



# Geometry, landmarks and the cerebral hemispheres: 2D spatial reorientation in split-brain patients

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A right-hemispheric superiority in spatial encoding based on geometric cues has been largely documented in a variety of species, together with a left-hemispheric specialization for encoding based on landmarks. In humans, hemispheric asymmetries for spatial encoding have been little explored. In this study, we compared a patient with a complete callosal resection (D.D.C.) and a patient with a wide callosal resection saving the splenium (A.P.), with healthy participants. In two 2D versions of the 'reorientation task', participants were asked to find the target corner of a rectangle-shaped environment, by exploiting either geometric information alone or the combination of geometric and landmark information. In Experiment 1, the landmark consisted of a coloured side of the rectangle; in Experiment 2, this cue was replaced by a coloured disc located inside the rectangle. In both experiments, the rectangular shape ensured the geometric cue. D.D.C. was always unable to recall the target, whereas A.P. correctly solved the task when only the geometric information was available, without difference with respect to the controls. Importantly, the performance of A.P. did not differ from controls' when the right hemisphere was tested with the landmark cues (the task being carried out using the left hand), whereas when the left hemisphere was tested (right-hand session) his performance was worse than controls' with the coloured side of the space, but it was better than controls' with the coloured disc. The results are discussed comparing them with data collected on other species, and with theories of spatial processing.

The ability to recognize places or to orient in space is crucial for survival, and it has been widely shown that the hippocampal formation is the core area in which spatial coding occurs (see Hartley, Lever, Burgess, & O'Keefe, 2014). In this region, in fact, different types of 'spatial cells' have been identified (e.g., place cells, head direction cells, grid cells, and boundary cells), and it has been documented that they encode different parameters concerning spatial position and orientation. One of the most exploited paradigms in the investigation of spatial abilities is the 'reorientation task' proposed by Cheng (1986), in which the author showed that rats use exclusively geometric cues when reorienting to a target in an enclosed environment. In particular,

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when rats were trained to find food at one corner of a rectangle-shaped arena in which walls and corners contained featurally distinctive characteristics, following disorientation and reintroduction in the arena, they behaved as if these features were absent. In these circumstances, they search for the hidden food both at the correct corner and at its rotational equivalent, showing that they ignored non-geometric information during spatial reorientation. Moreover, spatial coding has been studied in a variety of animal species, including fish, birds, and even insects (e.g., Lee, Spelke, & Vallortigara, 2012; Lee, Vallortigara, Ruga, & Sovrano, 2012; Lee, Vallortigara, Flore, Spelke, & Sovrano, 2013; Sovrano, Potrich, & Vallortigara, 2013; for a review, see Tommasi, Chiandetti, Pecchia, Sovrano, & Vallortigara, 2012). The conclusion of this line of research was that a 'geometric module', sensitive to the overall shape of the environment, would support animals in spatial navigation, independently from non-geometric cues available in the environment. At an evolutionary level, this evidence was explained making reference to the fact that, for instance, although trees can change their colours or shapes from season to season (featural cues), their mutual spatial relationships remain the same along seasons (geometric cues), allowing animals to correctly orient in the environment. Evidence of a geometric module at the basis of spatial orientation was then shown also in humans, in children up to 3 years of age (e.g., Hermer & Spelke, 1996). This finding has been attributed to the development of linguistic skills: Language would be necessary for integrating both geometry and landmark information in an unequivocal symbolic representation (see also Cheng, Huttenlocher, & Newcombe, 2013; Gouteux, Vauclair, & Thinus-Blanc, 2001; Lingwood, Blades, Farran, Courbois, & Matthews, 2015), so much so that it has been found that even in 5- to 7-year-old children, the reorientation performance correlates with the ability in the production of phrases specifying exactly the information needed to solve the task (Hermer-Vazquez, Moffet, & Munkholm, 2001). However, this interpretation has been questioned more recently (Learmonth, Newcombe, & Huttenlocher, 2001), because similar results have been described also in 18-month-old children (Learmonth, Newcombe, Sheridan, & Jones, 2008). Moreover, it has been found that 3–5-year-old children do not use landmarks to reorient in a small space, but they can use these cues in a larger space (Learmonth, Nadel, & Newcombe, 2002).

Moreover, not all experimental results are in agreement with the existence of a geometric module (e.g., Twyman & Newcombe, 2010). Lee and Spelke (2010) suggested a distinction between the geometric module and a landmark system, responsible for a different kind of spatial cognition based on the encoding of small objects, starting from the evidence that when landmarks were present as discrete elements within the space, children were unable to use geometric cues to reorient, whereas when landmarks were placed flush with the walls, children correctly solved the task by encoding the surface geometry. Doeller, King, and Burgess (2008) investigated the neurophysiological bases of these systems in a fMRI paradigm: The authors asked participants to learn the location of objects in a virtual environment comprising a discrete landmark, a circular boundary, as well as distant cues, finding that the geometry-based trials activate the posterior hippocampus, whereas the landmark-based trials involve the dorsal striatum. Moreover, they added evidence that the two systems work independently of each other, in a parallel manner, and that the ventromedial prefrontal cortex mediates the behavioural responses based on their outputs. Similar results were also obtained by Wegman, Tyborowska, and Janzen (2014), confirming the association between hippocampal activation and geometry encoding based on the configuration of multiple objects, and that between caudate

activation and single landmark encoding. Importantly, the very existence of an encapsulated module devoted purely to geometric processing has been overstepped more recently, also by the original proponent (e.g., Cheng, 2008; Cheng & Newcombe, 2005), in favour of a milder model in which geometric and non-geometric cues are not entirely independent of each other.

Since the seminal discovery by Cheng, the way in which geometric and featural cues are processed has been investigated for decades (e.g., Cheng *et al.*, 2013), both in animals and in humans, using the original three-dimensional (3D) reorientation paradigm, but also virtual computerized 3D versions, as well as simplified two-dimensional (2D) versions of the task. For instance, Gouteux *et al.* (2001) confirmed the use of geometric strategies for space processing in children until 5 years of age, using a 3D model of a rectangular space instead of a real navigable room. Moreover, spatial skills in adult humans were also investigated by presenting 2D images of schematic rectangular spaces (e.g., Kelly & Spetch, 2004; Spetch, 1995; Spetch, Cheng, & MacDonald, 1996; Spetch *et al.*, 1997). In this regard, Kelly and Spetch (2004) found that adults were able to use both geometric and featural cues to reorient, but also that when the two types of information were in conflict with each other, the responses were mainly based on the featural cues (see also Sturz, Gaskin, & Bodily, 2013; Sturz & Kelly, 2013).

Vallortigara and his co-workers explored the possible cerebral asymmetries in this field in a series of studies involving domestic chicks undergoing temporary monocular occlusion, exploiting the almost complete contralateral projections of the avian visual system (Della Chiesa, Speranza, Tommasi, & Vallortigara, 2006; Tommasi & Vallortigara, 2001, 2004; Vallortigara, Pagni, & Sovrano, 2004). The authors trained and tested chicks in navigable enclosures with different sizes and shapes (geometric cues), and by inserting different landmarks in the enclosure (featural cues). They consistently found that during the testing phase, the chicks who had been trained with the left eye in use were better at encoding geometry, revealing a right-hemispheric superiority in geometry processing, whereas those who had been trained with the right eye in use were better at encoding featural information, showing a left-hemispheric superiority in the encoding of beacons. A similar hemispheric lateralization was also found in pigeons (Prior, Lingenauber, Nitschke, & Güntürkün, 2002) and in rats (LaMendola & Bever, 1997), and it was confirmed in chicks with unilateral or bilateral hippocampal lesions (Tommasi, Gagliardo, Andrew, & Vallortigara, 2003).

As regards humans, the study of hemispheric competencies is more complex than in birds, mainly because the cerebral hemispheres are strictly interconnected to one another, mainly by means of the *corpus callosum* (CC). However, a specific neurosurgical condition allows neuroscientists to test the skills of each 'disconnected' hemisphere, namely the surgical resection of the callosal fibres, in patients suffering strong forms of epilepsy (Corballis, 2015; Gazzaniga, 1967, 1995, 2005, 2011). In the domain of spatial processing, Corballis and co-workers have consistently found a right-hemispheric superiority in split-brain patients (Corballis, 2003; Corballis, Funnell, & Gazzaniga, 1999, 2002; Funnell, Corballis, & Gazzaniga, 1999), also showing that in these patients, the visual information concerning colour, size, and luminance was not transferred from one hemisphere to the other (Corballis & Corballis, 2001). Nevertheless, although the right-hemispheric superiority in space encoding has been found in healthy participants (Vogel, Bowers, & Vogel, 2003) and has been confirmed in split-brain patients, the paradigm of the spatial reorientation has never been tested with callosotomized patients, in any of its versions. Similarly, hemispheric differences in a reorientation task have not been previously investigated in healthy participants,

due to a methodological difficulty: Brain asymmetries in the visual modality in humans are mostly investigated by means of the tachistoscopic presentation of lateralized stimuli, but the need to encode space and relative distances between landmarks in a spatial reorientation paradigm requires a presentation time longer than that used during tachistoscopic paradigms. In this regard, Pizzamiglio, Guariglia, and Cosentino (1998) investigated the spatial abilities of right brain-damaged patients with and without hemispatial neglect both when only geometric information was available, and when a coloured wall was added in a navigable room. They found that all patients and controls carried out the tasks with a better performance than expected by chance, but also that the performance of neglect patients was worse than that of the other two groups, whereas no difference was found between healthy participants and right brain-damaged patients without hemineglect.

Starting from these assumptions, in the present study we used a 2D version of the spatial reorientation paradigm to investigate the geometric/non-geometric encoding abilities of each hemisphere in D.D.C., a patient with a total callosal resection, in A.P., a patient with a wide anterior callosal resection, and in healthy participants. The main aim of the study was to explore the performance of the disconnected hemispheres, and thus, a simplified 2D version of the paradigm was used, asking participants to use either the left or the right hand to provide the responses. We did not expect to find evidence of cerebral lateralization in healthy participants in this specific task, because the use of one hand does not allow us to test the unilateral spatial skill in the intact brain. Moreover, because the presentation was central, the main condition for testing lateralization in controls was not satisfied. Finally, starting from different results found in children depending on the fact that landmarks were discrete elements or were adjoined to geometric cues (Lee & Spelke, 2010), in two different experiments, we presented the featural cue either as a coloured side of the environment (as in 'classic' reorientation tasks), or as a discrete landmark contained in the 2D space. It has been shown, for instance, that children can use different features of the walls in order to distinguish the sides of a room (Wang, Hermer, & Spelke, 1999), whereas they fail in distinguishing them by means of freestanding objects located inside the same room (Hermer & Spelke, 1996). Starting from this evidence, we aimed at investigating the possible difference in hemispheric asymmetries concerning the processing of coloured sides of the space, on the one hand (Experiment 1), and discrete elements placed within the same space, on the other hand (Experiment 2). For both kinds of featural cues, we expected to find the same cerebral asymmetries. Specifically, starting from the evidence of a right-hemispheric superiority for geometry processing in humans, as well as in chicks undergoing unilateral lesion and eye occlusion, together with a left-hemispheric superiority in featural encoding in animals (Tommasi *et al.*, 2003; Vallortigara *et al.*, 2004), we hypothesized that a complete callosotomy could reveal a clear right-hemispheric superiority for geometry encoding and a possible left-hemispheric superiority for featural encoding. Thus, we expected to find a better performance when the total split-brain patient was asked to carry out the reorientation task with his left hand, when only geometric cues were available, and possibly to find a reversed better performance when he was asked to use the right hand to reorient in featural trials. Moreover, considering the neuroimaging evidence, we hypothesized that a partial callosotomy involving the anterior portion of the CC and saving the posterior projections could lead to similar results as those expected with healthy participants as regards geometric encoding, involving more posterior

cerebral areas (i.e., absence of hemispheric asymmetries), whereas we expected to find a possible left-hemispheric superiority in featural encoding in the partial split-brain patient (involving more anterior cerebral areas; Hartley, Maguire, Spiers, & Burgess, 2003; Doeller *et al.*, 2008; Wegman *et al.*, 2014). Furthermore, we administered the tasks to healthy participants in order to have the possibility to compare the performance of the patients with that of a control group.

## EXPERIMENT I

In the first experiment, two callosotomized patients and a control group were presented with the image of a rectangular space (geometric cue) which could also contain a landmark consisting of a coloured side (featural cue). In the training phase, one of the corners was marked as the ‘target corner’ by presenting a red disc placed at that corner; in the testing phase, the task consisted in identifying the target corner (the red disc having been removed). Between the two phases, the spatial orientation of the rectangle was changed, and a blank screen was presented: These manipulations ensured a condition of spatial ‘disorientation’. Cerebral asymmetries were investigated by asking participants to point at the target corner of the figure, using either the left hand or the right hand, in two separate sessions. Due to the contralateral organization of the motor pathways in humans, the use of one hand in split-brain patients ensures contralateral hemispheric involvement (e.g., Gazzaniga, 1967; Levy, Trevarthen, & Sperry, 1972). Moreover, as it was previously shown that in the 3D version of the reorientation task, males perform better than females, but no difference in performance emerged between younger and older participants (Picucci, Caffo, & Bosco, 2009), sex but not age was matched between patients and controls.

## Materials and methods

### Participants

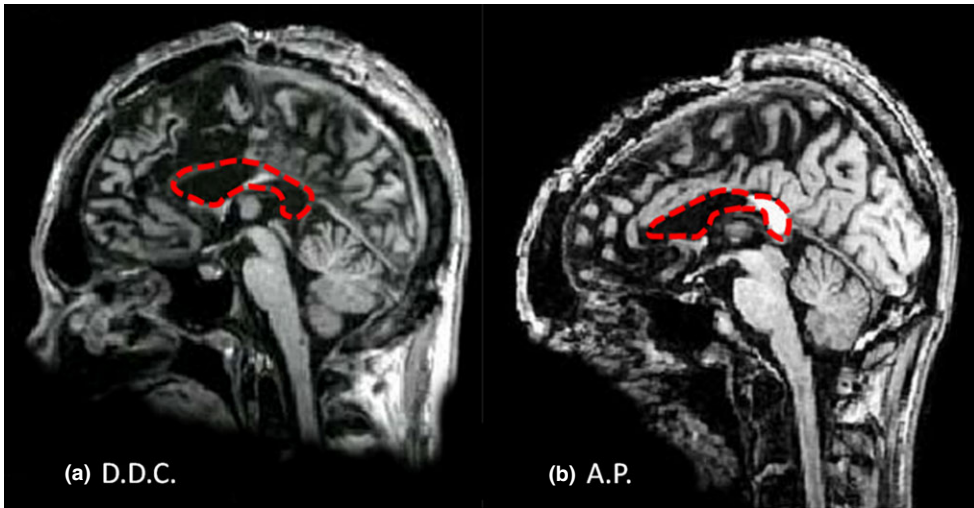
#### Patients

The experiment was administered to D.D.C., a patient with a total resection of the CC, and A.P., a patient with a large anterior resection of the CC.

D.D.C. is an Italian man, 35-year-old at the time of the test, who had the CC completely sectioned due to pharmacologically intractable epilepsy. He underwent a first partial resection of the CC in 1994, when he was 18 years old, and the complete resection in 1995; also the anterior commissure was partially sectioned (Figure 1a). As reported in previous studies (e.g., Fabri *et al.*, 2006), D.D.C.’s post-operative IQ was 83, as measured by means of the Wechsler Adult Intelligence Scale (WAIS), and his laterality quotient was +40, according to the Edinburgh Handedness Inventory (Oldfield, 1971). D.D.C. referred that he wrote with his left hand until he was 10, and then, he was forced to use the right hand.

A.P. is an Italian man, 47-year-old at the time of the test, who underwent the surgical resection of a large anterior portion of the CC in an attempt to reduce the spread of epileptic seizures. The surgery was carried out in 1993, when he was 28 years old, and it left intact only the splenium (Figure 1b). A.P.’s post-operative IQ was 87, as measured by means of the WAIS, and his laterality quotient was +10 (see Fabri *et al.*, 2006), according to the Edinburgh Handedness Inventory (Oldfield, 1971).

Both patients had no visual impairments or psychiatric symptoms.



**Figure 1.** Midsagittal MRI of patients: D.D.C.'s brain, showing the complete absence of callosal fibres (panel on the left), and A.P.'s brain, showing the callosal section which saves the splenium (panel on the right).

### *Controls*

The control group was composed of 16 self-reported right-handed males (age:  $22.06 \pm 0.79$  years) with normal or corrected-to-normal vision, free from neurological or psychiatric histories.

Informed consent was obtained from all participants prior to the beginning of the task, and the experimental procedures were conducted in accordance with the guidelines of the Declaration of Helsinki.

### *Stimuli*

The stimuli used in any single trial consisted of two images of a rectangle, one presented during the training phase of the trial and one during its testing phase. All rectangles were drawn by using the software Microsoft PowerPoint 2007 (Microsoft Corp., Redmond, WA, USA) and encompassed a white area measuring  $6 \times 12$  cm (height  $\times$  width;  $3.43 \times 6.86$  degrees of visual angle, seen at a distance of 72 cm, on a screen with a resolution of  $1280 \times 768$  pixels). The perimeter of the rectangle could be constituted either by four black sides (in the 'geometry-based trials') or by three black sides and one green side (in the 'geometry + landmark-based trials'). The green side constituted a 'landmark' and it could be one of the four sides of the area (randomly assigned: 25% for each side). In the rectangle presented during the training phase, one 'target corner' was marked by a red disc positioned in a corner. In 50% of the trials, the disc was placed between a short side on the left and a long side on the right, and in the other 50% of the trials, it was placed between a long side on the left and a short side on the right. The rectangle presented during the testing phase was the same as that presented during the training phase, but did not contain any disc.

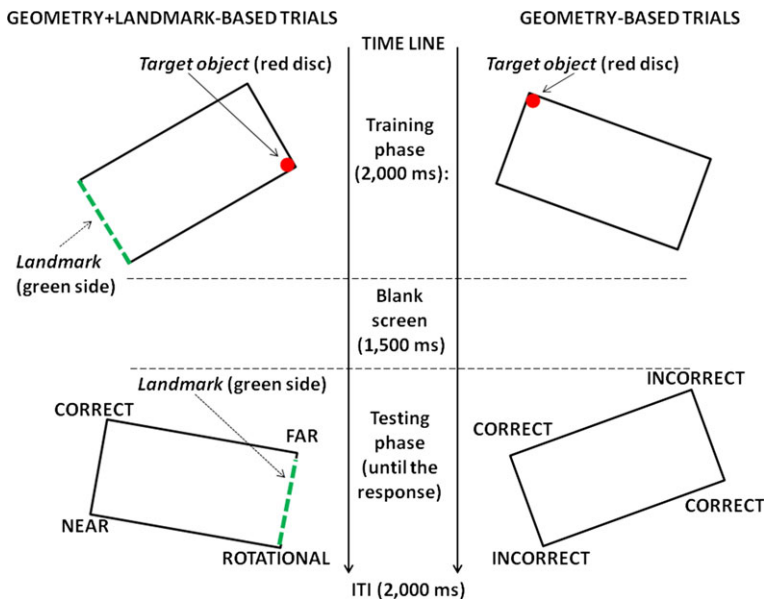
### *Procedure*

The paradigm was composed of two sessions comprising 48 trials. Each trial started with the training phase, in which the rectangle was presented in the centre of the screen for

2,000 ms and it was followed by a blank screen lasting 1,500 ms. In the following testing phase, the rectangle was presented again, as if it had been rotated with respect to the training phase. The image remained on the screen until the participant gave the response, and the next trial started after 2,000 ms from the response (ITI). In the training phase of the geometry + landmark-based trials, both the landmark and the target object (the red disc indicating the target corner) were present; in the training phase of the geometry-based trials, only the target object was present. In the testing phase of all trials, the target object was absent. Between training and testing phases, the spatial orientation of the rectangle changed invisibly to participants (Figure 2).

The starting orientation of the rectangle in the training phase was pseudo-randomized between  $15^\circ$  and  $180^\circ$  ( $0^\circ$  is referred to the position in which the rectangular shape is presented with the longer sides parallel to the horizontal axis), with steps of  $15^\circ$ , for a total of 24 possible starting positions. The starting orientation of the rectangle in the testing phase was obtained by adding a rotation to the starting position used in the training phase. The spatial rotation in the testing phase was pseudo-randomized within two ranges: from  $62^\circ$  to  $117^\circ$  and from  $242^\circ$  to  $297^\circ$  (step:  $5^\circ$ ) for a total of 24 possible rotations (12 within the first range and 12 within the second range).

Participants were asked to sit up straight in front of the computer screen, to maintain their gaze on it, and to avoid crossing either legs or arms. The instructions were presented on the computer screen, and then they were repeated verbally. Participants were informed that during the task, they would be required to use one hand to point at the target corner of the rectangle in the testing phase, defined as the corner in which the red disc had been presented during the training phase. Participants were tested individually in two sessions of 48 trials each. In a session, they were asked to respond using the right hand, and in the other session, they were asked to respond using the left hand (participants were asked to use the index finger of the left/right hand to physically point at



**Figure 2.** Schematic representation of geometry + landmark-based trials (on the left) and geometry-based trials (on the right) in Experiment 1.

the target corner on the computer screen). A.P. and eight healthy participants started with the left-hand session, D.D.C. and the remaining eight participants started with the right-hand session. During the task, the experimenter – positioned behind the participant – recorded the participant's responses and controlled the paradigm using a wireless mouse (after recording the participant's response on a sheet, a mouse click allowed the beginning of the following trial).

Participants were informed that the rectangle would be rotated between the training and the testing phases, either clockwise or counterclockwise. They were also informed that they could take all the time they needed to carry out each trial, without time limits, but they were asked to avoid talking and moving during each session, that lasted around 10 min.

Prior to the beginning of the experiment, four trials (two geometry-based trials and two geometry + landmark-based trials) were presented to familiarize with the task. The geometry-based trials and the geometry + landmark-based trials were both present in each experimental session, and their presentation order was pseudo-randomized within and between sessions. The paradigm was controlled by means of E-Prime software (Psychology Software Tools Inc., Pittsburgh, PA, USA).

## Results

In the geometry-based trials, a response was decoded as 'Correct corner' when participants pointed at both the correct target corner and the corner diagonally opposed to the correct target corner (Rotational corner); otherwise, the responses were decoded as 'Incorrect corner' (see Figure 2). In the geometry + landmark-based trials, the responses were decoded as: (1) 'Correct corner' when participants pointed at the target corner; (2) 'Near corner' when they pointed at the corner separated from the correct corner by the shorter side of the rectangle; (3) 'Far corner' when they pointed at the corner separated from the correct corner by the longer side of the rectangle; and (4) 'Rotational corner' when they pointed at the corner diagonally opposed to the correct corner (see Figure 2).

For both geometry-based and geometry + landmark-based trials, the frequency of each category of responses was computed for the left-hand session and for the right-hand session, separately. Table 1 shows the performance of control participants, D.D.C., and A.P.

### Control group

The mean number of responses for each category collected from the control group was transformed in percentage of response for each category, considering the left-hand session and the right-hand session separately. To compare the performance of participants in the two sessions, the percentage of each category of response collected in the left-hand session was compared with the percentage of the same category of response collected in the right-hand session, by means of *t*-tests: No significant differences were found according to the hand used (*t*-values comprised between  $-1.92$  and  $0.97$ ,  $p > .074$  for all comparisons).

Thus, the percentages of correct responses in both sessions were collapsed (left hand and right hand) and the resulting percentage was compared to the overall percentage of incorrect responses by means of *t*-tests. The results were significant both for the



**Table 1.** Frequencies (and percentages) of responses in Experiment 1 for the control group, D.D.C. (complete callosotomy), and A.P. (partial callosotomy), in geometry-based trials and in geometry + landmark-based trials, for the left-hand session (columns on the left) and for the right-hand session (columns on the right)

Trials	Corner	Left-hand session			Right-hand session		
		Control group	D.D.C.	A.P.	Control group	D.D.C.	A.P.
Geometry + Landmark	Correct	17.5 (72.92%)	8 (33.33%)	15 (62.5%)	16.68 (69.53%)	4 (16.67%)	11 (45.83%)
	Near	2.87 (11.98%)	9 (37.5%)	1 (4.17%)	2.87 (11.98%)	7 (29.17%)	3 (12.5%)
	Far	2.68 (11.2%)	6 (25%)	7 (29.16%)	3.5 (14.58%)	8 (33.33%)	6 (25%)
Geometry	Rotational	0.93 (3.9%)	1 (4.17%)	1 (4.17%)	0.93 (3.91%)	5 (20.83%)	4 (16.67%)
	Correct	18.37 (76.56%)	13 (54.17%)	16 (66.67%)	17.75 (73.95%)	12 (50%)	15 (62.5%)
	Incorrect	5.62 (23.44%)	11 (45.83%)	8 (33.33%)	6.25 (26.05%)	12 (50%)	9 (37.5%)

geometry + landmark-based trials, Correct:  $71.22 \pm 4.38$ , Incorrect:  $28.76 \pm 4.38$ ;  $t(15) = 4.85$ ,  $p < .001$ , and for the geometry-based trials, Correct:  $75.26 \pm 3.85$ , Incorrect:  $24.74 \pm 3.85$ ;  $t(15) = 6.55$ ,  $p < .001$ , showing that participants carried out the task with success. These results were also confirmed by means of single sample  $t$ -tests carried out comparing the percentage of correct responses against the chance response level for geometry + landmark-based trials, reference value: 25%;  $t(15) = 10.55$ ,  $p < .001$ , and for geometry-based trials, reference value: 50%;  $t(15) = 6.55$ ,  $p < .001$ .

#### D.D.C

A binomial distribution analysis revealed that D.D.C.'s responses were given at chance level, except for Rotational corner responses given using the left hand in the geometry + landmark-based trials, that were less frequent than expected by chance (see Table 2a). Moreover, chi-square tests were used to compare the frequency of each category of response by D.D.C. between the left-hand session and the right-hand sessions. Results revealed that there were no differences between the left-hand and the right-hand sessions (see Table 2b).

#### A.P

A binomial distribution analysis revealed that A.P.'s responses were not given at chance level in the left-hand session in both types of trials: The patient gave a higher number of Correct corner responses and a lower number of Incorrect responses than expected by chance, with the exception of Far corner responses in the geometry + landmark-based condition (see Table 3a). On the contrary, in the right-hand session, A.P.'s responses were given at chance level, with the exception of Correct corner responses in the geometry + landmark-based trials, that were higher than expected by chance (Correct corner responses in the geometry-based trials approached statistical significance; see Table 3a). Furthermore, chi-square tests were carried out to compare the frequency of each category of response between the left-hand session and the right-hand session. Results showed that there were no differences between the left-hand and the right-hand sessions (see Table 3b).

**Table 2.** Results of patient D.D.C. in Experiment I for each category of response. G + L: geometry + landmark-based trials; G: geometry-based trials. The first two columns show the significance level of the binomial test (LH: left-hand session; RH: right-hand session). The last two columns show the chi-square values and the associated significance levels for the comparisons between the left-hand and the right-hand sessions, in each category of response. Italics shows the significant results

D.D.C.	(a) Binomial distribution		(b) Chi-square	
	LH <i>p</i> -value	RH <i>p</i> -value	LH versus RH Chi-square	LH versus RH <i>p</i> -value
G + L: Correct	.112	.132	1.333	.248
G + L: Near	.066	.159	0.25	.617
G + L: Far	.185	.112	0.285	.592
G + L: Rotational	.008	.175	2.666	.102
G: Correct	.149	.161	0.04	.841
G: Incorrect	.149	.161	0.043	.834

**Table 3.** Results of patient A.P. in Experiment 1 for each category of response. G + L: geometry + landmark-based trials; G: geometry-based trials. The first two columns show the significance level of the binomial test (LH: left-hand session; RH: right-hand session). The last two columns show the chi-square values and the associated significance levels for the comparisons between the left-hand and the right-hand sessions, in each category of response. Italics shows the significant results

	(a) Binomial distribution		(b) Chi-square	
	LH <i>p</i> -value	RH <i>p</i> -value	LH versus RH Chi-square	LH versus RH <i>p</i> -value
A.P.				
G + L: Correct	<i>&lt;.001</i>	<i>.014</i>	0.615	.432
G + L: Near	.008	.075	1	.317
G + L: Far	.159	.185	0.077	.781
G + L: Rotational	.008	.132	1.8	.179
G: Correct	.044	.078	0.032	.857
G: Incorrect	.044	.078	0.058	.808

### Control group versus patients

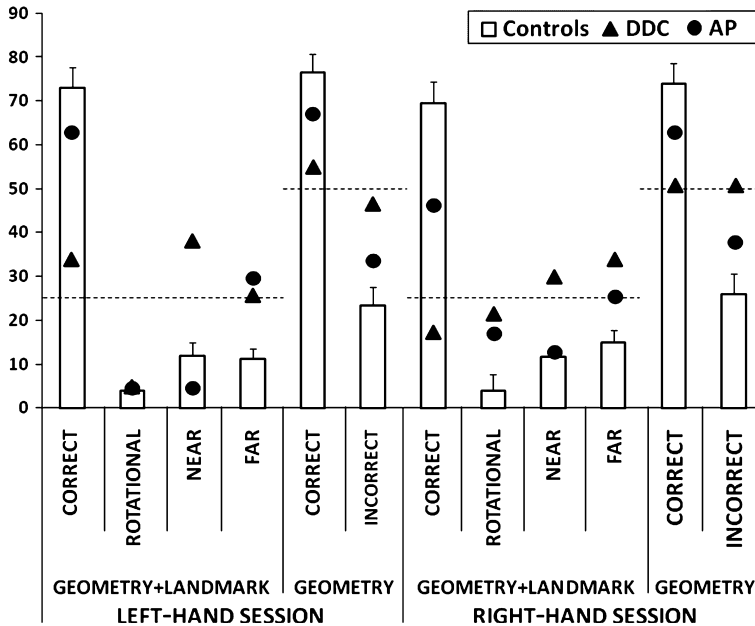
The percentages of each category of response collected from the control group in each session were compared with those of D.D.C. and A.P., by means of two separate series of exact *t*-tests, using the percentage of response by the patient as a reference value. The results were corrected for multiple comparisons by means of Bonferroni correction considering the two sessions separately (significant threshold:  $p = .008$ ).

The results showed that healthy participants gave more Correct corner responses and less Incorrect responses than D.D.C. for all of the categories of response, in both sessions (*t*-values comprised between  $-9.39$  and  $10.99$ ,  $p < .001$  for all comparisons), except for Rotational corner responses in the geometry + landmark-based trials using the left hand,  $t(15) = 0.14$ ,  $p = .892$  (see Figure 3).

With respect to A.P., healthy participants gave more Correct corner responses,  $t(15) = 4.93$ ,  $p < .001$ , and less Rotational,  $t(15) = -7.08$ ,  $p < .001$ , and Far corner responses,  $t(15) = -3.67$ ,  $p = .002$ , in geometry + landmark-based trials using the right hand; they gave less Far corner responses in the left-hand session,  $t(15) = -7.79$ ,  $p < .001$ . The comparisons concerning the other response categories did not reach statistical significance (*t*-values comprised between  $-2.54$  and  $2.75$ , Figure 3).

### Discussion

The first main result of Experiment 1 is that the patient with the complete callosotomy, D.D.C., failed to correctly carry out the task: Apparently, the complete hemispheric disconnection prevents the possibility of spatial encoding based upon both geometric and non-geometric cues in the 2D version of the reorientation task. This speculation has to be considered together with previous evidence of preserved performance by the same patient in a different set of spatial tasks (normal-backward discrimination task; as measured by Corballis *et al.*, 2010), showing that the results obtained in the present study are not indicative of a generalized spatial deficit in D.D.C. On the other hand, however, the patient with a wide but incomplete callosotomy (saving the most posterior interhemispheric connections), A.P., revealed residual abilities of spatial encoding. In fact, although the direct comparisons between



**Figure 3.** Results of Experiment I: percentage of each category of response for the left-hand session (on the left) and for the right-hand session (on the right), in geometry + landmark-based trials and in geometry-based trials. Columns represent the results of healthy participants (bars show standard errors), triangles represent the results of D.D.C., and circles represent the results of A.P. Dashed lines represent chance levels (25% for the geometry + landmark-based trials, and 50% for the geometry-based trials).

his results in the two sessions (left vs. right hand) did not show statistical differences, the performance of A.P. was higher than that expected by chance for all of the response categories in both the geometry + landmark-based trials and the geometry-based trials, in the left-hand session (with the only exception of the Far corner response). It has to be noted that also the Correct corner responses in the right-hand session were higher than chance in the geometry + landmark-based trials (and a non-significant trend in this direction can be noticed also in the geometry-based trials). Moreover, also the other conditions approach statistical significance ( $p < .19$  in all of the conditions, in both sessions) and this pattern of results can explain the absence of a significance difference between the left- and right-hand sessions. However, the comparison between his performance and that of healthy participants revealed that the control group had a better performance than A.P. in the Correct corner responses of the geometry + landmark-based trials in the right-hand session, as well as in the Far corner responses in both the left- and the right-hand sessions, whereas its performance did not differ from A.P.'s in the geometry-based trials carried out with both hands, and in the geometry + landmark-based trials carried out with the left hand. These results show that both cerebral hemispheres can solve the spatial reorientation based upon geometric processing and that the right hemisphere can also exploit a spatial encoding based upon featural cues (the left hemisphere showing more difficulties in this latter task). Finally, the control group did not show hemispheric asymmetries neither in the local-based trials, nor in the geometry-based trials.

## EXPERIMENT 2

A number of studies have shown that the processing of a single object placed inside an environment involves different cerebral areas than other types of non-geometric cues, such as coloured walls. For instance, in rodents it was found that the caudate nucleus is activated when objects are used as beacons and discrete landmarks (McDonald & White, 1994; Packard & McGaugh, 1996). Moreover, it has also been added that this activity is independent of hippocampal activity, as hippocampal lesions were shown not to influence the performance in this task (Pearce, Roberts, & Good, 1998; see also Mayer, Pecchia, Bingman, Flore, & Vallortigara, 2016). Importantly, a number of studies involving different species revealed an opposite hemispheric dominance for encoding geometric cues or discrete objects in reorientation tasks, with the right hemisphere being superior in geometry analysis and the left hemisphere being superior in navigation based upon discrete landmarks (Della Chiesa *et al.*, 2006; LaMendola & Bever, 1997; Prior *et al.*, 2002; Tommasi & Vallortigara, 2001, 2004; Tommasi *et al.*, 2003; Vallortigara *et al.*, 2004). To our knowledge, however, there is no evidence of human cerebral lateralization in this domain, and the aim of the present study was exactly to fill this gap and to compare the possible cerebral asymmetries in humans with those previously shown in other species, by presenting callosotomized patients and healthy controls with a modified version of the reorientation task used in Experiment 1. In this new task, a landmark was present in the 2D space, and it was located either in the centre of the space (thus not adding information with respect to the geometric information constituted by the shape of the environment, in the geometry-based trials), or in a different position with respect to the centre (thus constituting a landmark potentially useful to reorient, in the geometry + landmark-based trials). Starting from the results of the previous experiment, we expected to confirm the ability of the right hemisphere of the partially callosotomized patient to correctly carry out both the geometric and the geometry + landmark-based trials, and we hypothesized a left-hemispheric superiority when the landmark was available, based on the evidence coming from animals.

## Materials and methods

### *Participants*

The experiment was administered to patients D.D.C. (total callosotomy) and A.P. (large anterior callosotomy), and to a control group of 16 healthy participants who did not take part in Experiment 1. All healthy participants (age:  $24.44 \pm 1.4$  years) were male and right-handed, as self-reported, with normal or corrected-to-normal vision, free from neurological or psychiatric histories.

Informed consent was obtained by all participants prior to the beginning of the task, and the experimental procedures were conducted in accordance with the guidelines of Declaration of Helsinki.

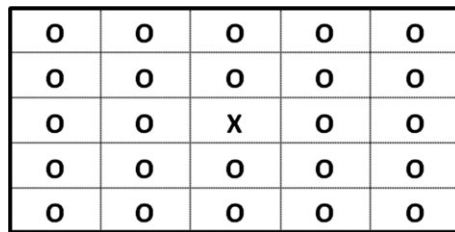
### *Stimuli and procedure*

The same stimuli as those described in Experiment 1 were used in this experiment, with two differences: (1) in the 'geometry + landmark-based trials', the landmark consisted of a green disc located in the rectangle at a number of possible positions excluding the centre. The landmark was present in the training phase, and it remained in the same position in the testing phase. Moreover, (2) in the geometry-based trials a centrally located landmark

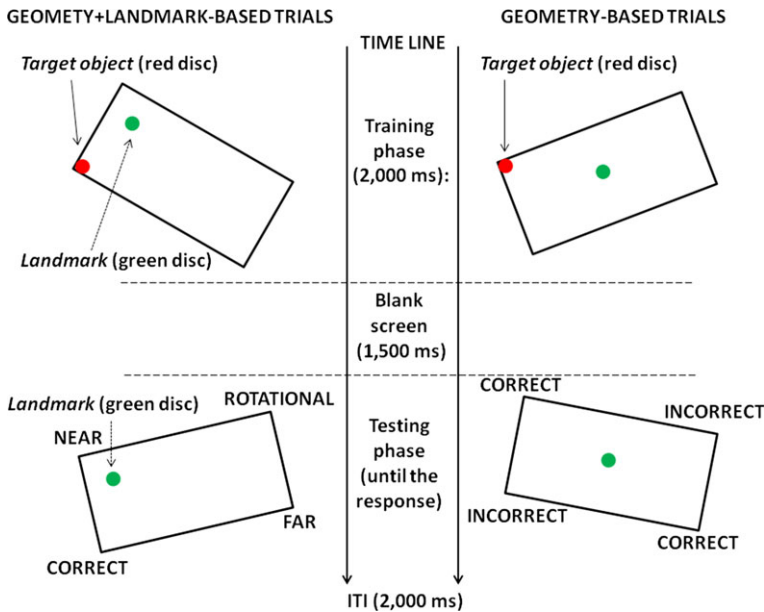
was present in the training phase and in the testing phase. The paradigm comprised 48 trials, of which 24 geometry-based trials with the central landmark, and 24 geometry + landmark-based trials with the landmark located in one of the 24 positions corresponding to the centres of a 5 × 5 grid subdividing the rectangle (Figure 4), and excluding the central position (see Figure 5).

The same procedure as in Experiment 1 was used, participants being asked to indicate the target corner using the left hand and the right hand, in two separate sessions. D.D.C. and eight healthy participants started with the left-hand session, and A.P. and the remaining eight participants started with the right-hand session.

Prior to the beginning of the experiment, four trials (two geometry-based trials and two geometry + landmark-based trials) were presented to familiarize with the task. The presentation order of the trials was pseudo-randomized within and between sessions.



**Figure 4.** Stimulus preparation for Experiment 2: in the geometry + landmark-based trials, the landmark could be positioned in any of the 24 cells in which the rectangle was subdivided, with the exception of the central cell (cross), which was used in the geometry-based trials.



**Figure 5.** Schematic representation of geometry + landmark-based trials (on the left) and geometry-based trials (on the right) in Experiment 2.

## Results

Data were analysed as in Experiment 1. Table 4 shows the performance of control participants, A.P., and D.D.C.

### Control group

To compare the performance of control participants in the two sessions, the percentage of each category of response collected in the left-hand session was compared to the percentage of the same category of response collected in the right-hand session, by means of *t*-tests: No significant differences were found according to the hand used (*t*-values comprised between  $-0.96$  and  $2.08$ ,  $p > .055$  for all comparisons).

The percentages of correct responses in the left- and right-hand sessions were collapsed, and the resulting percentage was compared to the overall percentage of all of the other (incorrect) categories of response, by means of *t*-tests. The results were significant both for the geometry + landmark-based trials, Correct:  $80.86 \pm 2.98$ , Incorrect:  $19.14 \pm 2.98$ ;  $t(15) = 10.36$ ,  $p < .001$ , and for the geometry-based trials, Correct:  $80.99 \pm 3.85$ , Incorrect:  $19.01 \pm 3.85$ ;  $t(15) = 8.05$ ,  $p < .001$ , confirming that participants carried out the task successfully. These results were also confirmed by means of exact *t*-tests carried out comparing the percentage of correct responses against the chance response level for the geometry + landmark-based trials, reference value: 25%;  $t(15) = 18.76$ ,  $p < .001$ , and for the geometry-based trials, reference value: 50%;  $t(15) = 8.05$ ,  $p < .001$ .

### D.D.C

A binomial distribution analysis revealed that D.D.C.'s responses did not differ from chance, except for Correct corner responses in the geometry + landmark-based trials of the left-hand session, that were given more frequently than expected by chance (see Table 5a). Moreover, chi-square tests were used to compare the frequency of each category of response by D.D.C. in the left-hand session and in the right-hand session. Results revealed that there were no differences between the left-hand and the right-hand sessions (see Table 5b).

### A.P

A binomial distribution analysis revealed that A.P.'s responses were not given at chance levels (see Table 6a): The patient gave a higher number of Correct responses and a lower number of Incorrect responses than expected by chance, except for Near corner and Far corner responses in the left-hand session which failed to differ from chance. Furthermore, chi-square tests were used to compare the frequency of each category of response between the left-hand session and the right-hand session. Results showed that there were no differences between the left-hand and the right-hand sessions (see Table 6b).

### Control group versus patients

The percentages of each category of response collected from the control group in each session were compared with those of D.D.C. and A.P. by means of two separate series of exact *t*-tests, using the percentage of response by the patient as a reference value. The

**Table 4.** Frequencies (and percentages) of responses in Experiment 2 for the control group, D.D.C. (complete callosotomy), and A.P. (large anterior callosotomy), in geometry + landmark-based trials and in geometry-based trials, for the left-hand session (columns on the left) and for the right-hand session (columns on the right)

Trials	Corner	Left-hand session			Right-hand session		
		Control group	D.D.C.	A.P.	Control group	D.D.C.	A.P.
Geometry + Landmark	Correct	19.37 (80.73%)	13 (54.17%)	18 (75%)	19.44 (80.99%)	6 (25%)	22 (91.67%)
	Near	1.93 (8.07%)	4 (16.67%)	3 (12.5%)	2.18 (9.11%)	7 (29.17%)	2 (8.33%)
	Far	1.5 (6.25%)	4 (16.67%)	3 (12.5%)	1.5 (6.25%)	6 (25%)	0 (0%)
Geometry	Rotational	1.18 (4.95%)	3 (12.5%)	0 (0%)	0.87 (3.65%)	5 (20.83%)	0 (0%)
	Correct	19.75 (82.29%)	13 (54.17%)	19 (79.17%)	19.12 (79.69%)	11 (45.83%)	21 (87.5%)
	Incorrect	4.25 (17.71%)	11 (45.83%)	5 (20.83%)	4.87 (20.31%)	13 (54.17%)	3 (12.5%)



**Table 5.** Results of patient D.D.C. in Experiment 2 for each category of response. G + L: geometry + landmark-based trials; G: geometry-based trials. The first two columns show the significance level of the binomial test (LH: left-hand session; RH: right-hand session). The last two columns show the chi-square values and the associated significance levels for the comparisons between the left-hand and the right-hand sessions, in each category of response. Italics shows the significant results

D.D.C.	(a) Binomial distribution		(b) Chi-square	
	LH <i>p</i> -value	RH <i>p</i> -value	LH versus RH Chi-square	LH versus RH <i>p</i> -value
G + L: Correct	<i>.001</i>	.185	2.578	.108
G + L: Near	.132	.159	0.818	.365
G + L: Far	.132	.185	0.4	.527
G + L: Rotational	.075	.175	0.5	.479
G: Correct	.149	.149	0.166	.683
G: Incorrect	.149	.149	0.166	.683

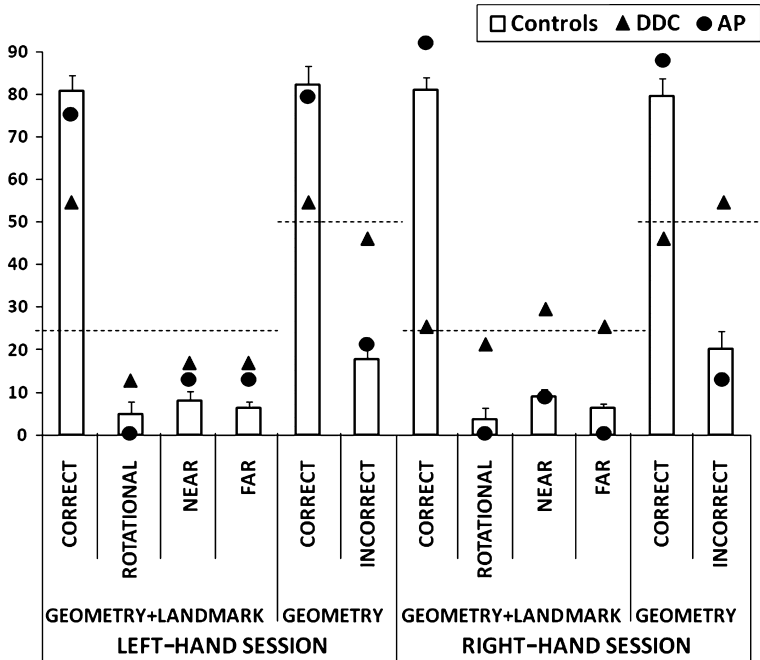
**Table 6.** Results of patient A.P. in Experiment 2 for each category of response. G + L: geometry + landmark-based trials; G: geometry-based trials. The first two columns show the significance level of the binomial test (LH: left-hand session; RH: right-hand session). The last two columns show the chi-square values and the associated significance levels for the comparisons between the left-hand and the right-hand sessions, in each category of response. Italics shows the significant results

A.P.	(a) Binomial distribution		(b) Chi-square	
	LH <i>p</i> -value	RH <i>p</i> -value	LH versus RH Chi-square	LH versus RH <i>p</i> -value
G + L: Correct	<i>&lt;.001</i>	<i>&lt;.001</i>	0.4	.527
G + L: Near	.075	.031	0.2	.654
G + L: Far	.075	.001	3	.083
G + L: Rotational	.001	.001	0	1
G: Correct	.002	<i>&lt;.001</i>	0.1	.752
G: Incorrect	.002	<i>&lt;.001</i>	0.5	.479

results were corrected for multiple comparisons by means of Bonferroni correction considering the two sessions separately (significant threshold:  $p = .008$ ).

The results showed that healthy participants gave more Correct responses and less Incorrect responses than D.D.C. for all of the categories of response, in both sessions and with both types of trials, left hand, Near corner:  $t(15) = 4.31$ ,  $p < .001$ ; all other conditions:  $t$ -values comprised between  $-18.62$  and  $19.85$ ,  $p < .001$ , except for Rotational corner responses in the geometry + landmark-based trials using the left hand,  $t(15) = -2.80$ ,  $p = .013$  (Figure 5).

Moreover, healthy participants gave less Correct corner,  $t(15) = -3.78$ ,  $p = .002$ , and more Far corner responses,  $t(15) = 6.21$ ,  $p < .001$ , than A.P. in the geometry + landmark-based trials using the right hand, and they made less Far corner errors than A.P. using the left hand in the geometry + landmark-based trials,  $t(15) = -4.39$ ,  $p < .001$ . The comparisons concerning the other response categories did not reach statistical significance ( $t$ -values comprised between  $-2.22$  and  $1.83$ ,  $p > .042$ ; Figure 6).



**Figure 6.** Results of Experiment 2: percentage of each category of response for the left-hand session (on the left) and for the right-hand session (on the right), in geometry + landmark-based trials and in geometry-based trials. Columns represent the results of healthy participants (bars show standard errors), triangles represent the results of D.D.C., and circles represent the results of A.P. Dashed lines represent chance levels (25% for the geometry + landmark-based trials, and 50% for the geometry-based trials).

## Discussion

The results of Experiment 2 confirmed that the complete hemispheric disconnection seems to impair spatial reorientation in the 2D version of the task here adopted: the responses of D.D.C. did not differ from chance levels, with the exception of the Correct corner response for the geometry + landmark-based trials in the left-hand session. If this result seems to suggest a right-hemispheric residual ability to solve the reorientation task when a discrete landmark is present, the comparison between the patient's and the control group's results revealed that the performance of D.D.C. was anyway worse than that of controls. As in Experiment 1, in the present task the control group did not show any difficulty in solving the task, and did not reveal hemispheric asymmetries. However, the really surprising results are those of A.P.: His performance confirmed that the partially disconnected hemispheres are capable to solve the 2D reorientation task; in fact, the results of A.P. are better than those expected by chance both in geometry-based and in geometry + landmark-based trials (with the exception of Far and Near corner responses in the left-hand session, which nevertheless approached statistical significance). Importantly, the performance of A.P. was not worse than that of the control group in all conditions except for the Far corner responses of the geometry + landmark-based trials carried out with the left hand, revealing an overall bilateral hemispheric ability to reorient based upon both geometry and landmarks (as found in healthy participants). Notably, his performance was even better than that of controls for the

geometry + landmark-based trials in the right-hand session (left hemisphere), for the Correct corner and Far corner responses.

## GENERAL DISCUSSION

To our knowledge, no previous studies in humans investigated hemispheric asymmetries during reorientation at a behavioural level, but the literature on animals allowed us to predict a right-hemispheric superiority in geometric encoding, as opposed to a left-hemispheric superiority in featural encoding (Della Chiesa *et al.*, 2006; Prior *et al.*, 2002; Tommasi & Vallortigara, 2001). We did not find hemispheric asymmetries in the control groups in any of the two experiments. We evaluated hemispheric asymmetries by asking participants to point the correct corner using either the left hand (right hemisphere), or the right hand (left hemisphere): We did not expect to observe cerebral lateralization in this task in healthy participants, because the use of one hand does not ensure a selective contralateral activation in the case of complete interhemispheric connections. However, the data collected with the control groups allowed us to compare the results obtained with the callosotomized patients. To this aim, we tested the patient D.D.C., with a complete interhemispheric disconnection, and the patient A.P., with a callosal disconnection saving the posterior portion of the CC: In both patients, the anterior cortices, including motor areas, were disconnected, allowing us to assume the use of one hand as a tool to investigate the 'response' of the contralateral hemisphere, in accordance with previous studies involving split-brain patients (e.g., Gazzaniga, 1967; Levy *et al.*, 1972). Whereas D.D.C. had an overall worse performance than the controls in both tasks and with both hands, the results of A.P. revealed that the intact splenium was sufficient for each hemisphere to solve the spatial task based only on the geometric cues (his scores were not statically different from those of the controls in the geometry-based trials, in both experiments). Moreover, the performance of A.P. did not differ from that of the controls in the geometry + landmark-based trials of both experiments using the left hand, confirming the ability of the partially disconnected right hemisphere to reorient on the basis of the a coloured side (Experiment 1) and an internal landmark (Experiment 2). Importantly, his performance deviated from that of the controls in the geometry + landmark-based trials only for the right-hand session in both experiments. In particular, in Experiment 1, in which the non-geometric cue was constituted by a coloured side of the rectangular shape, A.P. was unable to solve the task, and he made more errors and gave less correct responses than the controls; but in Experiment 2, in which the non-geometric cue was constituted by an internal landmark (a coloured disc inserted within the rectangular shape), A.P. correctly solved the task and he also outperformed the controls. This pattern of results shows a left-hemispheric inability to reorient basing upon featural cues as a coloured side of the space, but it shows the left-hemispheric intact ability in reorientation based upon discrete landmarks, as previously found with chicks (Della Chiesa *et al.*, 2006; Tommasi & Vallortigara, 2001, 2004; Tommasi *et al.*, 2003; Vallortigara *et al.*, 2004), rats (LaMendola & Bever, 1997), and pigeons (Prior *et al.*, 2002). It has to be highlighted in this regard that the performance of participants might be contingent upon the specific distance between the landmark and the target corner in the rectangular shape, in that (1) smaller distances between landmark and target might facilitate the task with respect to larger distances, and (2) hemispheric asymmetry can depend upon the distance between landmark and target. In domestic chicks, for instance, Tommasi and Vallortigara (2001) found a right-hemispheric superiority in relational spatial information (coding the distance between a

landmark and the walls of an enclosed arena), as opposed to a left-hemispheric superiority in coding absolute metric information. However, the low number of repetitions in the present study does not allow us to further investigate this aspect that should be considered in future studies.

The fact that we did not confirm the right-hemispheric superiority in geometric skills, even in case of the partial callosal disconnection (A.P.), can be explained by the fact that the neural substrates of geometric encoding has been shown to involve the posterior regions of the right hemisphere (Doeller *et al.*, 2008; Wegman *et al.*, 2014), which are not disconnected from the contralateral areas in patient A.P. (the splenium being intact). On the other hand, our results seem to suggest that the left-lateralized encoding of landmarks in humans takes place in a more anterior region, which does not exploit the interhemispheric exchanges supported by the splenium. These speculations are in agreement with neuroimaging results, showing the (posterior) hippocampal involvement in geometric processing, as opposed to the (anterior) striatum involvement in landmark encoding (Doeller *et al.*, 2008; Hartley *et al.*, 2003; Wegman *et al.*, 2014). In fact, it has been shown that the splenium connects not only left and right parietooccipital cortex, but together with the hippocampal commissure it connects also the parahippocampal cortex of the left and right hemispheres (Fabri, Pierpaoli, Barbaresi, & Polonara, 2014; Raybaud, 2010). To conclude, the present results show that, differently from what happens in other species, the human brain needs at least a partial interhemispheric connection in order to reorient, and we speculate that the hippocampal interhemispheric connections crucially subserve spatial processing. Nevertheless, further studies are necessary in this field in order to better disentangle the specific skills of each cerebral hemisphere in the processing of the different characteristics of space.

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