and excluded trials where the patient did not appropriately fixate the centre of the screen during stimulus presentation. We used permutation testing to compare observed to chance performance.

In Experiment 1 (Fig. 2), we explored to what extent Patients DDV and DDC can detect stimuli across the entire visual field using three response conditions: left hand, right hand, and verbally. Subjects were shown red circles in various locations of the visual field (50% of trials no stimulus was presented), and had to detect presence or absence either verbally or by indicating yes/no with either hand. Subsequently, for seen stimuli, they had to indicate the location of the stimulus. Both patients responded (nearly) perfectly in indicating presence of the stimulus (Patient DDV, hits: 100%, false alarms: 0%; Patient DDC, hits: 97.5%, false alarms: 7.7%), and were highly accurate in indicating location of the stimulus (average distance between pointed location and actual location: Patient DDV: 2.8°, Patient DDC: 4.5°). While presence and location performance was highly significantly above chance (all $P < 0.001$), the response type × visual half-field interaction did not approach significance in either patient or task (all $P > 0.5$).

This surprising finding of full detection awareness and above chance localization regardless of visual field of stimulation and response mode, led us to the question whether, in these patients, visual information is transferred (to a degree) across hemispheres. We tested this on Patient DDC by asking him to compare stimuli across hemispheres. In Experiment 2 (Fig. 3), Patient DDC indicated whether two stimuli (situated either within or between visual half-fields), had the same orientation, shape or identity. In keeping with earlier research (Corballis and Corballis, 2001), we found that he cannot compare stimuli across both visual half-fields (average performance 55.4% correct, which is not statistically better than chance performance, all stimulus categories $P > 0.25$), although he can make the same comparison within one visual half-field (average performance 90.4% correct, all $P < 0.001$). This suggests that
the areas involved in processing visual information do not have access to the information that is being processed in the other hemisphere.

We found further evidence that visual information is not shared between hemispheres in Experiment 3 (Fig. 3). Here we observed that Patient DDC was better at selecting the correct verbal label for an image when it had appeared in the right visual field than when it had appeared in the left visual field (Experiment 3A, left visual field: 73.4%, right visual field: 92.1%, left visual field versus right visual field: \( P < 0.001 \)). Yet, he was better at matching a stimulus to sample for items in left visual field, replicating earlier split-brain findings (Funnell et al., 1999) (Experiment 3B, left visual field: 95.5%, right visual field: 73%, left visual field versus right visual field: \( P < 0.001 \)). Note that, despite the seeming lack of transfer of visual information, we still observed no response type \( \times \) visual field interaction in Experiments 2 and 3 (all \( P > 0.12 \)). Thus, for instance, Patient DDC was better at matching to sample of stimuli in the left visual field even when he responded with the right hand. This suggests that processing of visual stimuli remains within each individual hemisphere, each with its own relative performances in various tasks, yet control over the report of the outcomes of this processing is undivided.

Finally, to assess whether the seeming unity in responding could be driven by unconscious processes, in the following three experiments, Patient DDC indicated confidence in his performance after each trial (Fig. 4). The idea behind obtaining confidence ratings is that these may reveal whether information is processed consciously or unconsciously. When information is processed unconsciously, the observer does not know when he gives correct or incorrect responses, and gives a uniformly low confidence (he always feels that he is guessing). However, when information is processed consciously, the observer knows quite accurately when he perceived an event and when he did not, leading to high confidence on correct, and low confidence on incorrect trials (Rosenthal, 2000; Lau and Rosenthal, 2011).

First, Patient DDC was tested on two visual matching experiments (shape and orientation). Second, he performed a detection and localization task of simple stimuli as in the first experiment (with the addition that the stimuli were presented equiluminantly with the background or with a large luminance difference). Patient DDC performed nearly flawlessly in detecting objects in Experiment 5 (no false alarms and two misses in 167 trials). This ceiling effect precluded meaningful metacognitive assessment of this aspect of the task. However, in the other two experiments and the localization of objects in Experiment 5, performance did not show a ceiling or floor effect, allowing us to investigate metacognitive abilities in these cases. This revealed that in all three experiments Patient DDC’s performance was better on high than on low confidence trials.
In conclusion, with two patients, and across a wide variety of tasks we have shown that severing the cortical connections between the two hemispheres does not seem to lead to two independent conscious agents within one brain. Instead, we observed that patients without a corpus callosum were able to respond accurately to stimuli appearing anywhere in the visual field, regardless of whether they responded verbally, with the left or the right hand—despite not being able to compare stimuli between visual half-fields, and despite finding separate levels of performance in each visual half-field for labelling or matching stimuli. This raises the intriguing possibility that even without massive communication between the cerebral hemispheres, and thus increased modularity, unity in consciousness and responding is largely preserved.

This preserved unity of consciousness may be especially challenging for the two currently most dominant theories of consciousness, the Global Workspace theory (Baars, 1988, 2005; Dehaene and Naccache, 2001) and the Integration Information theory (Tononi, 2004, 2005; Tononi and Koch, 2015). A core assumption of the Global Workspace theory is that cortical broadcasting of selected information by the ‘global workspace’ leads to consciousness. Thus severing of the corpus callosum, which prevents broadcasting of information across hemispheres, seems to exclude the emergence of one global workspace for both hemispheres. Rather, it seems that without a corpus callosum either two independent global workspaces emerge, or only one hemisphere will have a global workspace, while the other does not. In either case, an integrated global workspace, and thus preserved conscious unity, seems to be difficult to fit into this framework.

Also for Integration Information theory, conscious unity in the split-brain syndrome seems to be challenging. According to the Integration Information theory the richness of integration of information (called $\phi$, defined by how much information is represented, and how integrated the
information is) determines the level of consciousness. Moreover, only if the combined $\phi$ of two subsystems is larger than the $\phi$ per system, then the two subsystems combine to form one conscious entity. After removal of the corpus callosum, which all but eliminates communication between the cerebral hemispheres, integration of information is larger within each hemisphere than between hemispheres. Thus, according to the Integration Information theory, in the split-brain syndrome $\phi$ per hemisphere is larger than the combined $\phi$, thus leading to two independent conscious systems rather than one conscious agent (Tononi, 2005).

It thus seems that the current results provide a challenge for the Global Workspace and the Integrated Information theory of consciousness. However, the current results may fit well with the local recurrent processing theory of consciousness (Lamme and Roelfsema, 2000; Lamme, 2006; Block, 2007). This theory claims that local recurrent interactions between neural areas (for example between V1 and V5 in the visual system) are enough to create consciousness, even if these interactions are not part of a larger integrated network, and do not project their outcomes to a central processing unit. Thus, according to this theory, even in healthy subjects, relatively isolated processing in one hemisphere can lead to normal visual experiences. Therefore, the local recurrent processing theory suggests that consciousness in split-brain patients may be similar to consciousness in healthy subjects (and thus equally unified).

How should these results be compared to our classic textbook knowledge of the split-brain phenomenon? It is unlikely that our results can be explained by the anterior and posterior commissure still being (somewhat) intact, as this was also the case for many of the previously tested patients, and this did not seem to play an important role then (Gazzaniga et al., 1985; Seymour et al., 1994; Gazzaniga, 2005).

Another possible explanation to consider is that the current findings were caused by cross-cueing (one hemisphere informing the other hemisphere with behavioural tricks, such as touching the left hand with the right hand). We deem this explanation implausible for four reasons. First, cross-cueing is thought to only allow the transfer of one bit of information (Baynes et al., 1995). Yet, both patients could localize stimuli throughout the entire visual field irrespective of response mode (Experiments 1 and 5), and localizing a stimulus requires more than one bit of information. Second, visual capabilities differed per hemifield (Experiment 3: better matching for stimuli in left visual field, better labelling of stimuli in right visual field) and comparison of stimuli over hemifields was not possible (Experiment 2). This suggests that transfer of visual information did not occur. Yet, in these same experiments response type did not affect performance, suggesting that unity in control was not driven by any form of transfer of visual information. Third, we explicitly set up the experiments to prevent cross-cueing (e.g. hands were not allowed to touch each other, or the other half of the body). Moreover, we did not observe any indications of cross-cueing occurring. Fourth, as cross-cueing is a slow process, ipsilateral responses driven by cross-cueing should be considerably slower than contralateral responses. Yet, in one experiment where Patient DDC indicated, as quickly as possible, the colour of a circle appearing shortly to the left or the right of fixation, average ipsilateral and contralateral responses were almost equally fast, and equally accurate (ipsilateral reaction times: 1229 ms, ipsilateral accuracy: 88.4%; contralateral reaction times: 1307 ms, contralateral accuracy: 97%; No significant difference between ipsilateral and contralateral reaction times: $P=0.13$; or between ipsilateral and contralateral accuracy: $P=0.55$, see Supplementary material for details).

Finally, a possibility is that we observed the current results because we tested these patients well after their surgical removal of the corpus callosum (Patient DDC and Patient DDV were operated on at ages 19 and 22 years, and were tested 10–16 and 17–23 years after the operation, respectively). This would raise the interesting possibility that the original split brain phenomenon is transient, and that patients somehow develop mechanisms or even structural connections to re-integrate information across the hemispheres, particularly when operated at early adulthood. Even then, it remains the case that these patients’ minds have a curious property: somehow, their perception seems split, each hemisphere processing visual information independently, and at the best of their individual—yet different—abilities. When it comes to reporting this information to the outside world, however, the outcomes of the perceptual processes are unified in consciousness, verbalization and control of the body. This ‘split phenomenality’ combined with ‘unity of consciousness’ is difficult to grasp introspectively, and surely warrants further study, in a group of patients of which very few remain today.

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**Supplementary material**

Supplementary material is available at Brain online.
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