doi:10.1093/brain/awz179 BRAIN 2019: 142; 2207–2214 | 2207

BRAIN
A JOURNAL OF NEUROLOGY

REPORT

The antero-dorsal precuneal cortex supports specific aspects of bodily awareness

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See Pisella *et al.* (doi:10.1093/brain/awz187) for a scientific commentary on this article.

The precuneus is a functionally heterogeneous area located on the medial face of the parietal cortex, wedged between the occipital cortex and the paracentral lobule. In view of its topological positioning, this associative cortex is well-placed to play an important role in multisensory integration, specific aspects of which participate to bodily awareness. However, this potential implication remains unestablished. We assessed bodily awareness longitudinally in 14 rare patients who underwent a surgery for a low-grade glioma mainly infiltrating the precuneus. To determine the brain locus the most frequently affected in patients showing bodily awareness disorders, we first contrasted the resection cavity distributions of patients with versus without bodily awareness disorders. We next applied 'lesion network mapping' to identify the networks functionally coupled with lesion locations causing bodily awareness disorder. Bodily awareness disorders were observed in half of patients after surgery, especially alien hand, macrosomatognosia and fading limb. Importantly, a dissociation was revealed between the antero-dorsal precuneus (bodily awareness disorders) and postero-dorsal precuneus (no bodily awareness disorders). Furthermore, bodily awareness disorder-related regions were specifically connected to a network of sensorimotor regions while others were connected with the default network. Altogether, the present findings indicate a critical role of the antero-dorsal precuneus in specific aspects of bodily awareness and in the maintenance of body schema.

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Keywords: precuneusparietal cortex; body schema; bodily awareness; glioma

Abbreviations: BAD = body awareness disorder; SPL = superior parietal lobule

Introduction

The precuneal cortex (i.e. the medial aspect of the posterior parietal cortex) remains one of the most fascinating parts of the brain because of the limited understanding of its functional anatomy. Current literature suggests a role in a large array of highly-integrated cognitive processes (including social cognition, autobiographic memory, self-awareness

Received March 1, 2019. Revised April 13, 2019. Accepted April 28, 2019. Advance Access publication June 25, 2019

and many others; Cavanna and Trimble, 2006), but most of the available evidence remains correlative in nature because they are derived from functional MRI investigations. The precuneus is indeed rarely affected by focal or evolving lesions such as stroke injury or slow-growing tumours. As a consequence, neuropsychological data are almost non-existent. However, recent parcellation maps derived from resting-sate MRI favour the idea that the precuneus may be segregated into different functional areas, and thus involved in dissociated classes of cerebral functions (Margulies *et al.*, 2009; Zhang and Chiang-shan, 2012).

From an anatomical standpoint, the precuneal cortex is wedged between the medial occipital cortex and the paracentral lobule. Consequently, this associative parietal cortex is strategically well-placed to participate in some aspects of multimodal integration, the neural mechanism by which incoming information from different sensory modalities are assembled to provide individuals a coherent perceptual experience. Current literature suggests that some forms of cross-modal integration may play an important role in bodily awareness in general, especially integration of tactile, proprioceptive, vestibular and visual inputs (Berlucchi and Aglioti, 1997; Graziano, 1999; Graziano and Botvinick, 2002; Maravita *et al.*, 2003; Holmes and Spence, 2004; Dijkerman and De Haan, 2007). This optimal combining of sensory modalities may help the brain represent the body as a volumetric object in external space (Haggard and Wolpert, 2005), an amodal representation that needs to be updated during action to maintain coherence spatiotemporally. Dysregulation of such a mechanism may result in body awareness disorders (BADs), such as autotopagnosia or somatoparaphrenia (Haggard and Wolpert, 2005; De Vignemont, 2010).

In accordance with the established role of the parietal cortex in multisensory integration, most BADs have been reported following damage of either the inferior or the superior parietal lobule (SPL), most frequently in the right hemisphere (Vuilleumier *et al.*, 1997; Daprati *et al.*, 2010) knowing that some BADs are very rare. The potential role of the precuneus has been debated much less, and probably underestimated for the reasons mentioned above (i.e. rarely affected by neurological damage). However, sparse neuropsychological studies have reported associations between the precuneus (along with the neighbouring SPL) and different manifestations of BADs, in particular fading limb (Herbet *et al.*, 2014) and alien limb (Darby *et al.*, 2018), but the exact precuneal contribution to these abnormal body representations remains unestablished.

In this study, we assessed a series of rare patients longitudinally who presented with a low-grade glioma damaging the precuneal cortex. We hypothesized that the anterodorsal precuneus, a precuneal subarea which is functionally coupled with sensory-motor regions (Margulies *et al.*, 2009), should play a role in bodily perception and awareness.

Materials and methods

Patients

Fourteen patients with a histologically-proven low-grade glioma mainly infiltrating either the left or the right precuneus were recruited from Montpellier University Hospital's Department of Neurosurgery between 2011 and 2018. The exclusion criteria were: high-grade glioma, history of neurological or psychiatric disorders and previous radiotherapy. All patients were operated on under 'awake' surgery with a multifunctional mapping with direct electrostimulation. Our surgery approach has been extensively detailed elsewhere (Tate *et al.*, 2014).

The patient population consisted of six females and eight males, with a mean $\pm$ standard deviation (SD) age of 40.07 $\pm$ 11.08 years (22–55) and a mean educational level of 14.50 $\pm$ 2.79 years (9–17). All patients were right-handed, and for 11 of them the tumour was located in the right hemisphere. An overview of sociodemographic and clinical data is reported in Table 1.

The behavioural assessment was performed by a trained clinical neuropsychologist the day before, 5 days after surgery, and 3 months after surgery, as part of the routine care.

This study was conducted with our institution's ethical standards for a retrospective study. Patients provided informed consent.

Assessment of body awareness disorders

Based on the de Vignemont's BAD taxonomy (2010), several aspects of bodily awareness were systematically assessed in all patients peri-operatively. This included alien hand syndrome, tactile allochiria, anosognosia for hemiplegia, autotopagnosia for body parts or for body sensations, motor neglect, fading limb, finger agnosia, micro- or macrosomatognosia, supernumerary limb and tactile extinction. The way to assess these BADs is comprehensively described in the Supplementary material.

Assessment of other neurological impairments

Additionally, patients benefited from an extensive neuropsychological assessment. More specifically, the following neurological/neuropsychological syndromes were systematically checked: spatial neglect, auditory and visual extinction, optic ataxia, visual agnosia, constructional, and ideational apraxia. To examine the patients' executive functioning, the Trail Making Test, Stroop and phonological fluency tasks were used. Lastly, language abilities were assessed with a picture naming task, and semantic processing with the Pyramids and Palm Trees task and the semantic fluency task. All these assessments and the associated references are described in the Supplementary material.

Neuroanatomical data acquisition, normalization and lesion drawing

Structural MRI datasets were acquired 3 months after surgery as part of the standard care. In particular, high-resolution 3D

Table 1 Sociodemographic and clinical data

ID	Age	Education level	Sex	Manual laterality	Side	Resection volume, cm^3	Resection percentage, %	Quality	Type	Recurrence
P1	34	9	Male	Right	Right	12.35	96.5	Subtotal	OD	I
P2	50	16	Male	Right	Right	21.23	90	Subtotal	OD	I
P3	30	9	Male	Right	Right	44.4	90	Subtotal	OD	I
P4	42	17	Male	Right	Left	34.9	100	Complete	A	I
P5	40	14	Female	Right	Right	13.6	74	Subtotal	A	I
P6	35	17	Male	Right	Right	38.8	93.5	Subtotal	A	II
P7	45	14	Female	Right	Right	10.8	91	Subtotal	OD	I
P8	22	14	Male	Right	Right	26	93.5	Subtotal	A	I
P9	52	12	Male	Right	Right	47.4	87	Partial	OD	I
P10	55	17	Male	Right	Left	10.8	94.5	Subtotal	A	I
P11	55	17	Female	Right	Left	15.6	100	Complete	A	II
P12	46	15	Female	Right	Right	10.54	100	Complete	A	I
P13	32	17	Female	Right	Right	30.1	90	Subtotal	A	I
P14	23	15	Female	Right	Right	36.1	99	Subtotal	A	I

A = astrocytoma; OD = oligodendroglioma.
Recurrence: I = first surgery; II = second surgery.
Subtotal indicates a resection with a tumoral residue < 10 cm^3; partial indicates resection with a tumoral residue > 10 cm^3.

T_1-weighted sequences were retained for the purposes of the present study (3 T Siemens Skyrya scanner). The imaging parameters were as follows: 1 mm isometric voxel; reaction time = 1.7 s, echo time = 2.54 ms, inversion time = 0.92 s, field of view = 256 × 256 mm, flip angle = 9°.

To normalize individual imaging datasets spatially, we used SPM12 (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/), implemented in the MATLAB environment (release 2014b, The MathWorks), with standard parameters. At this stage, all 3-month normalized MRIs (MNI152 brain) were manually checked to ensure that all normalizations were of sufficient quality. Next, we contoured by hand the resection cavities and transformed them into binarized images using MRIcron software (http://people.cas.sc.edu/rorden/mricron/install.html). This work yielded 14 volumes of interest.

Subtraction plots

To determine which precuneal areas were the most frequently affected by the surgical procedure in patients showing BADs, we first overlapped the resection cavities of patients showing BADs and patients not showing BADs. Next, we contrasted both overlap maps using the MRIcron's 'subtraction plot' function. Note that resection cavity maps of patients with a left tumor (n = 3) were flipped for this analysis and the others described in the following.

Lesion network mapping

To identify the network of cortical regions functionally connected to lesion locations associated with BADs, we used 'lesion network mapping' (Boes *et al.*, 2015; Fox, 2018). This technique, which has been validated in several recent works (Darby *et al.*, 2018), has the advantage of avoiding the achievement of functional MRI in patients. In this study, resection cavity maps were used as seeds to generate resting-state functional connectivity maps based on the data from a local database of 18 healthy participants (Yordanova *et al.*, 2019). This seed-to-voxel analysis was performed with the Functional Connectivity (CONN) toolbox (Whitfield-Gabrieli and Nieto-Castanon, 2012). Next, the functional connectivity maps of resections cavities associated with BADs were contrasted with the functional connectivity maps of resection cavities not associated with BADs using a simple two-tailed t-test. The results were thresholded with a false discovery rate (FDR) correction of $P < 0.001$ and a voxel extent of 100 contiguous voxels. The preprocessing steps of the healthy participants' resting-state functional MRI data are fully detailed in Yordanova *et al.* (2019).

Data availability

The data that support the findings of this study are available from the corresponding author, upon reasonable request.

Results

Clinical and behavioural data

The resection cavity maps are overlaid onto the MNI152 standard space in Fig. 1A. As shown in Fig. 1, the surgical resection damaged different sectors of the precuneus, typically the anterior or the posterior part, and sometimes the whole precuneus (e.g. Patient P3). In most cases, the posterior cingulate gyrus (ventral or dorsal) and its underlying white matter connectivity (especially the cingulum) were also affected. Some resections extended laterally into the SPL. The average volume ± SD (range) of resected brain was 25.2 ± 13.4 cm^3 (10.5–47.3).

At the behavioural level, preoperatively, only one patient (Patient P11) showed BADs (alien hand and fading limb). These impairments were consecutive to the first surgery. The fading limb concerned the left entire hemi-body, and

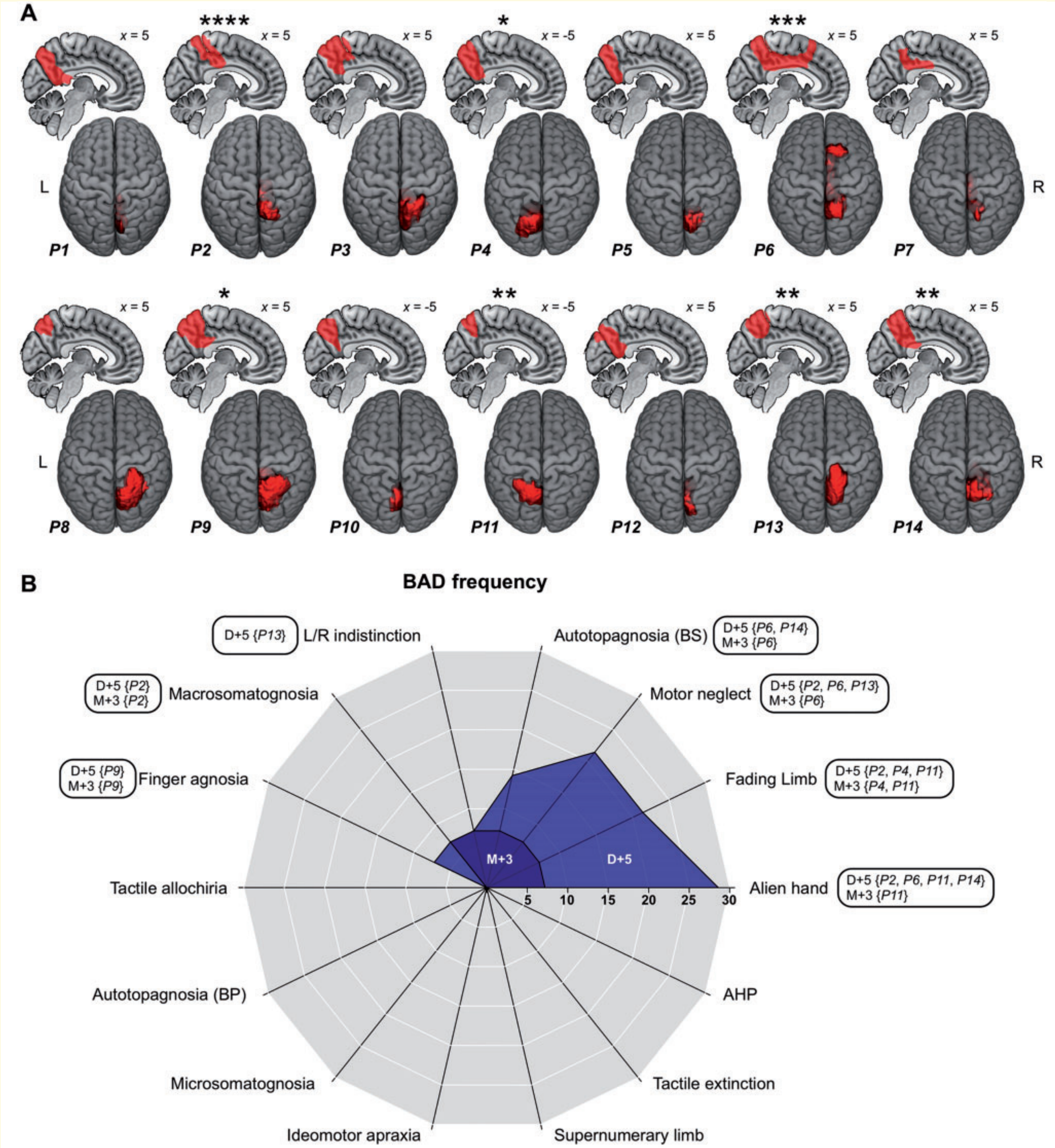

Figure 1 Neuroanatomical data and BAD frequency. (**A**) Individual resection cavities are plotted individually onto the standard MNI152 template using MRIcroGL (https://www.mccauslandcenter.sc.edu/mricrogl/home). The bells indicate the number of BADs observed in each patient (see also Supplementary Table 1). (**B**) Radar plot of BAD frequency observed both 5 days after surgery (D + 5), and 3 months after surgery (M + 3). Patients with BADs (P) are individually identified on the figure.

was characterized by severe difficulties in mentally representing and locating this part of the body in space (eyes closed), with an accompanying feeling of transparency.

Postoperatively, seven patients experienced at least one BAD (ranging from one to four). This included alien hand, fading limb, and macrosomatognosia, autotopagnosia for bodily sensations, left/right indistinction and motor neglect. Patients with BADs are shown in Fig. 1A and Supplementary Table 1. Figure 1B shows the frequency of BADs 5 days after and 3 months after surgery. In the following, we describe the most illustrative cases of BADs.

Patient P2 experienced four BADs just after surgery, including macrosomatognosia, alien hand, fading limb and motor neglect. Regarding the macrosomatognosia, the patient experienced his left leg as disproportionally larger than his right leg when it was not under visual control (and only during walking activities). This caused the patient to limp but only when he did not look at his legs. Additionally, at rest, the patient had difficulties in locating his left leg in space when it was not seen.

Patient P4 reported that, when he closed his eyes, he mentally felt his right hand as 'transparent' and had difficulties locating it in space. These manifestations diminished when he moved his arm.

Patient P6 experienced alien hand, motor neglect and autotopagnosia for bodily sensations. The latter impairment was characterized by an inability to locate tactile stimuli when they were applied below the contralesional knee. All stimulations were experienced as being applied at the level of the knee (verbally or by pointing with eyes closed) while they were actually applied to the foot, the ankle, the toes and the calf. In other locations, the patient was very precise both when stimulations were applied on the contralesional or the ipsilesional body side. Stimulations applied under the knee were identified as being applied to the same intensity as other stimulations.

Three months after surgery, six patients continued to experience BADs. Patients also experienced other cognitive disorders, especially in the immediate postoperative phase, including executive disorders, spatial neglect and constructional apraxia (Supplementary Fig. 1 and Supplementary Table 2).

The antero-dorsal precuneus is the most frequently damaged area in patients with body awareness disorders

The resection cavity distribution of patients showing at least one BAD 5 days after surgery (n = 7) were contrasted with the resection cavity distribution of patients not showing a BAD (n = 7). The results are displayed in Fig. 2. Patients with BADs were more frequently damaged at the level of antero-dorsal precuneus (maximum overlap of 71%). Conversely, other patients were more frequently affected into the postero-dorsal precuneus (maximum overlap of 71%). This pattern of results demonstrates a remarkable dissociation between the antero-dorsal and the postero-dorsal precuneus.

Lesion network localization of body awareness abnormalities

The results of the 'lesion network mapping' analysis are shown in Fig. 3. A clear dissociation was revealed. The resection cavity maps of patients with BADs were indeed strongly connected to a network of sensorimotor regions comprising the antero-dorsal precuneus, the paracentral lobule and the supplementary motor area, the SPL, the supramarginal gyrus, the insula and the premotor cortex. In contrast, the resection cavity maps of patients not experiencing BADs were clearly connected to areas of the default mode network.

Discussion

The present study provided first evidence for a role of the precuneus in different aspects of bodily awareness, with the description of body schema disorders which has been rarely reported, especially macrosomatognosia, fading limb and autotopagnosia for bodily sensations. Furthermore, neuroanatomical analyses indicated that the antero-dorsal sector of this area was likely to constitute the neural correlate of these BADs.

First, it is worth noting that we cannot entirely rule out the possibility that adjacent cortices might also participate in the development of BADs. For instance, Patient P2 had a resection extending towards the paracentral lobule; and in Patient P9, the resection also concerned a significant part of the SPL (Supplementary material). Given the established role of these brain areas in, somatosensory processing and crossmodal integration, respectively, (Dijkerman and De Haan, 2007), damage to these regions might, in principle, also lead to BADs. In the same way, it is known that the most anterior part of the posterior cingulate cortex functionally communicates with sensorimotor regions (Leech and Sharp, 2014). Consequently, the hypothesis according to which a lesion damaging this area might cause BADs appears to be valid. However, while some patients with a surgical resection extending to this structure had BADs (Patients P2 and P5), others had not (Patient P7).

Recent works have suggested a tri-parcellation of the precuneal anatomo-functional organization with anterior-to-posterior subdivisions (Margulies *et al.*, 2009; Zhang and Chiang-shan, 2012): an antero-dorsal 'sensorimotor' zone, a postero-dorsal 'cognitive' one and a 'visual' ventral one. Consistent with this, our 'lesion network mapping' analysis demonstrated that lesion locations associated with BADs were specifically coupled with areas known to be engaged in low-level or high-level sensorimotor processing, while other lesions were mainly connected with default mode network. In addition to confirming that most of the BADs identified in this study were possibly related to an impairment of sensorimotor integration, this pattern of results also suggests that dysregulation of the network emanating from the antero-dorsal precuneus is a possible mechanism leading to BADs. This is in agreement with the fact that the detected sensorimotor regions have been previously associated with BADs. For example, the superior parietal lobule has been associated with xenomelia (McGeoch *et al.*, 2011) and fading limb (Wolpert *et al.*, 1998), supramarginal gyrus

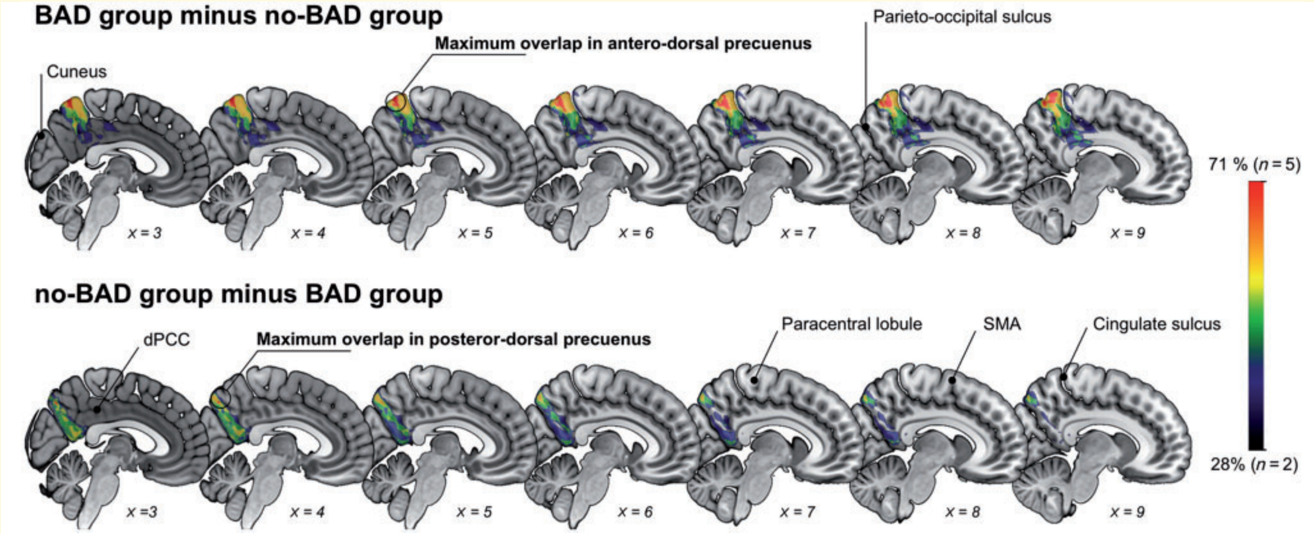

Figure 2 Subtraction plot results. The antero-dorsal precuneus was most frequently (and specifically) affected in patients with BADs versus others (the maximum overlap was 71% corresponding to 5/7 patients), while the postero-dorsal precuneus was most frequently damaged in patients without BADs versus others (the maximum overlap was also 71% corresponding to 5/7 patients). dPCC = dorsal posterior cingulate cortex; SMA = supplementary motor area.

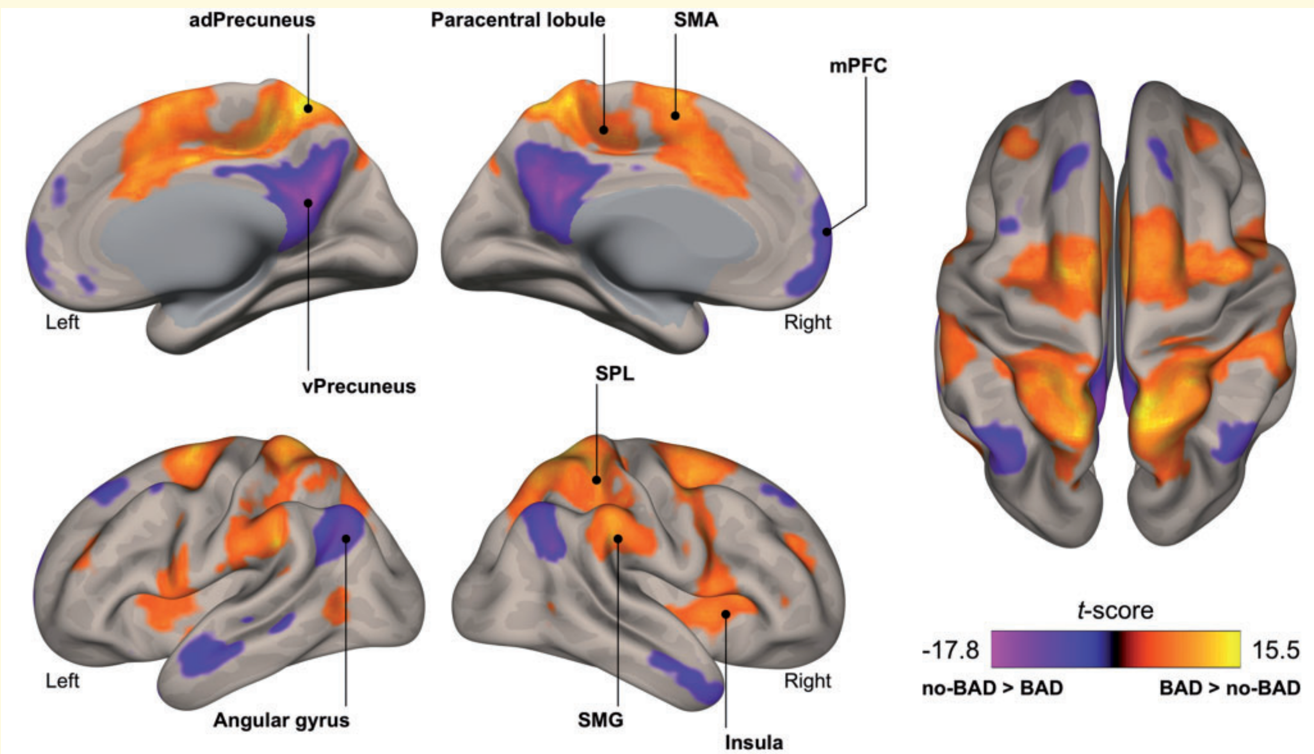

Figure 3 Lesion network mapping results. Lesions locations associated with BADs were specifically coupled with a network of sensorimotor area (red-to-yellow colour) while lesions locations not associated with BADs were specifically connected with areas of the default mode network (blue-to-purple colour). Only suprathresholded voxels are shown after FDR correction of $P < 0.001$. ad = antero-dorsal; mPFC = medial prefrontal cortex; SMA = supplementary motor area; SMG = supramarginal gyrus; v = ventral.

with asomatognosia (Feinberg *et al.*, 1990, 2010) the insula with somatoparaphrenia (Cereda *et al.*, 2002; Karnath *et al.*, 2005), and the supplementary motor area with macrosomatognosia (Weijers *et al.*, 2013).

The current study identified various forms of BADs, alien hand and fading limb being the most frequent. Because this work did not use specific experimental manipulations, rather conventional neurological and neuropsychological testing, it was not attempted to provide data about the underlying impaired mechanisms leading to BADs. However, the clinical characteristics of the observed BADs suggest that an impaired sensorimotor representation of the body might be the cause, not a higher cognitive one. Indeed, locating a member in space requires integration of both tactile and proprioceptive modalities coming from the contralesional body (Graziano, 1999; Holmes and Spence, 2004) or the maintenance of the representation of the current limb position. Selective disruption of these processes may lead to fading limb, as described in a previous study in which a patient presenting with a large left parietal cyst, mainly located in the SPL but extending to the precuneus, 'perceived her right arm and leg to drift and then fade unless she was able to see them' (Wolpert *et al.*, 1998). Further, deprivation of some tactile information may lead to alien hand, autotopagnosia for bodily sensations (Medina and Coslett, 2010) or to an overestimation of the size of specific body parts (as seen in macrosomatognosia) (Gandevia and Phegan, 1999; Haggard and Wolpert, 2005). In the latter case, this agrees with the fact that the only patient with a macrosomatognosia (of the leg) had a precuneal resection extending to the paracentral lobule (involved in the somatosensory representation of the leg).

At another level, it is worth noticing that patients frequently exhibited other neurocognitive deficits after surgery, especially spatial neglect and executive disorders. As previously discussed (Vallar and Ronchi, 2009), these impairments are often seen in BAD patients and might eventually participate in the development of BADs. However, in our study, patients with or without BADs indistinctively showed these neuropsychological abnormalities, suggesting no evident interactions (Supplementary material). It is also important to mention that, while spatial neglect was only transient for almost all patients, this was not the case for executive impairments that persisted chronically in a significant part of patients. These lasting deficits might be attributable to the damage of the posterior cingulate cortex, which was frequently lesioned. Indeed, the dorsal sector of this brain area is connected with the fronto-parietal networks involved in cognitive control (Leech *et al.*, 2011; Leech and Sharp, 2014).

To summarize, this study provides new insights into the role of the antero-dorsal precuneus in bodily awareness and perception. Future studies are needed to disentangle the exact neural mechanisms that might be sustained by this specific part of the cerebral cortex and causing BADs when disrupted.

Funding

No funding was received towards this work.

Competing interests

The authors report no competing interests.

Supplementary material

Supplementary material is available at *Brain* online.

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