



UvA-DARE (Digital Academic Repository)

Unified tactile detection and localisation in split-brain patients

de Haan, E.H.F.; Fabri, M.; Dijkerman, H.C.; Foschi, N.; Lattanzi, S. ; Pinto, Y.

DOI

[10.1016/j.cortex.2019.11.010](https://doi.org/10.1016/j.cortex.2019.11.010)

Publication date

2020

Document Version

Final published version

Published in

Cortex

License

CC BY-NC-ND

[Link to publication](#)

Citation for published version (APA):

de Haan, E. H. F., Fabri, M., Dijkerman, H. C., Foschi, N., Lattanzi, S., & Pinto, Y. (2020). Unified tactile detection and localisation in split-brain patients. *Cortex*, *124*, 217-223. <https://doi.org/10.1016/j.cortex.2019.11.010>

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.



Review

Unified tactile detection and localisation in split-brain patients

Edward H.F. de Haan^{a,b,*}, Mara Fabri^c, H. Chris Dijkerman^d, Nicoletta Foschi^e, Simona Lattanzi^c and Yair Pinto^{a,b}

^a Department of Psychology, University of Amsterdam, Amsterdam, the Netherlands

^b Amsterdam Brain & Cognition (ABC) Center, University of Amsterdam, the Netherlands

^c Department of Experimental and Clinical Medicine, Marche Politechnical University, Ancona, Italy

^d Department of Psychology, Utrecht University, the Netherlands

^e Epilepsy Center-Neurological Clinic, Azienda ‘Ospedali Riuniti’, Ancona, Italy

ARTICLE INFO

Article history:

Received 25 June 2019

Reviewed 18 September 2019

Revised 8 November 2019

Accepted 18 November 2019

Published online 7 December 2019

Keywords:

Epilepsy

Split-brain

Lateralisation

Tactile perception

Consciousness

ABSTRACT

In ‘split-brain’ patients, the corpus callosum has been surgically severed to alleviate medically intractable, severe epilepsy. The classic claim is that after removal of the corpus callosum an object presented in the right visual field will be identified correctly verbally and with the right hand but not with the left hand. When the object is presented in the left visual field the patient verbally states that he saw nothing but nevertheless identifies it accurately with the left hand. This interaction suggests that perception, recognition and responding are separated in the two isolated hemispheres. However, there is now accumulating evidence that this interaction is not absolute. Recently, we (Pinto et al., 2017) showed that accurate detection and location of stimuli anywhere in the visual field could be performed with both hands. In this study, we explored detection and localisation of tactile stimulation on the body. In line with our previous results, we observed that split-brain patients can signal detection and localisation with either hand anywhere on the body (be it the arm or the leg) but they remain unable to match positions touched on both arms or legs simultaneously. These results add to the evidence suggesting that the effects of removal of the corpus callosum may be less severe than sometimes claimed.

© 2019 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

The corpus callosum is the main route for communication between the two cerebral hemispheres (e.g., Gazzaniga, 2000; Innocenti, 1986; Wahl et al., 2007). In ‘split-brain’ patients, the corpus callosum has been surgically resected to alleviate

medically intractable, severe epilepsy. One of the Nobel Prize-winning discoveries in neuroscience is that lesioning the corpus callosum leads to a curious phenomenon. 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 but

* Corresponding author. Department of Psychology, University of Amsterdam, Room 16, G building, Nieuwe Achtergracht 129-B, Amsterdam, the Netherlands.

E-mail address: E.H.F.deHaan@uva.nl (E.H.F. de Haan).

<https://doi.org/10.1016/j.cortex.2019.11.010>

0010-9452/© 2019 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

nevertheless identifies the object accurately with the left hand only (Gazzaniga, 1967; Gazzaniga, Bogen, & Sperry, 1962; 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 (Cowey, 1979; Penfield & Boldrey, 1937; Sakata & Taira, 1994). Moreover, the left hemisphere is generally the site of language processing (Ojeman et al., 1989; Vigneau et al., 2006). Thus, it appears that severing the corpus callosum causes each hemisphere to gain its own conscious agent (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. This clinical observation features in many textbooks (Gazzaniga, 1998; Gray, 2002) and has influenced theoretical thinking about consciousness. Congruent with the idea that split-brain patients have two separate conscious agents, both the Global Workspace theory (Baars, 1988, 2005; Dehaene & Naccache, 2001) and the Information Integration theory (Tononi, 2004, 2005; Tononi & Koch, 2015) imply that without massive interhemispheric communication two independent conscious systems appear.

On closer examination, the response x visual field interaction appears less than absolute. First, Sperry (1968) himself already observed that there are clear exceptions. Second, there are a number of studies that failed to observe this interaction and found that responding was well-above chance with both hands (e.g., Corballis, 1995; Egly, Rafal, Driver, & Yves Starrveveld, 1994; Levy, Trevarthen, & Sperry, 1972). More recently, we (Pinto et al., 2017) performed a quantitative study into this 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 x visual field interaction was never observed. This result held across all tasks (detection, localization, orientation determination, labelling and visual matching), and all tested types of stimuli (isoluminant dots, simple shapes, oriented rectangles, objects). Pinto, de Haan, and Lamme (2017) and Corballis, Corballis, Berlucchi, and Marzi (2018) suggested that these effects are probably the result of intact subcortical routes. Savazzi et al. (2007), for instance, showed that the superior colliculus is likely to play a role in visual interhemispheric transfer. However, others, such as Volz and Gazzaniga (2017) have suggested that these effects might be caused by confounds as ipsilateral arm control and/or cross-cueing.

Most of the studies on (the lack of) interhemispheric transfer of information have been carried out in the visual domain but the somatosensory system is also separated with the perception of the right half of body being carried out by the left hemisphere and vice versa (e.g., Penfield and Boldrey (1937). Zaidel (1998) was one of the first to look at tactile perception. He investigated six patients with a complete commissurotomy using the Benton test of stereognosis looking separately at the left and the right hand. He observed deficits in stereognosis without primary somatosensory

impairment in both disconnected hemispheres. Object naming was worse with left hand than with the right hand but both were above chance. Interestingly, there was surprisingly good performance in a cross-hemisphere condition where one hand explored the stimulus and the multiple-choice card was explored in the opposite visual field. Fabri, Polonara, Quattrini, and Salvolini (2002) used fMRI to investigate brain activations in response to touch and painful stimulation in three split brain patients. They observed contralateral activation in SI and the parietal operculum during unilateral tactile stimulation of the hand. In contrast to the healthy subjects (Polonara, Fabri, Manzoni, & Salvolini, 1999), the patients showed no ipsilateral cortical activation (Fabri et al., 1999). With painful stimuli both controls and the split-brain patients showed contra- and ipsilateral activation in the parietal operculum and in the insular cortex in one case and in the posterior parietal cortex in one other patient. In a follow-up study, again with the three split-brain patients, Fabri et al. (2005) investigated inter-manual tactile recognition performance. Tactile finger localization was flawless with the same hand but deteriorated to around 80% correct when the patients had to respond with the other hand. Split-brain patients were impaired compared to healthy controls but still good at verbally identifying objects in the right hand (93%) and even more impaired but still above chance in the left hand (30%). Inter-manual object comparisons with either two the same or two different objects in each hand was difficult (68% correct). Thus, also in the somatosensory domain, there is enough data to doubt the classic description of the split-brain. This study is aimed a fine-grained assessment of basic tactile perception in a split-brain patient. We adopted the same basic approach as in Pinto, de Haan, et al. (2017) and Pinto, Neville, et al. (2017) to look at simple detection, localisation and cross-hemisphere matching. Our working hypothesis was that we would replicate our observations of extensive interhemispheric transfer for detection and localisation but an absence of cross-hemispheric matching with tactile stimulation. Such a correspondence in interhemispheric transfer of both visual and tactile stimulation would further delineate the circumstances in which the two hemispheres continue to “communicate” in split-brain patients.

1.1. Case description

Patient DDC also participated in the Pinto, de Haan, et al. (2017) and Pinto, Neville, et al. (2017) studies. During surgery, his corpus callosum was completely removed and most of the anterior commissure. Note that other than the removal of the corpus callosum, DDC has no brain damage, and he falls within the normal IQ range. See Pizzini et al. (2010) and Corballis et al. (2010) for detailed descriptions of this patient.

2. Experiment 1: Detection threshold

The first experiment was designed to measure DDC's tactile detection thresholds on the dorsum of his hands while he responded either with the stimulated or the other hand. The objective was to find out whether or not each of his two hemispheres only perceive half of his body. In essence, this

experiment is the tactile equivalent of the visual detection studies of Pinto, de Haan, et al. (2017) and Pinto, Neville, et al. (2017).

2.1. Method

Thresholds were determined with von Frey hairs (VFA; Touch-Test™ sensory evaluators, North coast medical Inc.) using a descending staircase procedure [Anema, van Zandvoort, de Haan, Kappelle, de Kort, Jansen & Dijkerman, 2009] starting with the thickest hair T (VFA 6.65 (= 300 g)). In half of the trials, the hairs touched his skin while in the other half the experimenter (EdH) made the same hand movement but stopped short of touching the skin. The hand that was stimulated was positioned under a cardboard cover in order to obscure it from the patient's vision. In addition, he was asked to close his eyes during the whole experiment and to concentrate on his hands. There were four trials per hair, and we moved on to the thinner hair after 3 or more correct responses. The following hairs were used respectively: R [VFA 6.10 (= 100 g)], P [VFA 5.46 (= 26 g)], N [VFA 5.07 (= 10 g)], L [VFA 4.74 (= 6 g)], J [VFA 4.31 (= 2 g)], I [VFA 4.17 (= 1.4 g)], H [VFA 4.08 (= 1 g)], G [VFA 3.84 (= .6 g)], F [VFA 3.61 (= .4 g)] and E [VFA 3.22 (= .16 g)]. Testing proceeded until he made 2 or more errors and we took the previous hair as the threshold. Stimuli were applied to the back of the hand and each trial started with the experimenter counting to three in Italian. DDC indicated detection of being touched with a thumbs up gesture while an absence of touch was signalled with the thumb down. There were four separate blocks in which the stimulated hand and the hand with which he responded were systematically varied. A second experimenter (YP), who could not see whether the hand had been touched, registered the responses.

2.2. Results

DDC's accuracy thresholds in von Frey hair thickness are summarised in Table 1. Overall, his performance (grand mean = 3.95) was slightly less sensitive than healthy subjects. Compared to 12 healthy controls [taken from Anema, van Zandvoort, de Haan, Kappelle, de Kort, Jansen and Dijkerman, 2009: mean = 2.44 (= .02 g); cut-off = 3.22 (= .16 g)] his performance is just outside the normal range. In addition, he appears slightly more sensitive in the crossed conditions, i.e. when he was asked to respond with the other hand than the one that was stimulated but differences were minimal. We performed statistics on the results in the following way. Per condition (of hair thickness) hits and correct rejections were coded as 1 and misses and false alarms as

0. If one condition was not tested then we assigned an equal amount of 1's and 0's to that condition, i.e. chance performance. We did so because conditions were only omitted because it was beyond the threshold of the participant. Permutation testing revealed that performance was similar irrespective of which hand was touched ($p = .4$) and irrespective of with which hand the participant responded ($p = .21$). However, there was a significant interaction as the participant performed somewhat better in the crossed conditions (responding with the other hand than the stimulated hand) than in the uncrossed conditions (stimulated and responding hand are the same), $p = .011$.

2.3. Discussion

DDC shows slightly increased detection thresholds for tactile stimulation on either hand but, if anything, his performance is somewhat better in the crossed than the uncrossed conditions. We suggest that one reacts faster in the other hand condition because in the same hand condition the patient has to wait until the trial is completed and the experimenter has removed his hand. Unfortunately, we did not record reaction times, so we cannot check this suggestion in a quantitative manner. Whatever the explanation of this interaction, it clearly invalidates the claim that sensory information of touch can only be used by one hemisphere for manual output. Therefore, the classic interaction between side-of-stimulation x response-hand (where performance should be much better in the uncrossed conditions) is not observed. This finding suggests that response selection and action control remains unified in this split-brain patient.

3. Experiment 2: Tactile localisation

Having shown that the detection of tactile stimuli is not split in DDC, the next question we investigated was whether the localisation of tactile stimuli might also be unified across the two hemispheres. We carried out two separate, comparable tasks on the inner side of his arms and on the frontal side of his legs.

3.1. Method

DDC was asked to roll up the sleeves of his shirt up to above his elbow or the legs of his trousers. The to be stimulated arm or leg was positioned under a cardboard cover in order to obscure it from sight. Tactile stimulation was applied to the skin with the rubber tip of a pencil and was well above threshold. A response sheet (see Fig. 1) with the four stimulation sites on the arm (1a) or the leg (1b) was placed on top of the cardboard cover. The four stimulation sites were separated equidistantly on the underarm and the upper leg. Each of the four positions was stimulated seven times in a pseudo-random fashion (total number of trials is 28). Each trial started with the experimenter counting to three in Italian, and DDC indicated where he thought he had been touched by pointing to one of the four positions on the response sheet. There were four separate blocks in which the stimulated hand and the hand with which he responded were systematically varied. A

Table 1 – DDC's tactile detection thresholds (accuracy) in von Frey hair thickness.

Von Frey threshold	Right hand responded	Left hand responded
Right hand stimulated	4.17	3.84
Left hand stimulated	3.61	4.17

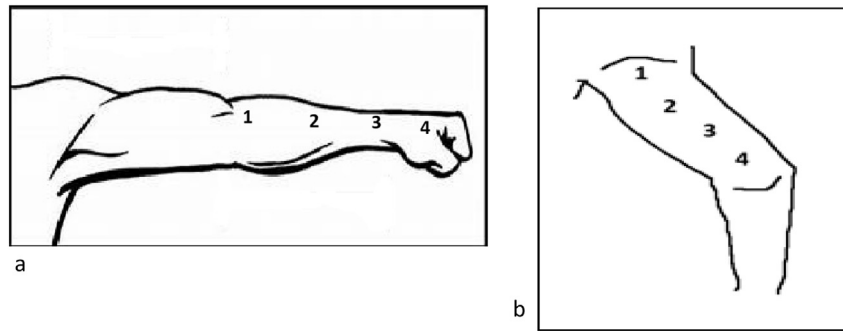


Fig. 1 – The response sheets on which DDC had to indicate where he thought he had been touched on the arm (1a) and the leg (1b).

second experimenter (YP), who could not see where his hand had been touched, registered the responses. His errors were calculated as the average distance from the correct position in terms of positions (maximum is 3).

3.2. Results

For each trial, the distance between the correct and the indicated position was calculated on an interval scale (correct = 0, an adjacent position = 1, etc.). Subsequently, these distances were averaged per condition. The results are summarised in Table 2. We performed permutation tests to determine statistics. His performance is well above chance-level in all four conditions (arms: all p s < .001, legs: all p s < .001). An important observation is that, again, the classic interaction between side-of-stimulation x response-hand is not observed (arms: $p = .77$, legs: $p = .1$). Moreover, there was no effect of with which hand the participant responded (arms: $p = .77$, legs: $p = .33$). When the legs were stimulated, accuracy did not depend on which leg was stimulated ($p = .51$). Also, there was no indication of a relatively better or worse performance in relation to the proximal or distal part of the underarm ($p = .78$). Average distance error per position 1: .31, position 2: .43, position 3: .43, and position 4: .29. However, there was an effect of which arm was stimulated ($p = .0016$), with better localization of stimuli on the left arm (average distance .19) than on the right arm (average distance .54).

Table 2a – Average localisation error in terms of position on his arm.

Average distance in positions	Right hand responded	Left hand responded
Right hand stimulated	.54	.54
Left hand stimulated	.17	.21

Table 2b – Average localisation error in terms of position on his leg.

Average distance in positions	Right hand responded	Left hand responded
Right leg stimulated	.25	.425
Left leg stimulated	.325	.275

3.3. Discussion

The results are clear cut. He performs well above chance level in all four conditions, and more importantly, for each hand his performance is almost identical whether he used his ipsi- or contralateral hand for responding. This suggests that apart from detection, tactile localisation is also unified in DDC. An interesting observation is that his localisation is relatively better on the left arm. This finding is reminiscent of our findings in DDC showing a relatively better localisation performance in his left compared to his right visual hemifield (Pinto et al., 2017). Perhaps, this reflects a generalised (visual and tactile) right hemisphere advantage for spatial processing, or alternatively a noisier processing in the left hemisphere due to the epilepsy.

4. Experiment 3: Cross arms localisation: same / different

The observation that both detection and localisation of tactile stimuli are unified across the two hemispheres in the split-brain patient DDC raises the question whether the removal of his corpus callosum has had no effect on his somatosensory processing. It could be that both hemispheres have access to the sensory information from the whole body (perceptual unity) or that only response selection and action control (action unity) remain unified in this split-brain patient. Here, in the third experiment, we investigate whether he is able to compare where he has been touched simultaneously on both his arms.

4.1. Method

As in the previous experiment, DDC was asked to roll up the sleeves of his shirt up to above his elbow. Both arms were positioned under a cardboard cover in order to obscure it from sight (see Fig. 2). Simultaneous tactile stimulation was applied to the skin with the rubber tip of two pencils and was well above threshold. The distance between the four stimulation sites on each arm was equidistant. Each trial started with the experimenter counting to three in Italian, and then stimulated both arms at the same time. In half of the trials (36), the same positions were stimulated on both arms, and the twelve

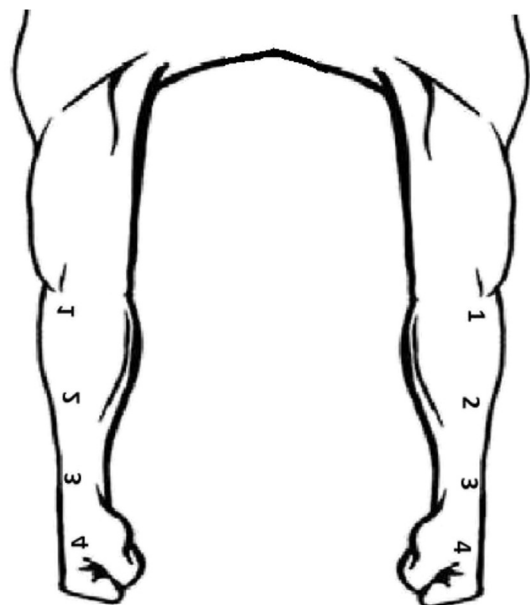


Fig. 2 – Graphic representation of the stimulation sites on his two arms.

possible (all different permutations) “different” trials appeared three times. Thus, the total number of trials was 72. DDC reported verbally whether he thought he had been stimulated in a symmetrical fashion (“same”) or in two different positions (“different”) on both arms. A second experimenter (YP), who could not see where his arms had been touched, registered the responses.

4.2. Results

DDC showed no sign of extinction and he indicated that he always felt the double stimulation. He scored below but not significantly different from chance ($p = .19$). The total number correct was 30/72. He is clearly not able to perform this task. Despite his poor performance, he maintained during the test session that he was quite confident about his responses.

4.3. Discussion

The absence of a corpus callosum has left DDC unable to compare simultaneous, tactile stimulation across the two arms. This impairment appears to be complete as he performs at chance level. Again, this finding is reminiscent of his inability to compare visual stimulation across fixation. Interestingly, he seems largely oblivious to this inability.

5. General discussion

This study was designed to investigate the classic observation of a stimulation-side \times response-hand interaction in split brain patients with tactile instead of visual stimulation. The wiring of the somatosensory system is similarly crossed, with the perception of touch on the left half of the body being processed by the right hemisphere and vice versa. There is

now substantial evidence from the visual domain that this interaction is not always observed (e.g., Corballis, 1995; Pinto et al., 2017; Savazzi et al., 2007). Notably, split brain patients appear able to signal detection and localisation of visual stimuli with both hands equally well. Here the main question was, thus, whether or not detection and localisation of touch on one half of the body can only be signalled by the ipsilateral hand.

Previous research with somatosensory stimulation had, at least, suggested that the processing of touch is not completely separated either (e.g., Fabri et al., 2005; Zaidel, 1998). Our current findings corroborate this suggestion. In fact, there was no hand difference for detecting and localizing touch. Both hands can be used to signal detection and localization of touch anywhere on the body. Note that our findings are in line with several other findings that suggest that the processing of somatosensory information (of which touch is one aspect) is less than completely segregated in a split-brain patient. In other words, although our findings contradict some claims, they are certainly not extraordinary or revolutionary. Fabri et al. (2002) used fMRI to demonstrate contra- and ipsilateral activation in response to painful stimuli in healthy controls and split-brain patients, and Lepore, Lassonde, Veillette, and Guillemot (1997) showed that detection thresholds for temperature discrimination were similar for within- and between-side comparisons in split brain patients and comparable to the discrimination performance of healthy subjects. Our finding is also in line with a recent study by Dosso, Chua, Weeks, Turk, and Kingstone (2018) who looked at the interaction between proprioceptive perception of the left and the right hand positioned either in the left or the right visual half-field in two split brain patients. They concluded that each hemisphere can accurately represent the full visuomotor space, and suggested that this whole field perception is subserved by subcortical connections between the hemispheres.

Some (e.g., Volz & Gazzaniga, 2017) have suggested that these observations do not represent the true split-brain state-of-affairs as the absence of an interaction could be due to confounding factors, such as “cross-cueing” or “ipsilateral hand control”. Cross-cueing is, in their view, something that the patients have developed over years of practice learning to cope with a split-brain. As localising the position where one has been touched is not an everyday requirement, we feel that this is not a likely explanation for touch localisation. Ipsilateral hand control is still controversial as far as it concerns the ability of one hemisphere to move the ipsilateral hand in a coherent fashion while the other hemisphere (that is dominant for that arm) has no intention to move that hand. For instance, observations during the Wada test (Wada, 1960), where one hemisphere is temporarily anaesthetised in order to establish language dominance in the context of functional surgery, has systematically shown that the contralateral hand is paralysed after the drug takes effect. In addition, the pointing response that is required in Experiment 2 (taking the hand out of the stimulation box and then to move the index finger to the correct position on the drawing on top of the box) is too elaborate given the proximal ipsilateral innervation of the arm. Therefore, we suggest that these possible confounding factors cannot explain our current results. These results are in line with Polonara, Mascioli, Salvolini, Fabri, and

Manzoni (2009) who showed that proximal body regions of each side (face, trunk, proximal limbs) and hand are represented in both hemispheres, and also argue against the “cross-cueing” or “ipsilateral hand control” hypothesis. Yet, although it may be difficult to explain our results with a simple cross-cueing account, more complex versions cannot be ruled out. Therefore, although our results advance this debate, they do not conclusively decide it.

Analogous to our observations in the visual domain (Pinto et al., 2017), we found that DDC was unable to compare touched locations across the midline, performing this task at chance-level. This finding is in line with a study by Lassonde, Sauerwein, Chicoine, and Geoffroy (1991) who showed that after surgery the performance of three adult split-brain patients deteriorated to chance-level on a task where they had to indicate on which finger they were touched by touching the corresponding finger on their other hand with the thumb. Intra-manual matching, where the finger had to be touched with thumb of the touched hand, remained perfect. Clearly, the absence of the corpus callosum prevents detailed sensory information being transferred between the two hemispheres. Therefore, the ‘split brain paradox’, i.e. the demonstration that each hemisphere is able to signal the position of stimulation anywhere (in the visual field and on the body) while they are unable to compare these positions across the midline, has been firmly established in two different sensory domains. Based on the subjective report from the patients, who feel “normal” and unaltered after surgery (e.g., Bogen, 1965), it seems possible that they are able to respond consciously to stimulation anywhere in the visual world or their body, and that this information is provided via subcortical routes (e.g., Savazzi, et al., 2007; Pinto, de Haan, & Lamme, 2017; Corballis et al., 2018). This unified consciousness of vision and somatosensation does, however, not support the matching of information across the midline. Possible explanations are (1) that the information transfer via the subcortical connections is degraded (compared to callosal transfer), (2) that it is only at the response selection phase that unity is achieved, or (3) that this unified consciousness has access to but cannot integrate the information from both hemispheres in real-time. Future studies should be geared towards distinguishing between these options.

We argue that our current findings are not revolutionary or radically different from what has been previously claimed. For instance, Sperry, Gazzaniga, and Bogen (1969, pages 279–280) have noted “Onset and presence or absence of tactile stimulation of the left hand can be reported verbally as can also a distinction between stimuli applied to the wrist or palm, thumb or palm, and thumb or little finger”. The importance of the current results is that they unequivocally, and quantitatively, show that tactile perception of presence and location of stimuli is unified in split-brain patients. Moreover, this information cannot be used for comparisons across the side of the body. Thus, although the patient knows, for both arms, which location is stimulated, he cannot indicate whether the same location was stimulated on both arms. This puzzling finding - if both locations are known to the patient, why can he not compare them? - neatly fits the model of the split-brain we recently put forward (Pinto, de Haan, et al., 2017). In this model

all perceptual information (from both fields, and the entire body) is available to one conscious agent, yet the information is not automatically integrated. That is, the subject experiences two independent streams of information, thereby hampering comparisons across these streams. Note that although previous studies have provided partial or qualitative support for the claims of our model, no study so far has collected the quantitative data needed to check our model. In the current study we investigated the “unified consciousness” part of the model, i.e. ability to report on presence and location of tactile stimuli across the entire body irrespective of response type (left hand or right hand). Moreover, we checked the “split perception” part, i.e. inability of the patient to compare the location of tactile stimuli across arms. Thus, the current study is the first to quantitatively verify crucial predictions of our model of the split-brain syndrome within one investigation.

In summary, in this study we carried out the tactile equivalence of the Pinto, de Haan, et al. (2017) and Pinto, Neville, et al. (2017) visual tests for the detection, location, and matching across the midline. In line with our previous results, we observed that split-brain patients can signal detection and localisation with either hand anywhere on the body (be it the arm or the leg) but they remain unable to match positions touched on both arms or legs simultaneously. Our study further clarifies the remaining unity of tactile perception in split-brain patients, and is in line with several previous studies into this domain. Further studies are needed to explore the extent of conscious unity in split-brain patients, and whether this unity extends to other processes in perception, memory and cognition.

Acknowledgements

This work was supported by an European Research Council Advanced grant FAB4V (#339374) to Edward de Haan. The Authors are grateful to Gabriella Venanzi for scheduling patient's exam.

REFERENCES

- Anema, H. A., van Zandvoort, M. J. E., de Haan, E. H. F., Kappelle, L. J., de Kort, P. L. M., Jansen, B. P. W., et al. (2009). A double dissociation between somatosensory processing for perception and action. *Neuropsychologia*, 47(6), 1615–1620. <https://doi.org/10.1016/j.neuropsychologia.2008.11.001>.
- Baars, B. J. (1988). *A cognitive theory of consciousness*. Cambridge University Press.
- Baars, B. J. (2005). *Global workspace theory of consciousness: Toward a cognitive neuroscience of human experience*. *Progress in Brain Research*, 150, 45–53.
- Bogen, J. E., Fisher, E., & Vogel, P. (1965). Cerebral commissurotomy: A second case report. *JAMA*, 194, 1328–1329.
- Corballis, M. C. (1995). Visual integration in the split brain. *Neuropsychologia*, 33, 937–959.
- Corballis, M. C., Birse, K., Paggi, A., Manzoni, T., Pierpaoli, C., & Fabri, M. (2010). Mirror-image discrimination and reversal in the

- disconnected hemispheres. *Neuropsychologia*, 48, 1664–1669. <https://doi.org/10.1016/j.neuropsychologia.2010.02.011>.
- Corballis, M. C., Corballis, P. M., Berlucchi, G., & Marzi, C. A. (2018). *Perceptual unity in the split brain: The role of subcortical connections*. *Brain* (2018).
- Cowey, A. (1979). Cortical maps and visual perception the Grindley memorial lecture. *The Quarterly Journal of Experimental Psychology: QJEP*, 31, 1–17.
- Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition*, 79, 1–37.
- Dosso, J. A., Chua, R., Weeks, D. J., Turk, D. J., & Kingstone, A. (2018). Attention and awareness: Representation of visuomotor space in split-brain patients. *Cortex*, 122, 253–262. <https://doi.org/10.1016/j.cortex.2018.08.029>.
- Egly, R., Rafal, R., Driver, J., & Yves Starveveld, Y. (1994). Covert orienting in the split brain reveals hemispheric specialization for object-based attention. *Psychological Science*, 5, 380–383.
- Fabri, M., Del Pesce, M., Paggi, A., Polonara, G., Bartolini, M., Salvolini, U., et al. (2005). Contribution of posterior corpus callosum to the interhemispheric transfer of tactile information. *Cancer Biotherapy & Radiopharmaceuticals*, 24, 73–80.
- Fabri, M., Polonara, G., Quattrini, A., & Salvolini, U. (2002). Mechanical noxious stimuli cause bilateral activation of parietal operculum in callosotomized subjects. *Cerebral Cortex*, 12, 446–451.
- Fabri, M., Polonara, G., Quattrini, A., Salvolini, U., Del Pesce, M., & Manzoni, T. (1999). Role of the corpus callosum in the somatosensory activation of the ipsilateral cerebral cortex: An fMRI study of callosotomized patients. *European Journal of Neuroscience*, 11, 3983–3994.
- Gazzaniga, M. S. (1967). The split brain in man. *Scientific American*, 217, 24–29.
- Gazzaniga, M. S. (1998). The problem of consciousness. In *Cognitive neuroscience - the biology of the mind* (pp. 542–543). New York, NY, USA: W. W. Norton & Company.
- Gazzaniga, M. S. (2000). Cerebral specialization and interhemispheric communication: Does the corpus callosum enable the human condition? *Brain*, 123, 1293–1326.
- Gazzaniga, M. S., Bogen, J. E., & Sperry, R. W. (1962). Some functional effects of sectioning the cerebral commissures in man. *Proceedings of the National Academy of Sciences of the United States of America*, 48, 1765–1769.
- Gray, P. (2002). The nervous system. In *Psychology* (pp. 160–161). New York, NY, USA: worth publishers.
- Innocenti, G. M. (1986). General organization of callosal connections in the cerebral cortex. In *Sensory-motor areas and aspects of cortical connectivity* (pp. 291–353). Springer.
- Lassonde, M., Sauerwein, H., Chicoine, A.-J., & Geoffroy, G. (1991). Absence of disconnection syndrome in callosal agenesis and early callosotomy: brain reorganization or lack of structural specificity during ontogeny? *Neuropsychologia*, 29, 481–495.
- Lepore, F., Lassonde, M., Veillette, N., & Guillemot, J.-P. (1997). Unilateral and bilateral temperature comparisons in callosal and split-brain subjects. *Neuropsychologia*, 35, 1225–1231.
- Levy, J., Trevarthen, C., & Sperry, R. W. (1972). Perception of bilateral chimeric figures following hemispheric deconnection. *Brain*, 95, 61–78.
- Ojemann, G., Ojemann, J., Lettich, E., & Berger, M. (1989). Cortical language localization in left, dominant hemisphere: An electrical stimulation mapping investigation in 117 patients. *Journal of Neurosurgery*, 71, 316–326.
- Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain: a Journal of Neurology*, 60, 389–443.
- 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 Science*, 21, 835–851.
- Pinto, Y., Neville, D. A., Otten, M., Corballis, P. M., Lamme, V. A. F., de Haan, E. H. F., et al. (2017). Split brain: Divided perception but undivided consciousness. *Brain*, 140, 1231–1237.
- Pizzini, F., Polonara, G., Mascioli, G., Beltramello, A., Foroni, R., Paggi, A., et al. (2010). Diffusion tensor tracking of callosal fibers several years after callosotomy. *Brain Research*, 1312, 10–17. <https://doi.org/10.1016/j.brainres.2009.11.030>.
- Polonara, G., Fabri, M., Manzoni, T., & Salvolini, U. (1999). Localization of the first (SI) and second (SII) somatic sensory areas in human cerebral cortex with fMRI. *AJNR. American Journal of Neuroradiology*, 20, 199–205, 1999.
- Polonara, G., Mascioli, G., Salvolini, U., Fabri, M., & Manzoni, T. (2009). Cortical representation of cutaneous receptors in primary somatic sensory cortex of man: A functional imaging study. In F. Columbus (Ed.), *Somatosensory cortex: Roles, interventions and traumas* (pp. 51–77). Nova Science Publishers, Inc.
- Sakata, H., & Taira, M. (1994). Parietal control of hand action. *Current Opinion in Neurobiology*, 4, 847–856.
- Savazzi, S., Fabri, M., Rubboli, G., Paggi, A., Tassinari, C. A., & Marzi, C. A. (2007). Interhemispheric transfer following callosotomy in humans. Role of the superior colliculus. *Neuropsychologia*, 45, 2417–2427.
- Sperry, R. (1984). Consciousness, personal identity and the divided brain. *Neuropsychologia*, 22, 661–673.
- Sperry, R. W. (1968). Hemisphere disconnection and unity in conscious awareness. *The American Psychologist*, 23, 723.
- Sperry, R. W., Gazzaniga, M. S., & Bogen, J. E. (1969). Interhemispheric relationships: The neocortical commissures; syndromes of hemisphere disconnection. In P. J. Vinken, & G. W. Bruyn (Eds.), *Handbook of Clinical Neurology*, 4 pp. 273–290. New York: John Wiley and Sons, Inc.).
- Tononi, G. (2004). An information integration theory of consciousness. *BMC Neuroscience*, 5, 42.
- Tononi, G. (2005). Consciousness, information integration, and the brain. *Progress in Brain Research*, 150, 109–126.
- Tononi, G., & Koch, C. (2015). Consciousness: Here, there and everywhere? *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 370. <https://doi.org/10.1098/rstb.2014.0167>.
- Vigneau, M., Beaucousin, V., Hervé, P. Y., Duffau, H., Crivello, F., Houdé, O., et al. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *Neuroimage*, 30, 1414–1432.
- Volz, L. J., & Gazzaniga, M. S. (2017). Interaction in isolation: 50 years of insights from split-brain research. *Brain*, 140, 2051–2060.
- Wada, J. A. (1960). Intracarotid injection of sodium amyltal for the lateralization of cerebral speech dominance: Experimental and clinical observations. *Journal of Neurosurgery*, 17, 266–282.
- Wahl, M., Lauterbach-Soon, B., Hattingen, E., Jung, P., Singer, O., Volz, S., et al. (2007). Human motor corpus callosum: Topography, somatotopy, and link between microstructure and function. *Journal of Neuroscience*, 27, 12132–12138.
- Wolman, D. (2012). A tale of two halves. *Nature*, 483, 260–263.
- Zaidel, E. (1998). Stereognosis in the chronic split brain] hemispheric differences, ipsilateral control and sensory integration across the midline. *Neuropsychologia*, 36, 1033–1047.