

UNIVERSITÀ POLITECNICA DELLE MARCHE Repository ISTITUZIONALE

Revisiting the attentional bias in the split brain

This is the peer reviewd version of the followng article:

Original

Revisiting the attentional bias in the split brain / Hausmann, Markus; Corballis, Michael C.; Fabri, Mara. -In: NEUROPSYCHOLOGIA. - ISSN 0028-3932. - STAMPA. - 162:(2021). [10.1016/j.neuropsychologia.2021.108042]

Availability: This version is available at: 11566/292964 since: 2024-04-12T16:33:20Z

Publisher:

Published DOI:10.1016/j.neuropsychologia.2021.108042

Terms of use:

The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. The use of copyrighted works requires the consent of the rights' holder (author or publisher). Works made available under a Creative Commons license or a Publisher's custom-made license can be used according to the terms and conditions contained therein. See editor's website for further information and terms and conditions. This item was downloaded from IRIS Università Politecnica delle Marche (https://iris.univpm.it). When citing, please refer to the published version.

note finali coverpage

(Article begins on next page)

Hausmann, M., Corballis, M. C., Fabri, M. (2021). Revisiting the attentional bias in the split brain. *Neuropsychologia, in* press. <u>https://doi.org/10.1016/j.neuropsychologia.2021.108042</u>

Revisiting the attentional bias in the split brain

Markus Hausmann¹, Michael C. Corballis², Mara Fabri³,

¹Department of Psychology, Durham University, United Kingdom

²Department of Psychology, University of Auckland, New Zealand

³Department of Experimental and Clinical Medicine, Politechnic University of Marche,

Ancona, Italy

Running title: Attentional bias in the split brain

Address for correspondence:

Markus Hausmann Department of Psychology Durham University South Road Durham DH1 3LE United Kingdom

Email: markus.hausmann@durham.ac.uk

Abstract

Previous research has revealed a strong right bias in allocation of attention in split brain subjects, suggesting that a pathological attention bias occurs not only after unilateral (usually right-hemispheric) damage but also after functional disconnection of intact right-hemispheric areas involved in allocation of attention from those in the left hemisphere. Here, we investigated the laterality bias in spatial attention, as measured with the greyscales task, in two split-brain subjects (D.D.C. and D.D.V.) who had undergone complete callosotomy. The greyscales task requires participants to judge the darker (or brighter) of two left-right mirror-reversed luminance gradients under conditions of free viewing, and offers an efficient means of quantifying pathological attentional biases in patients with unilateral lesions. As predicted, the results of the two split-brain subjects revealed a pathological rightward bias in allocation of attention, suggesting strong dependence on a single hemisphere (the left) in spatial attention, which is opposite to what one expects from people with intact commissures, and is remarkable in that it occurs in free viewing. In that sense both split-brain patients are behaving as though the brain is indeed split, especially in D.D.C. who had undergone partial resection of the anterior commissure in addition to complete callosotomy, whereas the anterior commissure is still intact in D.D.V. The findings support the view that the commissural pathways play a significant role in integration of attentional processes across cerebral hemispheres.

<u>key words</u>: corpus callosum, hemineglect, hemispheric asymmetry, laterality, spatial attention, split brain

Introduction

After several decades of neuropsychological research, there is still no general agreement on the neural mechanisms underlying the lateral bias in allocating attention. One potential explanation is that both hemispheres allocate visuospatial attention to the contralateral hemispace, whereas the right hemisphere is responsible for allocating attention also to the ipsilateral right hemispace (Heilman and Van Den Abell, 1980; Weintraub and Mesulam, 1987). Therefore, right-hemisphere damage in the temporal-parietal junction and superior and middle temporal gyri can induce inattention to left hemispace (i.e., spatial hemineglect; for review see Karnath and Rorden, 2012), whereas left-hemisphere damage has only modest effects on allocating attention. This has been interpreted as evidence for right-hemisphere dominance in spatial attention, and is further supported by the small but consistent leftward bias (contralateral to the dominant right hemisphere) in attention allocation in neurologically healthy participants, called pseudoneglect (Bowers, 1980, for review see Jewell and McCourt, 2000).

Several different behavioural tasks are commonly used to quantify the spatialattention bias in patients with right- (and left-) hemisphere lesions, and also to quantify the extent of right pseudoneglect in healthy controls. These include visual line bisection (Schenkenberg et al., 1980), the landmark task (Milner et al., 1992) and the greyscales task (Mattingley et al., 1994). Visual line bisection requires participants to place a mark relative to the perceived midpoint of horizontal lines of different lengths and positioned in different locations. The deviation of the mark from the veridical midpoint determines the direction and extent of the visuospatial bias. Hemineglect patients will typically deviate largely towards the right of the veridical midpoint in this task because the left hemispace is not represented. In contrast,

healthy controls produce a marginal tendency to deviate to the left from the true midpoint, slightly neglecting the right (Bradshaw et al., 1986). Other tasks used to quantify direction and magnitude of the spatial attentional bias in patients and healthy controls include the landmark task (Milner et al., 1992), in which participants need to judge deviations from the true midpoint of pre-bisected horizontal lines, and the greyscales task (Mattingley et al., 1994), which requires a comparative luminance ('darkness') judgement to be made between two horizontal lines containing mirror-imaged linear contrast gradients. Although all these tasks are well-established and revealed good test-retest reliability, they are not strongly intercorrelated, suggesting that each task measures to some extent different aspects of visuospatial attention (Learmonth et al., 2015).

Previous research has shown that visuospatial attention is not only affected after right-hemisphere lesions in temporo-parietal areas, and to some extent after right-frontal lesions (Saj et al., 2018), but also when these areas are functionally disconnected from homotopic areas in the contralateral left hemispheres. This suggests that the bias in allocation of attention results from the integration of visuospatial information of both left and right hemisphere which requires interhemispheric communication via the corpus callosum.

Some indirect evidence for this idea comes from differences between the hands in manual line bisection of healthy adults. Pseudoneglect is generally larger with the left hand, which is dominantly controlled by motor areas of the contralateral right hemisphere (e.g., Beste et al., 2006; Hausmann et al., 2002). Neurotypical children aged 10 years or below, in contrast, showed a phenomenon called *symmetrical neglect* – a line-bisection bias with the left hand towards the left and with the right hand towards the right. Although the number of callosal fibres reaches its

maximum in utero (LaMantia and Rakic, 1984), quantitative MRI has shown that the total midsagittal callosal area increases in size up to the age of 18 years, particularly in the regions of the midbody and splenium (Giedd et al., 1996). Symmetrical neglect might therefore be due to immature development of the corpus callosum, so that allocation of visuospatial attentional for each hand is controlled almost exclusively by the corresponding contralateral hemisphere (e.g., Bradshaw et al., 1988; Dobler et al., 2001; Hausmann et al., 2003a; Roeltgen and Roeltgen, 1989).

More direct evidence comes from studies in patients with functional callosal disconnection. For example, Kashiwagi et al. (1990) reported a left hemineglect in a patient with callosal infarction in the trunk and genu of the corpus callosum, with rightward errors in line bisection, but only when the right hand was used. Heilman et al. (1984) found a symmetrical neglect (i.e., left bias with the left hand and right bias with the right hand) in a 43-year-old right-handed woman with a haemorrhage in the region of the corpus callosum with the most anterior extent of the infarction at the junction of the genu and the body. The posterior one-fourth to one-fifth of the body and all of the splenium were intact. Similarly, Goldenberg (1986) investigated a 46year-old right-handed woman, who suffered destruction of the anterior two third of the corpus callosum due to pericallosal haemorrhage and ischemia and also found some evidence of symmetrical neglect in visual line bisection, but this was dependent on the position of the line. The right hand showed a right bias, but only when the line itself was in left hemispace or in the centre, but not when it was in right hemispace. The left hand showed a left bias in all line positions, but it was greatest in right hemispace. Goldenberg (1986) concluded that some callosal transfer of visual information was possible but may have been degraded. The results are similar in two right-handed patients with hydrocephalus and general thinning of the corpus

callosum who also showed features of functional disconnection when performing the line-bisection task (Jeong et al., 2006). In both patients, it was found that each hand was biased towards its own hemispace, providing further support for the idea that "each hand is biased to operate in and towards its own hemispace and that hydrocephalus can induce a form of *callosal neglect*" (Jeong et al., 2006, p. 348). These studies suggest that partial callosal infarction or damage of anterior regions of the corpus callosum as well as general thinning of the corpus callosum can result in a spatial-attention bias which is similar to symmetrical neglect (i.e., right bias with the right hand and left bias with the left hand) found in younger children whose corpora callosa have not yet fully matured.

There are only a few studies of *callosal neglect* in split-brain patients with complete commissurotomy, and the findings are partly inconsistent. Plourde and Sperry (1984) investigated three patients with complete surgical section of the corpus callosum on a rod-bisection task and found some systematic biases, but again depending on the hand used and the location of the rod. Although all patients made substantial errors, there was no clear indication overall of spatial hemineglect. One patient of this study (R.Y.) showed a robust right bias which was similar to that in a control group of right-handed patients who had sustained right-hemisphere damage. Somewhat paradoxically, however, this occurred only when he used his left hand. In contrast, patients N.G. and L.B. erred more to the left (N.G. always) with the left hand. When using the right hand, both patients erred to the right, if rods were presented in the centre or in the left hemispace. This pattern indicates some degree of symmetrical neglect. Although one patient (L.B.) tested by Plourde and Sperry (1984) did not show a consistent bias, he showed evidence of left hemineglect under more stringent conditions. When asked to judge whether single horizontal lines,

flashed for 100 ms, extended further to the left or right of a central fixation mark, L.B. showed a strong bias to judge the right side longer (Corballis, 1995). However, L.B.'s strong right bias was not observed in judgments about the larger of two circles or the longer of two horizontal lines in opposite hemifields, suggesting that the bias was not due to a compression of perceived space in the left hemifield (Corballis and McLean, 2000).

Further direct evidence that the bias in allocating attention might be directly related to the extent of callosal resection comes from a visual line-bisection study which included four patients with anterior (L.P. and R.V.), posterior (M.C.) and complete callosotomy (D.D.V.) (Hausmann et al., 2003b). D.D.V. showed a strong rightward attention bias, suggesting left hemineglect. The two patients with anterior callosotomy showed biases similar to neurotypical adults (i.e., pseudoneglect in L.P.) and children (i.e., symmetrical neglect in R.V.). This difference in biases might be explained by the extent of the resection of the corpus callosum. In R.V., only a small portion of the splenium was spared, so there was relatively little transfer of attentiondependent information, and neglect was a function of the hemisphere controlling the hand. In L.P., by contrast, the posterior body and splenium were clearly spared, enabling the right hemisphere to play a role regardless of the hand used. M.C. (posterior callosotomy) showed a pattern very different from the other three patients. M.C. showed a very large left bias, implying right hemineglect. The reason why the bias was in the opposite direction to that shown by D.D.V. is unclear. However, given that the left bias was particular pronounced when the right hand was used might suggest that M.C.'s left hemisphere is dominant for visuospatial attention.

Previous research on a pathological spatial-attention bias in split-brain patients focused predominantly on the line-bisection task (see above). As mentioned earlier,

the biases across tasks are not strongly correlated with another (Learmonth et al., 2015), suggesting that each task measures specific aspects of visuospatial attention and/or involve additional cognitive processes. This might also explain why patients with right-hemisphere damage and hemineglect symptoms can exhibit pronounced dissociations in performance across tasks, depending on the specific location of the damage in the attention network (e.g., Chechlacz et al., 2012; Halligan et al., 2003; Kerkhoff, 2001). For example, damage to the right inferior parietal lobe negatively affected the allocation of attention to the ipsilesional hemispace in visual line bisection, whereas lesions in the right dorsolateral prefrontal cortex and temporal lobe negatively affected visuomotor exploration and object-centred perception (Verdon et al., 2010).

It is important to note that the paper-pencil version of the visual line-bisection task which was used in many split-brain studies reported earlier (e.g. Hausmann et al., 2003b) involves the integration of both visuospatial *and* motor abilities. Therefore, in the present study, we examined the attentional bias in two patients with complete callosotomy with the greyscales task which does not require a unilateral manual response. The motor demands required for visual line bisection but not greyscales task performance might also explain why the attention bias observed in the greyscales task revealed only weak (non-significant) correlation with visual line bisection (Mattingley et al., 2004; Nicholls and Roberts, 2002), and it might explain why the attention bias measured with the greyscales task has been found to be stronger and more consistent than for visual line bisection (Friedrich, Hunter, & Elias, 2016).

By testing two patients with complete callosotomy, D.D.C. and D.D.V (the latter also took part in Hausmann et al., 2003b), we hope to gain clearer insight into

the role of the corpus callosum in the integration of spatial attention when no manual response is required. Following the empirical evidence as summarised above, we hypothesised a strong right bias in spatial attention in both patients.

Methods

Subjects

Two right-handed split-brain subjects (D.D.C. and D.D.V) who had undergone complete callosotomy to treat drug-resistant epilepsy took part in the present study. D.D.V. shows the anterior commissure still intact whereas D.D.C. has a partial resection of it. D.D.V. was a 46-year-old man at the time of testing. He had his second operation, which completed the callosotomy at the age of 22 years. His post-operative intelligence scores (IQ) according to the Wechsler Adult Intelligence Scale (WAIS) was 81. D.D.C. was a 36-year-old man at the time of testing. His age at surgery was 19 years. His post-operative intelligence scores (IQ) according to the Wechsler Adult Intelligence Scale (WAIS) was 83. Both participants are right-handed according on the Edinburgh Handedness Inventory (Oldfield, 1971). However, D.D.C. was originally left-handed and was made to write with the right hand ever since primary school (Fabri et al., 2005). Both patients were chronically treated with antiepileptic medication. They were tested in Ancona, Italy, in September 2010. The extent of the callosal resections of both patients is shown in Figure 1. For more information about D.D.C. and D.D.V., see Fabri et al. (2005; 2006).



Figure 1. Magnetic resonance imaging scans of midsagittal brain slices obtained from T1-weighted spin-echo sequences showing the extent of callosal resection in D.D.C. and D.D.V.

Procedure and materials

The greyscales task was originally described by Mattingley et al. (1994). The original greyscales stimuli consist of horizontal rectangles, 49 pixels high which change in 50 increments from black on one side to white on the other. Changes in brightness were achieved by adding pixels to successive increments. For example, a stimulus 400 pixels long was divided into 50 increments (each 8 pixels/lines wide). At the dark end, no white pixels were placed in the first increment. In the second increment, one white pixel was added to each vertical line within the increment. In the third increment, two white pixels were added to each vertical line. This process continues until the 50th increment was reached, where 49 white pixels were added, making this increment appear completely white. To create the impression of a smooth change in brightness, the vertical position of the pixels within each line was

randomized which makes the stimuli look slightly different despite the fact that they contain exactly the same number of white and dark pixels.

The paper-pencil version of the greyscales task used here is based on the one developed by Nicholls et al. (1999), and contained 40 pairs of greyscales stimuli. Each stimulus was created by Nicholls et al. using a computer-graphics package and printed in landscape orientation onto sheets of white A4 paper. Each stimulus card consisted of a pair of horizontal rectangles, one immediately above the other. Each rectangle was 20 mm high (2.29° VA) and had a length of 105 mm (12.12° VA) (short lines) or 125 mm (14.48° VA) (long lines). Each rectangle was defined by a fine (0.5 mm) black outline, and was shaded continuously from black at one end to white at the other. For each stimulus pair, one rectangle was darker at the right end and the other was darker at the left end (i.e. the two rectangles were mirror images of one another; see Fig. 2). Both rectangles within a pair had the same length. Greyscales stimuli of each length were presented twenty times in pseudorandom order, with the positions of the rectangles (top/bottom) counterbalanced, making a total of 40 items.



Figure 2. Sample stimulus pair from the greyscales task. The figure illustrates a long greyscales stimulus (125 mm) on a DinA4 page (with permission from Mike Nicholls).

The factors of length (long, short) and orientation (upper stimulus dark on left and lower dark on right - or vice versa) were equally represented. The order of the 40 greyscales stimuli was identical for all participants. The viewing distance was approximately 500 mm. Each participant's body midline was aligned with the center of the pages. The number at the bottom of the page faced toward the participant.

In the first experimental run, participants were asked to select the stimulus that appeared overall darker. In the second run, a few minutes later, participants were asked to go through the same set of stimuli again and select the stimulus that appeared overall brighter. Participants indicated their response by calling out "upper" or "lower" stimulus. Participants did not rush their decisions. The average response time was less than 3000 ms. Participants' verbal response was recorded by the experimenter (M.H.) on the scoring sheet. These were then transcribed as leftward or rightward. Thus, if responses of "upper" or "lower" corresponded to rightward and leftward in the 'darker' condition, respectively, "upper" and "lower" corresponded to leftward and rightward in the "brighter" condition, respectively. The response bias was calculated as: ((20 - sum of leftward responses) / 20) x 100. For both conditions, we calculated separate response biases. Scores can range between -100 and +100. Negative values indicate a leftward bias, whereas positive values reflect a rightward bias. Further details for using the paper-pencil version of the greyscales task can be found here:

https://www.researchgate.net/publication/239612589 Guidelines on using the pap er version of the greyscales task

After participants completed the greyscales task, they were asked to indicate on a 5-point scale (1 = identical, 5 = completely different) how similar they found the two greyscales stimuli in brightness. D.D.V. and D.D.C. were also asked to point to the start and end points of the entire stimulus with their preferred hand, to ensure that the entire greyscale stimulus was perceived.

Results

To analyse whether split-brain participants revealed a significant attention bias in each condition ('darker', 'brighter'), we calculated exact binomial probabilities (onetailed) for the number of leftward responses (or fewer) out of 40 responses/trials. Descriptive statistics for both participants are shown in Figure 3.

D.D.C. did not show a single leftward response out of 40 trials in the 'darker' condition (p < .0001) and in the 'brighter' condition (p < .0001), indicating a maximal rightward bias of 100% in both conditions. When we asked D.D.C. how similar in brightness he found the two stimuli shown in each trial, his response was 3.5 on a 5-point scale, suggesting that D.D.C. perceived the two identical (but mirror-reversed) stimuli as being different.

Similarly, D.D.V. showed only 2 leftward responses out of 40 trials in the 'darker' condition (p < .0001), and 15 leftward responses out of 40 trials in the 'brighter' condition (p = .077), corresponding to response biases of 90% and 25%, respectively. When the analysis for the 'brighter' condition was performed separately for long line and short lines, the binomial test revealed a significant response bias of for long lines (5 leftward responses out of 20 trials, p = .02) and no bias for shorter lines (10 leftward responses out of 20 trials, p = .59, *ns*). When D.D.V. was asked how similar the two greyscales rectangles stimuli shown in each trial appeared in brightness, his response was 2.5 on a 5-point scale, suggesting that D.D.V.

perceived the two identical (but mirror reversed) stimuli as being different, albeit slightly less different compared to D.D.C. Also, both participants were able to identify the start and end points of the greyscale stimulus by pointing with the preferred hand, indicating that the entire greyscales stimulus was perceived.

This suggests that the strong rightward bias in the greyscales task occurred despite of both patients being able to perceive the entire stimulus, and not only the stimulus part located in the right hemispace.



Figure 3. Response bias in the 'darker' and 'brighter' condition of the greyscales task. A positive score indicates a bias in spatial attention towards the right hemispace (i.e., spatial neglect of left hemispace). A response bias of 100% indicates no single leftward responses.

Discussion

As predicted, a significant rightward bias was shown by both split-brain subjects (D.D.C. and D.D.V.) who had undergone complete callosotomy. Although significant response biases were observed in both split-brain subjects, the bias was maximal (100%) in D.D.C. across both conditions, whereas in D.D.V., the rightward response bias was particularly pronounced in the 'darker' condition, albeit also occurred in the 'brighter' condition when only longer lines were considered. D.D.V.'s right bias in the greyscales task matches the previously reported pronounced right line-bisection bias which was observed for both hands, albeit more pronounced with the left hand (Hausmann et al., 2003a).

The rightward bias in D.D.C., and to some extent in D.D.V., was similar in size to the pronounced rightward bias found in 78 stroke patients with right-hemisphere damage, who revealed a mean bias of 83.50% and a median of 100% (Mattingley et al., 2004), suggesting that the rightward bias in both split-brain subjects with complete callosotomy was similar to right-hemisphere damaged patients (with or without spatial neglect). The same study found a large left bias (mean: -56.20%; median = -87.50%) in patients with left-hemisphere damage and small left bias, pseudoneglect (mean: -21.30%; median: -25.00%) in age-matched healthy controls. However, it is important to note that (a) for the patient groups, performance on clinical tests of neglect (i.e., cancellation and line bisection) did not predict their greyscales scores, and (b) pathological biases were also present in patients without clinical neglect or visual-field defects, suggesting that the attentional bias measured by the greyscales task is dissociated from clinical spatial neglect and visual-sensory loss.

To interpret the bias found in the current study in the right context, it is also important to note that D.D.C. and D.D.V. were 36 and 46 years of age, respectively,

at the time of testing. According to a recent large-scale study investigating the visuospatial bias in the greyscales task across the adult life span (Friedrich et al., 2016), participants in their 30s and 40s revealed a mean leftward bias of -10.84% (SD = 15.26, Cohen's d = -1.42) and -7.97% (SD = 14.98, Cohen's d = -1.06), respectively. This indicates that the bias of both split-brain patients differed not only in size but also in direction for this particular age group of healthy controls.

We are not aware of any visual-field deficits, as D.D.V. and D.D.C. were both able to point to the start and end point of the greyscale stimulus, and there is no MRI evidence for damage of visual areas and pathways caused by the commissurotomy or epilepsy. Also, the attention bias in patients with visual-field deficits, such as left hemianopia after right-hemispheric damage would predict a strong attention bias in the opposite left ('blind') direction as has been frequently shown in patients with homonymous hemianopia, for example in the visual line-bisection task (e.g., Hausmann et al., 2003c).

The rightward bias was consistent (100%) in D.D.C. The reason why the rightward bias across conditions was somewhat less consistent in D.D.V. is not entirely clear. A simple explanation could be the less than perfect (i.e. medium) test-retest reliability of the greyscales task, as reported for healthy controls (Learmonth et al., 2015). This study found a strong laterality bias only during the first test session, not during retest. For D.D.V., the present study also found a strong bias (90%) in the first test (i.e., darker condition) and a smaller bias (25%) during retest (i.e., brighter condition). However, it is unlikely that test-retest reliability issue can account for the results in the present study because it should have affected both patients, not only D.D.V.

We also do not consider D.D.V.'s and D.D.C.'s lower IQ scores of 81 and 83, respectively, a major issue, as both IQ scores are classified as only "below average" (Weiss et al., 2006) and fall in the lower normal IQ range. Also, the greyscales task is cognitively not very demanding and can be administered even to young children whose cognitive/perceptual capabilities have not fully developed. It is also unlikely that patients had problems in following verbal instructions because D.D.V. and D.D.C. participated in many (more demanding) experiments previously (e.g., Corballis, 1995; 2005; Pinto et al., 2017a; Hausmann et al., 2003b) and none of them reported that both patients had any issues in this respect.

An alternative explanation for D.D.V.'s inconsistent attention is that he may be somewhat unusual among patients with complete callosotomy due to a marked dependence on the left hemisphere in visual tasks (Corballis et al., 2005). In that study, D.D.V. was unusually poor at responding to flashes of light in the left visual field in a simple reaction-time task. He responded to only one light flash out of 60 in the left visual field when responding with his right hand, and only 13 out of 60 in the left visual field when he used his left hand. He had little difficulty responding to right visual-field flashes with either hand, and was much faster at responding to flashes in both fields than at responding to flashes in either field, indicating that flashes in the left visual field were at least registered. This detection deficit of single left visual-field flashes contrasts with the performance of other split-brain patients, who did not show this deficit in similar tasks (e.g., Berlucchi et al., 1995; lacoboni and Zaidel, 1995; Corballis, 1998), and might suggest that D.D.V. shows an unusual left hemisphere dominance, even when using his left hand.

The present study included two split brain patients who had undergone complete callosotomy. Therefore, the present study cannot contribute much to the

question where in the commissural system spatial attention is integrated across hemispaces. However, previous research suggested a qualitative and quantitative bias depending on which callosal subareas were surgically resected or damaged (e.g., Hausmann et al., 2003b). Patients with complete callostomy, such as D.D.V. and D.D.C, showed a strong rightward attention bias. Similar to D.D.V., a split-brain subject (M.C.) who had undergone partial callosotomy of the splenium, isthmus, and central callosal body also showed a pronounced response biases in visual line bisection. However, the strong spatial-attention bias in M.C. was in the opposite direction to that shown by D.D.V., probably because M.C. showed an unusual left hemispheric dominance for spatial attention. Patients who had undergone partial callosotomy or damage which is restricted to anterior subareas of the corpus callosum showed biases similar to neurotypical adults (i.e., pseudoneglect) or children (i.e., symmetrical neglect), suggesting that the attention bias is proportional to the extent of callosal disconnection and depends on the portion of the splenium spared (Hausmann et al., 2003b). The relevance of posterior callosal subareas in spatial attention is supported by the fact that the splenium connects posterior tempoparietal regions of the cortex and damage to these areas typically result in hemineglect (for review see Karnath and Rorden, 2012).

It should be noted, however, that two of the commissurotomized patients investigated by Plourde and Sperry (1984), and who had undergone complete surgical section of the corpus callosum along with the anterior and hippocampal commissures, did not show a consistent rightward spatial-attention bias in a tactile rod-bisection task, although all patients showed large deviations on individual trials. The third patient also even showed left neglect when using his left hand. The findings

by Plourde and Sperry suggest that attention bias in all patients was confounded by the hand used.

The majority of studies reviewed above suggest that the manual response can be a confounding factor. Typically, the attention bias is more pronounced when the left hand is used for bisecting lines, because the left hand is controlled by the attention-dominant right hemisphere. The present study used the greyscales task which is independent from manual responses and required participants to respond verbally. One could argue that the strong rightward bias in the greyscales task occurred simply because, similar to a right-hand response, the verbal response involves the language-dominant left hemisphere, which is also assumed to allocate attention to only the right hemispace. However, we consider this unlikely in the case D.D.V., at least, because his right bias in the greyscales task is very similar to his right bias in visual line bisection for both hands (Hausmann et al., 2003b).

In a series of experiments, a recent split-brain study on D.D.C. and D.D.V. (Pinto et al., 2017a) suggested that both patients can only respond to stimuli when stimulus perception and manual response were processed in the same hemisphere, that is a left-hand response to stimuli presented in the left hemispace and a righthand response *and* verbal response to stimuli in the right hemispace. However, Pinto et al. (2017a) also reported that D.D.C. and D.D.V. showed full awareness of the presence of stimuli, and well above chance level recognition of their location, orientation and identity, throughout the entire visual hemispace. This has been interpreted by the authors as evidence against the view of two independent conscious agents within one brain, and in support for a 'conscious unity, split perception model' (Pinto et al., 2017b). However, this interpretation has been challenged recently because the authors cannot rule out that both hemispheres could

interacted closely via cross-cueing (Volz et al., 2018) or subcortical connectivity (Corballis et al., 2018), and ignored the fact that the anterior commissure is intact in D.D.V. and partially resected in D.D.C.

It is important to note that D.D.C. and D.D.V. correctly identified the start and end points of greyscales stimuli when asked to point to these locations with either hand. This suggests that the strong rightward bias in the greyscale task occurred despite of both patients being able to perceive the entire stimulus, and not only the stimulus part located in the right hemispace. This finding supports the view that perception and spatial awareness are relatively independent processes and the bias in allocation of attention might be representational (Bisiach, 1993).

Acknowledgements

We thank Dr Nicoletta Foschi, Dr Tullio Manzoni and Dr Aldo Paggi for their help and cooperation, Mrs Gabriella Venanzi for scheduling the patients' exams, and Dr Gabriele Polonara for providing the MR scans of the patients' brains.

References

- Berlucchi, G., Aglioti, S., Marzi, C. A., Tassinari, G., 1995. Corpus callosum and simple visuomotor integration. *Neuropsychologia*, 33, 923-936. https://doi.org/10.1016/0028-3932(95)00031-W
- Beste, C., Hamm, J.P., Hausmann, M., 2006. Developmental changes in visual line bisection in women throughout adulthood. *Dev Neuropsychol*, 30, 753-767. https://doi.org/10.1207/s15326942dn3002_6

- Bisiach, E., 1993. Mental representation in unilateral neglect and related disorders. *Q J Exp Psychol A*, 46, 435–461. https://doi.org/10.1080/14640749308401056
- Bowers, D., Heilman, K.M., 1980. Pseudoneglect: effects of hemispace on a tactile
 line bisection task. *Neuropsychologia*, 18, 491-498. https://doi.org/10.1016/0028-3932(80)90151-7
- Bradshaw, J.L., Bradshaw, J.A., Nathan, A., Nettleton, N.C., Wilson, L., 1986.
 Leftward errors in bisecting the gap between two points: Stimulus quality and hand effects. *Neuropsychologia*, 24, 849-855. https://doi.org/10.1016/0028-3932(86)90084-9
- Bradshaw, J.L., Spataro, J.A., Harris, M., Nettleton, N.C., Bradshaw J., 1988. Crossing the midline by four to eight year old children. *Neuropsychologia*, 26, 221-235. https://doi.org/10.1016/0028-3932(88)90076-0
- Chechlacz, M., Rotshtein, P., Humphreys, G.W., 2012. Neuroanatomical dissections of unilateral visual neglect symptoms: ALE meta-analysis of lesion-symptom mapping. *Front Hum Neurosci*, 6, https://doi.org/10.3389/fnhum.2012.00230
- Corballis, M.C., 1995. Line bisection in a man with complete forebrain commissurotomy. *Neuropsychology*, 9, 147-156. https://doi.org/10.1037/0894-4105.14.4.519
- Corballis, M.C., 1998. Interhemispheric neural summation in the absence of the corpus callosum. *Brain*, 121, 101-113. https://doi.org/10.1093/brain/121.9.1795
- Corballis, M.C., McLean, A., 2000. Interhemispheric comparison in a man with complete forebrain commissurotomy. *Neuropsychology*, 14, 519-525. https://doi.org/10.1037/0894-4105.14.4.519

- Corballis, M.C., Corballis, P.M., Berlucchi, G., Marzi, C.A., 2018. Perceptual unity in the split brain: The role of subcortical connections. *Brain, 141*, e1. https://doi.org/10.1093/brain/awy085
- Corballis, M.C., Corballis, P.M., Fabri, M., Paggi, A., Manzoni. T., 2005. Now you see it, now you don't: Variable hemineglect in a commissurotomized man. *Cogn Brain Res*, 25, 521–530. https://doi.org/10.1016/j.cogbrainres.2005.08.002
- Dobler, V., Manly, T., Atkinson, J., Wilson, B.A., Ioannou, K., Robertson, I.H., 2001.
 Interaction of hand use and spatial selective attention in children. *Neuropsychologia*, 39, 1055-1064. https://doi.org/10.1016/S0028-3932(01)00038-0
- Fabri, M., Del Pesce, M., Paggi, A., Polonara, G., Bartolini, M., Salvolini, U., Manzoni,
 T. (2005). Contribution of posterior corpus callosum to the interhemispheric
 transfer of tactile information. *Cogn Brain Res*, 24, 73–80.
 https://doi.org/10.1016/j.cogbrainres.2004.12.003
- Fabri, M., Polonara, G., Mascioli, G., Paggi, A., Salvolini, U., Manzoni, T., 2006.
 Contribution of the corpus callosum to bilateral representation of the trunk midline in the human brain: an fMRI study of callosotomized patients. *Eur J Neurosci, 23,* 3139–3148. https://doi.org/10.1111/j.1460-9568.2006.04823.x
- Friedrich, T.E., Hunter, P.V., Elias, L.J., 2016. Developmental Trajectory of
 Pseudoneglect in Adults Using the Greyscales Task. *Dev Psychol*, 52(11), 1937–
 1943. https://doi.org/10.1037/dev0000202
- Giedd, J.N., Rumsey, J.M., Castellanos, F.X., Rajapakse, J.C., Kaysen, D., Vaituzis, A.C., Vauss, Y.C., Hamburger, S.D., Rapoport, J.L., 1996. A quantitative MRI

study of the corpus callosum in children and adolescents. *Dev Brain Res*, 91, 274-280. https://doi.org/10.1016/0165-3806(95)00193-X

- Goldenberg, G., 1986. Neglect in a patient with partial callosal disconnection. *Neuropsychologia*, 24 397-403. https://doi.org/10.1016/0028-3932(86)90025-4
- Halligan, P.W., Fink, G.R., Marshall, J.C., Vallar, G., 2003. Spatial cognition:
 evidence from visual neglect. *Trends Cogn Sci*, 7(3): 125–133.
 https://doi.org/10.1016/S1364-6613(03)00032-9
- Hausmann, M., Ergun, G., Yazgan, Y., Güntürkün, O., 2002. Sex differences in linebisection as a function of hand. *Neuropsychologia*, 40, 235–240. https://doi.org/10.1016/S0028-3932(01)00112-9
- Hausmann, M., Waldie, K. E., Allison, S. D., Corballis, M. C. (2003c). Line bisection following hemispherectomy. *Neuropsychologia*, 41, 1523-1530.
 https://doi.org/10.1016/S0028-3932(03)00076-9
- Hausmann, M., Waldie, K.E., Corballis, M.C., 2003a. Developmental changes in line bisection: A result of callosal maturation? *Neuropsychology*, 17, 155-160. https://doi.org/10.1037/0894-4105.17.1.155
- Hausmann, M., Corballis, M.C., Fabri, M., 2003b. Line bisection in the split brain. *Neuropsychology*, 17, 602–609. https://doi.org/10.1037/0894-4105.17.4.602
- Heilman, K., Bowers, D., Watson, R., 1984. Pseudoneglect in a patient with partial callosal disconnection. *Brain*, 107, 519-532.
 https://doi.org/10.1093/brain/107.2.519
- Heilman, K.M., Van Den Abell, T., 1980. Right hemisphere dominance for attention:
 The mechanism underlying asymmetries of attention (neglect). *Neurology*, 30, 327–330. https://doi.org/10.1212/WNL.30.3.327

- Iacoboni, M., Zaidel, E., 1995. Channels of the corpus callosum: Evidence from simple reaction time to lateralized flashes in the normal and the split brain. *Brain*, 118, 779-788. https://doi.org/10.1093/brain/118.3.779
- Jeong, Y., Tsao, J.W., Efros, D.B., Heilman, K.M., 2006. Callosal Neglect in Hydrocephalus. *Neurocase*, 12(6), 346-349. https://doi.org/10.1080/13554790601100422
- Jewell, G., McCourt, M.E., 2000. Pseudoneglect: a review and meta-analysis of performance factors in line bisection task. *Neuropsychologia*, 38, 93-110. https://doi.org/10.1016/S0028-3932(99)00045-7
- Karnath, H.-O., Rorden, C., 2012. The anatomy of spatial neglect. *Neuropsychologia*, 50, 1010-1017. https://doi.org/10.1016/j.neuropsychologia.2011.06.027.
- Kashiwagi, A., Kashiwagi, T., Nishikawa, T., Tanabe, H., Okuda, J., 1990. Hemispatial neglect in a patient with callosal infarction. *Brain*, 113, 1005-1023. https://doi.org/10.1093/brain/113.4.1005
- Kerkhoff, G., 2001. Spatial hemineglect in humans. *Prog Neurobiol*, 63(1), 1–27. https://doi.org/10.1016/S0301-0082(00)00028-9
- LaMantia, A.S., Rakic, P., 1984. The number, size, myelination, and regional variation of axons in the corpus callosum and anterior commissure of the developing rhesus monkeys. *Soc Neurosci Abstracts*, 10, 1081.
- Learmonth, G., Gallagher, A., Gibson, J., Thut, G., Harvey, M., 2015. Intra- and intertask reliability of spatial attention measures in pseudoneglect. *PLoS ONE* 10(9): e0138379. https://doi.org/10.1371/journal.pone.0138379
- Mattingley, J.B., Berberovic, N., Corben, L., Slavin, M. J., Nicholls, M.E.R., Bradshaw, J.L., 2004. The greyscales task: a perceptual measure of attentional

bias following unilateral hemispheric damage. *Neuropsychologia*, 42, 387–394. https://doi.org/10.1016/j.neuropsychologia.2003.07.007

- Mattingley, J.B., Bradshaw, J.L., Nettleton, N.C., Bradshaw, J.A., 1994. Can task specific perceptual bias be distinguished from unilateral neglect. *Neuropsychologia*, 32, 805-817. https://doi.org/10.1016/0028-3932(94)90019-1
- Milner, A. D., Grechmann, M., Pagliarini, L. (1992). To halve or not to halve: an analysis of line bisection judgements in normal subjects. *Neuropsychologia*, 30(6), 515-526. https://doi.org/10.1016/0028-3932(92)90055-q
- Nicholls, M.E.R., Bradshaw, J.L., Mattingley, J.B., 1999. Free-viewing perceptual asymmetries for the judgement of shade, numerosity and size. *Neuropsychologia*, 37, 307-314. https://doi.org/10.1016/S0028-3932(98)00074-8
- Nicholls, M.E., Roberts, G.R., 2002. Can free-viewing perceptual asymmetries be explained by scanning, pre-motor or attentional biases? *Cortex*, 38(2), 113-136. https://doi.org/10.1016/S0010-9452(08)70645-2
- Oldfield, R.C., 1971. The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, 9, 97-113. https://doi.org/10.1016/0028-3932(71)90067-4
- Pinto, Y., Neville, D.A., Otten, M., Corballis, P.M., Lamme, V.A.F., de Haan, E.H.F.,
 2017a. Split brain: divided perception but undivided consciousness. *Brain*, 140,
 1231–1237. https://doi.org/10.1093/brain/aww358
- Pinto, Y., de Haan, E.H., Lamme, V.A.F., 2017b. The split-brain phenomenon revisited: a single conscious agent with split perception. *Trends Cogn Sci*, 21, 835–851. https://doi.org/10.1016/j.tics.2017.09.003

- Plourde, G., Sperry, R.W., 1984. Left hemisphere involvement in left spatial neglect from right-sided lesions. *Brain*, 107, 95-106. https://doi.org/10.1093/brain/107.1.95
- Roeltgen, M.G., Roeltgen, D.P., 1989. Development of attention in normal children: a possible corpus callosum effect. *Dev Neuropsychol*, 5, 127-139. https://doi.org/10.1080/87565648909540428
- Saj, A., Verdon, V., Hauert, C.-A., Vuilleumier, P., 2018. Dissociable components of spatial neglect associated with frontal and parietal lesions. *Neuropsychologia*, 115, 60-69. https://doi.org/10.1016/j.neuropsychologia.2018.02.021
- Schenkenberg, T., Bradford, D.C., Ajax, E.T., 1980. Line bisection and unilateral visual neglect in patients with neurological impairment. *Neurology*, 30, 509-517. https://doi.org/10.1212/WNL.30.5.509
- Verdon, V., Schwartz, S., Lovblad, K.O., Hauert, C.A., Vuilleumier P., 2010.
 Neuroanatomy of hemispatial neglect and its functional components: a study using voxel-based lesion-symptom mapping. *Brain*, 133 (3), 880–94.
 https://doi.org/10.1093/brain/awp305
- Volz, L.J., Hillyard, S.A., Miller, M.B., Gazzaniga, M.S., 2018. Unifying control over the body: consciousness and cross-cueing in split-brain patients. *Brain*, 141, 1-3. https://doi.org/10.1093/brain/awx359
- Weintraub, S., Mesulam, M.M., 1987. Right cerebral dominance in spatial attention. Further evidence based on ipsilateral neglect. *Arch Neurol,* 44, 621–625. https://doi.org/10.1001/archneur.1987.00520180043014

Weiss, L. G., Saklofske, D. H., Prifitera, A., Holdnack, J. A. (2006). WISC-IVAdvanced Clinical Interpretation. Practical Resources for the Mental HealthProfessional. Burlington (MA): Academic Press.