Neuropsychologia 51 (2013) 1453–1462

Contents lists available at SciVerse ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Body ownership and attention in the mirror: Insights from somatoparaphrenia and the rubber hand illusion

Paul M. Jenkinson [a,*], Patrick Haggard [b], Nicola C. Ferreira [c], Aikaterini Fotopoulou [d,*]

[a] Department of Psychology, University of Hertfordshire, UK
[b] Institute of Cognitive Neuroscience, University College London, UK
[c] Wolfson Centre for Age-Related Diseases, King's College London, UK
[d] Division of Psychology and Language Sciences, University College London, UK

ARTICLE INFO

Article history:
Received 8 October 2012
Received in revised form
12 March 2013
Accepted 15 March 2013
Available online 16 April 2013

Keywords:
Somatoparaphrenia
Perspective
Rubber hand illusion
Body ownership
Attention

ABSTRACT

The brain receives and synthesises information about the body from different modalities, coordinates and perspectives, and affords us with a coherent and stable sense of body ownership. We studied this sense in a somatoparaphrenic patient and three control patients, all with unilateral right-hemisphere lesions. We experimentally manipulated the visual perspective (direct- versus mirror-view) and spatial attention (drawn to peripersonal space versus extrapersonal space) in an experiment involving recognising one's own hand. The somatoparaphrenic patient denied limb ownership in all direct view trials, but viewing the hand via a mirror significantly increased ownership. The extent of this increase depended on spatial attention; when attention was drawn to the extrapersonal space (near-the-mirror) the patient showed a near perfect recognition of her arm in the mirror, while when attention was drawn to peripersonal space (near-the-body) the patient recognised her arm in only half the mirror trials. In a supplementary experiment, we used the Rubber Hand Illusion to manipulate the same factors in healthy controls. Ownership of the rubber hand occurred in both direct and mirror view, but shifting attention between peripersonal and extrapersonal space had no effect on rubber-hand ownership. We conclude that the isolation of visual perspectives on the body and the division of attention between two different locations is not sufficient to affect body ownership in healthy individuals and right hemisphere controls. However, in somatoparaphrenia, where first-person body ownership and stimulus-driven attention are impaired by lesions to a right-hemisphere ventral attentional-network, the body can nevertheless be recognised as one's own if perceived in a third-person visual perspective and particularly if top-down, spatial attention is directed away from peripersonal space.

1. Introduction

The sense of body ownership has been defined as the feeling that one's body belongs to oneself (Gallagher, 2000). A long tradition of experimental studies has attempted to study this facet of bodily self-consciousness by focusing on the self-attribution of body parts. Typically, in such studies participants are asked to make conceptual judgements about the ownership of body parts presented in extrapersonal space, as for example in video screens or photographs (e.g. Frassinetti, Maini, Romualdi, Galante, & Avanzi, 2008; Saxe, Jamal, & Powell, 2006). A different tradition of studies has sought to investigate feelings of body ownership as a more intuitive and less doxastic awareness of the body as one's own (see de Vignemont, 2011; Tsakiris, 2010 for discussion). Such studies have taken advantage of the malleability of bodily representations. For example, in the Rubber Hand Illusion (RHI; Botvinick & Cohen, 1998), a rubber-hand viewed in peripersonal space (i.e. space near to the body) is experienced as part of one's body if the subject's own hand is synchronously touched out of view.

Despite the progress in understanding the sense of body ownership through such experimentally induced illusions, it remains difficult to tease apart the phenomenally elusive components of body ownership. It seems even harder to create convincing and lasting conditions of subjective body disownership (de Vignemont, 2011; Longo, Schuur, Kammers, Tsakiris, & Haggard 2008; Newport & Gilpin, 2011). By contrast, neurological patients with symptoms such as asomatognosia (lack of recognition regarding the existence or ownership of one's limbs; Vallar & Ronchi, 2009) show a clear and long-lasting, subjective experience of body disownership; denying ownership of their affected body

* Corresponding authors.
E-mail addresses: p.jenkinson@herts.ac.uk (P.M. Jenkinson), a.fotopoulou@ucl.ac.uk (A. Fotopoulou).

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http://dx.doi.org/10.1016/j.neuropsychologia.2013.03.029

parts for days, weeks or months. Sometimes this denial is accompanied by delusions about the affected arm (somatoparaphrenias; Gerstmann, 1942). The particular application of terms like asomatognosia and somatoparaphrenia remain unclear. Typically, somatoparaphrenia is regarded as a positive or productive variant of asomatognosia (in the Jacksonian sense; Jackson, 1932), and it may take several clinical forms (see Vallar & Ronchi, 2009). In the version of the syndrome that we will be focusing on here, patients recognise the existence of a limb attached to their body, but judge this as belonging to someone else. For example, the affected limb may be attributed to another person, such as a friend, relative or doctor.

Somatoparahrenia occurs more frequently in patients with right-hemisphere lesions and is of variable duration, lasting from days to years (Vallar & Ronchi, 2009). Only a handful of single-case studies have documented clinical interventions that can lead to temporary remission of the disorder (Bisiach, Rusconi, & Vallar, 1991; Rode et al., 1992; Verret & Lapresle, 1978) and controlled, experimental investigations are equally rare (Aglioti, Smania, Manfredi, & Berlucchi, 1996; Bottini, Bisiach, Sterzi, & Vallar, 2002; Fotopoulou et al., 2011; Moro, Zampini, & Aglioti, 2004; van Stralen, van Zandvoort, & Dijkerman, 2011). Somatoparaphrenia is frequently associated with sensorimotor loss and related higher-order impairments such as neglect, but double dissociations have been noted between somatoparaphrenia and most of these deficits (Cogliano, Crisci, Conson, Grossi, & Trojano, 2012; Vallar & Ronchi, 2009). Such deficits therefore seem to be important contributing factors of the symptom, but they may not be sufficient conditions for somatoparaphrenia to arise.

Given the temporary remission of somatoparaphrenia by vestibular stimulation (Bisiach et al., 1991). Vallar and Ronchi (2009) have argued that somatoparaphrenia involves a defective higher-order spatial representation of the body and impaired multisensory integration (cf. similar "dyschiria"; Bisiach & Berti, 1987; and defective internal body representation explanations; Daprati, Sirigu, Pradat-Dieh, Franck & Jeannerod, 2000). In a previous experimental study (Fotopoulou et al., 2011), we were able to show that viewing one's affected arm through a conventional mirror, placed in the frontal plane, systematically reinstated ownership for the arm in two patients with somatoparaphrenia. As soon as the mirror was removed, and patients had only direct view of their arm, they again denied its ownership. Thus, patients alternated between claiming and denying ownership of their arm every few seconds. These findings suggested a dissociation between the processes that support self-recognition of the body in direct and mirror view.

Looking at our body in a mirror creates visual feedback of ourselves from a third-person perspective (or "from the outside"; see Vogeley & Fink, 2003). This mirror view of the body is subject to several unusual properties (Gregory, 1997), one being that the mirror image is left-right reversed, such that the left side of the body is located on the left side of the mirror space. In addition, the image of the body is observed in a location that is distant to the physical location of the body; nevertheless, viewing one's body in the mirror activates representations of peripersonal space (Maravita, Spence, Clarke, Husain, & Driver, 2000). More generally, the third-person perspective afforded by a mirror involves both a translocation of the egocentric (i.e. body-centered/viewer dependent) viewpoint, and engagement of allocentric (i.e. object-centered/view independent) operations (Vogeley & Fink, 2003).

These properties may be particularly relevant to somatoparaphrenia, given that the first-person perspective appears to play a special role in the sense of body ownership, with sensory, motor and other bodily signals being integrated in egocentric coordinates (Petkova, Khoshnevis, & Ehrsson, 2011; but see Lenggenhager, Tadi, Metzinger, & Blanke, 2007). In addition, it has been shown that peripersonal space and extrapersonal space (i.e. space beyond manual reach; Berti & Frassinetti, 2000) are coded independently in patients with unilateral neglect (Cowey, Small, & Ellis, 1994; Halligan & Marshall, 1991; Vuilleumier, Valenza, Mayer, Reverdin, & Landis, 1998). Moreover, recent studies show that both extrapersonal space processing and allocentric judgments draw upon the ventral 'perception-related' stream of visual processing, whereas both near-space processing and egocentric judgments draw upon the 'action-related' dorsal stream (Chen, Weidner, Weiss, Marshall, & Fink, 2012; Lane, Ball, Smith, Schenk, & Ellison, 2013; Neggers, Van der Lubbe, Ramsey, & Postma, 2006). Although previous studies of somatoparaphrenia have looked at the role of processing the body in left versus right space (Moro et al., 2004), the relation between visual perspective (first vs. third), attentional fractionating of space (peripersonal vs. extrapersonal), and body ownership remains unclear.

Several recent lesion mapping studies have compared the lesions sites of patients with body ownership disturbances and hemispatial neglect to those of patients with hemispatial neglect but without body ownership disturbances (Baier & Karnath, 2008; Feinberg, Venneri, Simone, Fan, & Northoff, 2010; Gandola et al., 2012; Invernizzi et al., 2013). Although such studies find differences in the lesions selectively associated with spatial neglect versus somatoparaphrenia, debates surround the issue of which of the identified cortical (e.g. insular cortex; Baier & Karnath, 2008; frontal lobe lesions; Feinberg et al., 2010), or subcortical (e.g. basal ganglia; Gandola et al., 2012; Invernizzi et al., 2013) regions are selective to somatoparaphrenia as opposed to neglect, hemiplegia or anosognosia. Importantly, given the clinicoanatomical aim of such studies, patients are typically categorised into groups according to a clinical assessment of body ownership, which is subsequently used in comparisons of lesion extent and location between groups with and without disownership. Such investigations may thus not take into account the frequently reported multidimensional and variable, within- and between-patients phenomenology of disownership. By contrast, correlating lesion patterns with statistically significant differences in performance between systematically varied experimental conditions has the advantage of potentially revealing more complex and heterogeneous patterns of neurocognitive impairments in such syndromes (see Fotopoulou, 2013 for discussion). This methodological advantage has been recently demonstrated in a related syndrome, anosognosia for hemiplegia; lesion analysis of patients classified on the basis of experimental rather than psychometric or clinical performance revealed different lesion-behaviour relations (see Fotopoulou, Pernigo, Maeda, Rudd, & Kopelman, 2010; Moro, Pernigo, Zapparoli, Cordioli, & Aglioti 2011).

The current study examined the role of: (i) visual feedback (direct vs. mirror) and, (ii) selective spatial attention (peripersonal vs. extrapersonal space) in body ownership. We aimed to confirm our previous finding of improved limb ownership following mirror self-observation (Fotopoulou et al., 2011), and extend them by studying how directing attention to different spatial locations may further enhance the effects of perspective afforded by vision alone. We manipulated spatial attention in a right-hemisphere stroke patient (GR) with neglect and somatoparaphrenia, by placing an orienting stimulus either near to the affected hand (peripersonal space), or well in front of the body, near to the mirror (extrapersonal space). Based on the idea that somatoparaphrenia involves an impaired first person representation of the body (Fotopoulou et al., 2011), we predicted that focusing attention in the extrapersonal, mirror space would enhance the visual processing of the reflected, third person perspective of the body and hence improve limb mirror recognition in somatoparaphrenia. By contrast, we predicted that focusing attention in the peripersonal, left hand space would diminish the visual processing of the reflected, third person perspective of the body and hence increase disownership of the hand in the mirror. These same factors were tested in three hemiplegic control patients with neglect but no somatoparaphrenia, in order to determine the combined effect of visual perspective and attention on body ownership in patients with neglect, and provide matched data against which GR's experimental and lesion-mapping results could be compared.

Given that extrapersonal space processing and allocentric judgments draw on a network of mainly right-hemisphere ventral areas (including the lateral occipital complex and hippocampus) compared with peripersonal space processing and egocentric judgments, which involve a dorsal processing stream (superior parietal lobule/precuneus) (Chen et al., 2012; Lane et al., 2013; Neggers et al., 2006), we further anticipated that areas linked with near-space processing and egocentric judgements would be more impaired in GR, whereas the areas supporting allocentric judgements and extrapersonal space would be relatively intact and thus facilitate body ownership when the body was perceived in the mirror and attention was placed in the mirror space.

Finally, because healthy and right-hemisphere controls showed ceiling effects in all relevant ownership conditions of a previous experiment (Fotopoulou et al., 2011), we included in the current study a novel control experiment. We studied the sense of ownership in healthy subjects using the Rubber Hand Illusion, while manipulating the same factors of perspective (direct vs. mirror views of the rubber hand) and attention in space (peripersonal vs. extrapersonal). This experiment was considered particularly useful for controlling for the potential effects of dividing the loci of attention in the critical comparisons.

2. Case report

Patients involved in this study were the same as those described fully in a previous report by Fotopoulou et al. (2011). To avoid redundancy, here we provide only a summary of the key clinical and neuropsychological characteristics of interest.

GR is a 78-year-old right-handed woman, a retired tailor, with seven years of formal education. Prior to her stroke she was mobile and independent and had no relevant medical or psychiatric history. She suffered a sudden left-sided hemiplegia and was admitted to hospital, whereupon a CT scan confirmed a diagnosis of right Middle Cerebral Artery (MCA) infarction.

Upon clinical examination, 35 days post-admission, GR showed no evidence of a confusional state, but exhibited total left hemiplegia, left spatial inattention, left hemisensory loss, homonymous hemianopia and facial weakness. She was generally aware of her motor and cognitive difficulties (e.g. the occurrence of her recent stroke and subsequent inability to manage activities of daily living independently), but was clearly anosognosic about the specific motor deficits of her "own" left arm (see Marcel, Tegnér & Nimmo-Smith, 2004, for further details of the extension, specificity, and partiality of anosognosia), and had formed the firm belief that her left arm belonged to her granddaughter when viewing it directly in both left and right visual fields (see Fotopoulou et al., 2011, for further details of dissociations in GR's motor awareness). GR's belief did not change when she touched the arm simultaneously, with or without vision. Attempts to reason with GR, including referring to the appearance of the hand or her hospital tag, at best led to her saying 'I do not know' and at worse strengthened her conviction. When asked to point to or touch her left arm, GR would search to the left of her actual (left) arm, and would often ask the examiner to help her find it. GR never claimed that her left leg belonged to someone else, and she seemed aware of its paralysis. GR remained somatoparaphrenic (in both testing and spontaneous behaviour) until her discharge from hospital one week later. At a six-month follow-up she had only partial movement in her leg but no somatoparaphrenia, or anosognosia. Visuospatial left neglect and left arm paralysis persisted.

A detailed neuropsychological and sensorimotor assessment was conducted 36–48 days from onset (see Supplementary Material, Table S1). GR's neurological and neuropsychological profile was compared with three age-matched, right-hemisphere control patients (all male), who were recruited from the same acute rehabilitation stroke unit (see Fotopoulou et al., 2011, for full details and descriptions). All participants gave fully-informed written consent.

GR did not differ significantly from the controls in terms of age, post-morbid intelligence, somatosensory function, visuospatial neglect, or executive functions including inhibition and abstract reasoning. However, she had fewer years of formal education and a larger delay prior to testing compared to controls. GR exhibited a statistically greater (albeit small) deficit in the right visual hemifield compared with controls, and significantly greater personal neglect as measured by the One Item test.

2.1. Lesion mapping and analysis

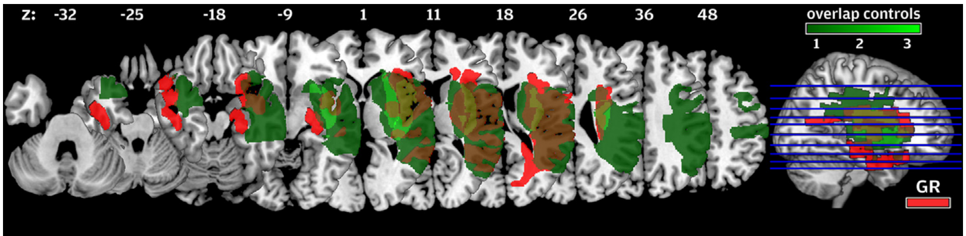
All lesions were caused by a single ischaemic or haemorrhagic, right Middle Cerebral Artery (MCA) stroke, and excluded damage to the left hemisphere. An independent researcher (S.P.), blind to the groups and hypothesis of the study drew all lesions, and a second independent researcher (V.M.), also blind to the aims of the study, double-checked each lesion mapping for accuracy. Any disagreements between these two researchers were resolved via consultation with a third independent expert (a senior neurosurgeon). Lesions were mapped on slices of the T1-weighted MRI scan template (ICBM152) from the Montreal Neurological Institute (standard MNI space; $2 \times 2 \times 2$ mm). The template was first rotated to match the orientation of the MRI or CT patient scan, and the scan images of the patient brain was normalised and aligned to superimpose to the rotated template slices in MRIcro software (www.mricro.com; Rorden & Brett, 2000). The patients' lesions were then outlined on the rotated template and subsequently rotated back to match the stereotaxic space of the MNI T1-weighted template. The derived tridimensional volumes representing the lesions of each patient were superimposed onto the 'Automated Anatomical Labelling' template (Tzourio-Mazoyer et al. 2002) to determine the lesion voxels of the different cerebral structures. The lesion involvement of white matter structures and connections was achieved by means of the lesion plots' overlap with the 'white matter parcellation map' template (Mori et al., 2008). Fig. 1 illustrates these lesion plots and provides a quantitative summary of the voxels involved in each affected area (qualitative descriptions of these lesions, based on clinician reports and a qualitative assessment, and individual lesion plots can also be found in Fotopoulou et al., 2011).

GR's lesions overlapped considerably with those of the control patients, and included areas commonly associated with body ownership, such as the insula, frontal lobes, and temporoparietal junction (see Baier & Karnath, 2008; Craig, 2009; Feinberg et al., 2010; Fotopoulou et al., 2010; Olausson et al., 2005; Tsakiris, 2010). However, GR showed quantitatively more unique lesion voxels in limbic regions (amygdala and hippocampus), the inferior frontal gyrus (opercular and triangular parts), and associated white matter connections (fornix, terminal stria, and uncinate fasciculus).

3. The mirror-attention experiment

3.1. Materials and method

An experimental mirror-attention task was used to investigate the effect of visual perspective and attention on limb ownership. GR was asked to identify the owner of her left (paralysed) arm whilst looking



	Regions (AAL)	GR only lesion: Area %	GR only lesion: Voxels	Common lesion: Area %	Common lesion: Voxels	Common lesion: Voxels Sum	Common lesion: Max Overlap	Controls only lesion: Area %	Controls only lesion: Voxels	Controls only lesion: Voxels Sum	Controls only lesion: Max Overlap
Gray Matter	Amygdala	37%	733	4%	73	150	3	6%	122	125	2
	Hippocampus	33%	2472	12%	886	1821	3	16%	1202	1415	2
	ParaHippocampal	26%	2366	<1%	28	56	2	4%	392	392	1
	Frontal Inf Orb	10%	1395	2%	288	576	2	8%	1066	1066	1
	Temporal Pole Sup	9%	960	11%	1185	2385	3	41%	4412	4413	2
	Frontal Inf Tri	8%	1390	1%	136	287	3	1%	119	119	1
	Calcarine	8%	1254	<1%	10	20	2	<1%	19	19	1
	Fusiform	8%	1534	<1%	49	98	2	6%	1221	1221	1
	Olfactory	7%	150								
	Insula	7%	977	69%	9739	27168	4	14%	1936	2439	3
	Precentral	2%	593	1%	148	296	2	16%	4311	4311	1
	Frontal Inf Oper	2%	273	20%	2183	4870	3	18%	2030	2030	1
	Rolandic Oper	1%	65	82%	8786	17996	3	10%	1076	1076	1
	Cuneus	1%	94								
	Postcentral	1%	157	2%	758	1516	2	30%	9269	9269	1
	Caudate	1%	56	5%	408	903	3	51%	4012	4282	2
	Pallidum	1%	22	25%	552	1477	3	63%	1388	1945	2
	Frontal Sup Orb	<1%	22								
	Frontal Mid	<1%	26					3%	1025	1025	1
	Occipital Sup	<1%	37								
	Precuneus	<1%	130								
	Thalamus	<1%	38	2%	192	384	2	10%	823	823	1
	Temporal Sup	<1%	46	48%	12021	25212	4	38%	9683	9925	2
	Temporal Mid	<1%	20	23%	8060	16129	3	59%	20963	21001	2
	Heschl			93%	1796	4051	3				
	Putamen			43%	3628	9563	4	57%	4828	8054	3
	SupraMarginal			1%	173	346	2	78%	12335	12335	1
	Temporal Pole Mid			<1%	22	44	2	28%	2694	2694	1
	Temporal Inf							16%	4610	4610	1
	Angular							46%	6435	6435	1
	Parietal Inf							19%	2024	2024	1
	Occipital Mid							3%	437	437	1
	Parietal Sup							<1%	47	47	1
White Matter	Fornix / Stria term	40%	447	13%	151	302	2	4%	41	41	1
	Uncinate fasciculus	29%	108	57%	213	426	2	5%	20	20	1
	Tapetum	28%	167	6%	38	76	2	<1%	1	1	1
	Post thal rad	16%	625	25%	978	1956	2	13%	508	508	1
	Ant corona rad	13%	917	15%	1056	2316	3	11%	777	1072	2
	Post corona rad	9%	334	15%	565	1208	3	29%	1071	1075	2
	Cerebral peduncle	5%	120								
	Splenium corpus call	3%	382								
	Sup corona rad	3%	221	38%	2827	7218	3	20%	1517	1652	2
	Cingulum (hippoc.)	3%	30								
	Post limb of int caps	2%	93	31%	1175	2356	3	28%	1047	1114	2
	Retrolen part int caps	2%	61	24%	601	1586	4	49%	1212	1464	3
	Sup long fascic	1%	68	32%	2084	4780	3	67%	4403	4658	2
	Sup fronto-occ. fasc.	1%	3	25%	125	250	2	74%	375	375	1
	Genu corpus call	<1%	11	<1%	2	4	2	2%	149	149	1
	Ant limb of int caps	<1%	2	10%	290	580	2	79%	2398	2919	2
	External capsule	<1%	6	47%	2615	6807	4	48%	2705	4638	3
	Sagittal stratum (*)			10%	225	535	3	70%	1564	1786	2

Fig. 1. Regional lesion plot of GR (in red). The green colours represent the lesion voxels of the three control patients. The number of overlapping lesions is illustrated by different colours coded for increasing frequencies, from dark green (lesion in one control patient) to light green (lesion voxels overlap in three control patients). The table provides a quantitative estimate of the region plots lesioned in (from left to right) (i) GR but not in the control patients; (ii) the three control patients and GR; and (iii) the control patients excluding GR. For each region, the number (n) and percentage (n%) of lesioned voxels are shown. MNI = Montreal Neurological Institute. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

at it either directly (first-person visual perspective), or using a large (36 × 25 cm) frontally-positioned mirror, which provided visual feedback of GR's upper body (including the affected arm, shoulder, upper torso and face, but not the right arm or hand) in a third-person visual perspective. Direct observation of the left arm was obstructed in the mirror condition by placing a large piece of card above GR's hand. Additionally, in order to manipulate spatial attention independent of this shift in visual gaze, GR was instructed to direct her attention to either mirror space or space near to her left hand on different trials. A hand held metallic clicker was used to produce an audible reminder as to where GR should direct her attention. The cue comprised three clicks in quick succession (duration approximately 1 s), followed by a jittered interval of between 1 and 3 s, and a single repeat of the three clicks in the same location. The clicker was placed left of GR's mid-sagittal plane, either next to the mirror, which was located in front of GR's body at a distance beyond manual reach (extrapersonal space), or next to GR's left arm (peripersonal space), which was positioned comfortably to the left of her midline with the hand extending to the mid-sagittal plane. A pre-experimental bedside assessment established that GR was able to accurately orient her attention, and describe what she could see, in each of these spatial locations. Ownership regarding the affected (left) limb was tested in three separate conditions: (i) direct observation of the left arm with attention/clicker near the arm (peripersonal space), (ii) mirror observation of the left arm with attention/clicker near the mirror (extrapersonal space), and (iii) mirror observation of the left arm with attention/clicker near the arm (peripersonal space). Six trials of each condition were performed in a pseudo-random order during a single test session. In addition, the main experiment was replicated in a second session conducted two days later. Results of this second session were identical to those of the first. A further series of supplementary control conditions (see Section 3.2) also replicated the main factors of interest and produced similar results (see Supplementary Materials for details).

Each trial began with an episodic or semantic memory question to avoid perseveration and distract the patient while the mirror was presented/removed. GR was then instructed to direct her attention (in peri- or extra-personal space), and look at her left hand (directly or via the mirror), while the sound of the clicker provide an additional cue as to where she should focus her attention. Once it had been established that her gaze had shifted, GR was immediately asked 'Whose hand is this?' GR's responses could be classified into one of three categories: (1) ownership (i.e. she acknowledged that the arm was her own), (2) disownership (i.e. she attributed the arm to someone else), and (3) 'don't know'. 'Don't know' responses could either indicate uncertainty between responses, or unawareness of ownership (asomatognosia) without projection of ownership onto another. If not spontaneously reported in her response, GR was also asked to state whether the hand she was describing was the left or right. To avoid confusion, GR's right hand was located to the right of her body in a relaxed position throughout the experiment.

3.2. Supplementary control conditions

In addition to the main experiment, we tested GR under various supplementary control conditions designed to specify the results of the main experiment and control for several confounding variables. Details of these control conditions, together with their results, can be found in the Supplementary Materials.

3.3. Statistical analyses

Results of the main experimental mirror-attention task were analysed by comparing GR's responses during each of the three main conditions with those of the control patients, using the Revised Standardised Difference Test (RSDT; Crawford & Garthwaite, 2005). Standard deviations of 0.0 and correlations of 1.0 were replaced by 0.001 and 0.999 when controls performed at ceiling, to allow the RSDT to be calculated. All tests were 2-tailed with alpha set at 0.05.

4. Results of mirror-attention experiment

Table 1 summarises the performance of GR and the three control patients. All controls correctly recognised their paralysed left arm as their own on 100% of trials in all conditions. GR did not make any 'don't know' responses, however, she failed entirely to recognise her paralysed arm as being her own when looking directly at it with the clicker located near her arm (i.e. both visual gaze and attention located in peripersonal space). By contrast, she showed a complete and statistically significant remission of somatoparaphrenia when the left arm was viewed in the mirror and attention focused in extrapersonal space (by the mirror) (t (2)=85.906, $p < 0.001$). A less dramatic, but statistically significant 50% improvement in ownership was found when GR observed the left arm via the mirror, but the clicker was in peripersonal space next to the hand (t (2)=60.722, $p < 0.001$). In all instances, the improvement in limb ownership remained only so long as the mirror was in place, with limb disownership returning whenever the mirror was removed.

Table 1
Percentage of correct ownership recognitions made by GR and control hemiplegic patients during the mirror-attention task.

Condition	GR	Controls mean (SD)
Direct view-peripersonal space	0	100 (0)
Mirror view-extrapersonal space	100	100 (0)
Mirror view-peripersonal space	50	100 (0)

5. Rubber hand illusion control experiment

5.1. Materials and methods

In addition to the main experiment in GR, we sought to explore the role of perspective and spatial attention on limb ownership in a group of 20 young healthy controls (5 males, 15 females; mean age=31.20, SD=11.62) using conditions similar to those tested in GR. In order to manipulate body ownership, we made use of the well-known rubber hand illusion (RHI; Botvinick & Cohen, 1998). During the RHI, a lifelike prosthetic hand was placed on a raised platform in front of the subject at their midline, while their own left hand was positioned out of sight beneath the platform and rubber hand, also at the subject's midline. A black cape covered the participants left shoulder and the proximal end of the rubber hand in order to obscure vision of the subjects own hand, and create the impression that the rubber hand was attached to the subject (see Fig. 2). An experimenter then used two small paintbrushes to synchronously stroke the subject's own (unseen) hand and the rubber hand for 5 min, while the subject watched the rubber hand. This manipulation typically results in a stronger sense of ownership for the rubber hand, while asynchronous stroking of the two hands leads to a weaker or no effect (see Tsakiris, 2010; Eshkevari, Rieger, Longo, Haggard, & Treasure, 2012). Drawing on existing studies of the RHI (Longo, Schuur, Kammers, Tsakiris, & Haggard 2008), the effect of the stroking was assessed by asking the subject five questions: (1) how much does it seem that the touch you are feeling is where you see the rubber hand being stroked? (2) How much does it seem as if you might have more than one left hand? (3) How much does it seem as though the rubber hand is your hand? (4) How much does it seem as though you are losing the sense of where your own hand is? (5) How much does it seem as though you are losing the sense of owning your hand? The full set of questions was asked after 5 min of stroking, with subjects responding to each item using a 7-point scale (0=not at all, 6=very much).

Subjects completed all conditions of a 2 (view of rubber hand: direct, mirror) by 3 (attention: own hand, rubber hand, mirror) fully-factorial design, which comprised six experimental conditions (see Fig. 2) and a control condition (direct rubber hand view with rubber hand attention), in which the subject's own hand and the rubber hand were stroked asynchronously. In the direct view conditions subjects looked directly at the rubber hand while it was stroked by the experimenter, while in the mirror view conditions direct vision of the rubber hand was obscured by a piece of card, and the subject viewed the rubber hand in a large (30 cm × 40 cm) frontally-positioned mirror which was located at a distance beyond manual reach. The mirror was covered during trials of the direct view condition (see Fig. 2). The subject's own left hand was never visible.

In order to manipulate spatial attention, prior to each condition we told the subject that, in addition to looking at their hand directly or in the mirror, they should pay attention to the space from which they heard a sound emitted by a beeper. The beeper (Sony handheld recorder) made a pre-recorded, repetitive tone once every 2–5 s (jittered), and was placed in one of three positions: (i) beside the mirror (mirror space), (ii) beside the rubber hand (rubber hand space), or (iii) beside the subject's own left hand (own hand space). The beeper served as a reminder for the subject to continually attend to the given location. The ability to correctly and easily discriminate the spatial location of the emitted sound was established in a pilot study, during which three healthy subjects

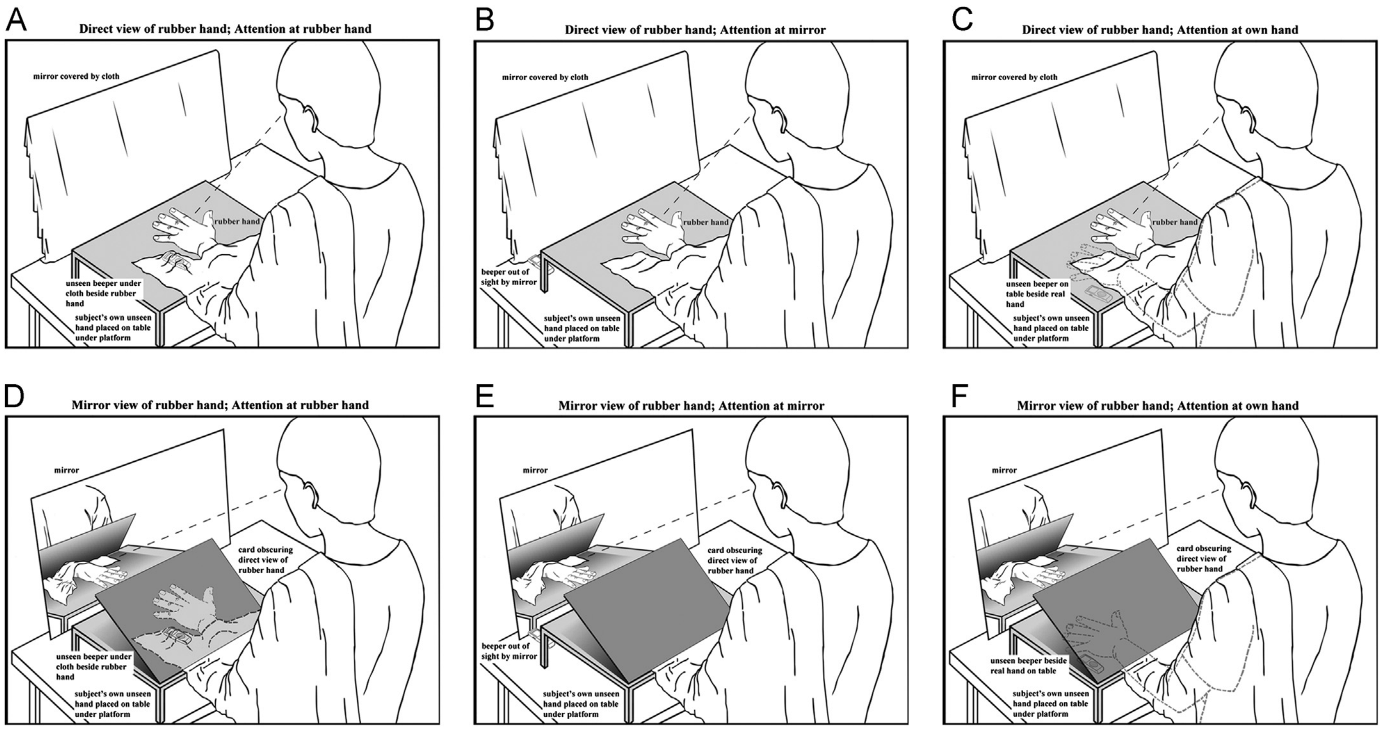


Fig. 2. Setup of the rubber hand illusion experiment. Healthy subjects viewed the rubber hand directly (pictures A, B & C) or via the mirror (pictures D, E & F), while attention shifted from the rubber hand (pictures A & D), mirror (pictures B & E), or own hand (pictures C & F).

identified the spatial location of the beeper with 100% accuracy (beeper placed in each of the three locations in a pseudo-random order and identified with eyes closed).

The order of conditions was counterbalanced between subjects. Results were analysed using repeated measures ANOVA and Bonferonni corrected post-hoc *t*-tests. Alpha was set at 0.05 and all tests were 2-tailed.

5.2. Results

To check the ability to induce the RHI we performed a 2 (stroke: synchronous, asynchronous) by 5 (question: 1–5) repeated-measures ANOVA on data from the condition in which vision of the rubber hand was direct and attention was focused on the rubber hand. There was a main effect of stroking ($F(1,19)=5.24$, $p=0.034$), question ($F(4,76)=15.61$, $p<0.001$) and an interaction between stroking and question ($F(4,76)=9.99$, $p<0.001$), indicated that, similar to previous RHI studies (Longo et al., 2008), synchronous stroking was only effective in changing responses to some of the questions (see Table 2). Post-hoc repeated measures *t*-tests revealed that questions one (How much does it seem that the touch you are feeling is where you see the rubber hand being stroked?) and three (How much does it seem as though the rubber hand is your hand?) were affected by our experiment ($t(19)=4.04$, $p=0.005$ and $t(19)=2.88$, $p=0.05$ respectively. All other $ps>0.1$).

Subsequent 2 (view: direct, mirror) by 3 (attention: mirror, rubber hand, own hand) repeated measures ANOVA of questions one and three revealed no main effect of View (both $ps>0.1$), indicating that although the illusion could be induced, it was not affected by whether the rubber hand was observed directly or in the mirror (see Table 3). The main effect of attention was similarly non-significant for question three ($F(2,38)=2.19$, $p=0.126$), but a significant difference was found between the three locations as measured by question one ($F(2,38)=3.75$, $p=0.033$), with strength of the RHI being significantly greater when attention was on the rubber hand compared with when attention was focused on the subject's own hand. Post-hoc comparisons revealed no significant differences when spatial attention was directed towards the mirror compared with spatial attention being directed at either the rubber hand or participants' own hand (all $ps>0.1$).

6. Discussion

We found that providing GR with mirror feedback of her arm as seen "from the outside" (or from a third-person visual perspective), evoked a complete but temporary remission of somatoparaphrenia. This contrasted her complete disownership of the same limb when observed directly (from a first-person visual perspective). These findings confirm our previous observations (Fotopoulou et al., 2011), on the remission of somatoparaphrenia through mirror feedback. In addition, the current study showed for the first time how this shift in body ownership was modified by a simple manipulation of attention; specifically, although GR showed an almost complete denial of her arm when viewing it directly, she showed a dramatic improvement in limb ownership (100% recognition) when viewing herself in a mirror and directing her attention to extrapersonal space (close to the mirror). When GR viewed herself in the mirror, but directed her attention to peripersonal space (close to the body), she showed a less pronounced improvement in limb ownership (50%). Thus, simply directing selective attention to different sectors of space elicited a change in her sense of body ownership, over and above that produced by the contents of visual feedback.

6.1. Body disownership: perspectives and attention

Looking at one's image in a frontal mirror activates a representation of space near to the body, despite the image of one's body being located at a distant location (Maravita et al., 2000). We propose that when GR looks at herself in a mirror, she is therefore presented with an image of how she looks from the

Table 2
Ratings for each RHI question during synchronous and asynchronous stroking.

Question	Stroke	
	Asynchronous	Synchronous
1. How much does it seem that the touch you are feeling is where you see the rubber hand being stroked?	2.40 (2.23)	4.75 (1.45)**
2. How much does it seem as if you might have more than one left hand?	1.65 (2.13)	1.30 (1.49)
3. How much does it seem as though the rubber hand is your hand?	2.30 (2.25)	3.95 (1.82)*
4. How much does it seem as though you are losing the sense of where your own hand is?	2.35 (2.21)	2.70 (1.87)
5. How much does it seem as though you are losing the sense of owning your hand?	1.80 (2.02)	2.05 (2.11)

Note: Values are mean (SD). Responses to each question given on a 7-point scale (0=not at all, 6=very much).

* $p=0.05$.

** $p=0.005$

Table 3
Responses to questions one and three during the rubber hand illusion, mirror-attention experiment.

Attention	View	
	Direct	Mirror
Question 1		
Rubber hand	4.75 (1.45)	4.55 (1.57)
Own hand	4.05 (1.80)	4.05 (1.61)
Mirror	4.35 (1.93)	4.65 (1.69)
Question 3		
Rubber hand	3.95 (1.82)	3.60 (2.26)
Own hand	3.50 (2.14)	2.90 (1.94)
Mirror	3.70 (2.16)	3.75 (2.05)

Values are mean (SD). Min=0, Max=7.

outside (i.e. a third-person perspective of herself), yet her affected body parts are to an extent represented as being located in peripersonal space. Focusing attention on the mirror may allow GR to further enhance the processing of signals related to her body in a third-person perspective as seen in the mirror space. Her increased body ownership may thus be linked with such processing of bodily signals in extrapersonal space. The extent to which this effect involves a competition versus integration of different body representations, or alternatively a more 'precise' processing of signals about prediction errors (see Fotopoulou, 2012; 2013 for discussion) remains to be explored in further studies.

It might alternatively be suggested that GR's change in limb ownership following our manipulation of spatial attention was simply a result of increased task difficulty (i.e. of having to split auditory and visual attention, or attend to two different locations in space). However, several findings from our study render such explanations unlikely. Firstly, splitting spatial attention did not alter the performance of right-hemisphere control patients, or the strength of the RHI in the healthy controls. Moreover, GR's performance was similar when we used vision or touch as alternative means of orienting attention. This suggests that changes in GR's body ownership were not simply a result of her attention being diminished because it was divided between various sensory modalities and locations. Attending to two sensory modalities can, in fact, be more efficient when attention is spatially divided rather than focused (Santangelo, Fagioli, & Macaluso, 2010).

It might also be argued that GR failed to orient her attention to the required spatial location, or was unable to divide her attention successfully. Unfortunately, we did not formally assess the presence of auditory neglect in GR, nor her divided attention capacity or eye gaze during the task; however, we did assess and control for visuospatial and personal neglect in all our patients, and our pre-experimental checks established that GR and all controls were able to shift spatial attention, and describe accurately what they saw, in the various stimulus locations. We also attempted to control attention during the task by providing an orienting cue in the required location (i.e. the clicker/ beeper), and observed where subjects were looking. Existing research demonstrates the ability of neglect patients to orient attention to their neglected side in order to detect an auditory stimulus (Soroker, Calamaro, Glicksohn, & Myslobodsky, 1997), and shows that the presence of attentional impairments such as unilateral neglect would not necessarily abolish GR's ability to divide her attention (see Lux, Thimm, Marshall, & Fink, 2006). Indeed, the required shift in selective attention was the only change between conditions in our main experiment that produced dramatically different reports of body ownership.

Our supplementary control manipulations (see Supplementary Materials) further demonstrated that GR did not suffer from a general inability to make correct, doxastic ownership judgments, since she was able to correctly attribute ownership of other body parts and objects. GR's correct identification of the examiner's arm in the mirror shows that her improved ownership is specific to seeing her own arm in the mirror, and not due to the visual coherence of the image (i.e. other arms viewed in the mirror are not incorporated into GR's own body representation). Finally, GR's ability to correctly recognise the laterality of her left arm in the mirror demonstrates her capacity to perform the mental transformation of an image that is left-right reversed. This findings allows us to discount the possibility that improved ownership in GR was an artefact of her misrecognising or considering the image in the mirror to be her right hand.

6.2. *Permanent updating of body ownership*

GR's improved limb ownership lasted only for as long as the mirror was present, and reverted to an almost complete disownership moments after its removal (see also Verret & Lapresle, 1978). This finding suggests that GR was unable to permanently integrate the first- and third-person body representations afforded by direct and mirror views in order to form a coherent, stable and updated sense of body ownership. The effects of vestibular stimulation are also noted to be temporary (Bisiach et al., 1991; Rode et al., 1992). Moreover, similar, temporary improvements in awareness have also been noted in anosognosic patients with verbal perspective-taking tasks (Fotopoulou, 2008; Fotopoulou, Conway, Solms, Tyrer, & Kopelman, 2008; Marcel et al., 2004). It remains to be ascertained whether persistent training with either mirrors, or with verbal perspective-taking tasks, can enhance these patients' ability to form an updated and coherent body representation and what kind of additional deficits underlie such lack of updating (see Fotopoulou, 2012, 2013 for discussion).

6.3. *The rubber hand illusion mirror experiment*

Our rubber hand illusion experiment aimed to examine, in healthy controls, dynamic changes of body ownership relating to similar manipulations of spatial perspective and attention as in the main experiment with GR. Even though the 'extra' rubber hand required in the RHI renders direct matching of conditions between the two experiments impossible, the results of the two experiments can be considered in parallel to an extent (see Zeller, Gross, Bartsch, Johansen-Berg, & Classen, 2011). Given that healthy subjects do not feel a sense of ownership for the rubber hand when it is rotated 180 degrees from the position of their own hand (Costantini & Haggard, 2007), we expected to find differences between rubber hand ownership in conditions of direct versus mirror view. However, consistent with Bertamini, Berselli, Bode, Lawson and Wong (2011) we found that the illusion could be induced in the mirror, and with no difference in the strength of the illusion when viewing the rubber hand directly or in the mirror. It is likely that, given our life-long exposure to mirrors, mirror-based visual information about the body can be readily transformed to egocentric coordinates and combined with other bodily signals in personal and peripersonal space (tactile stimulation in the present case; see also Maravita et al., 2000). It is perhaps this well-established representation of the body in mirror view that also allows somatoparaphrenic patients to show intact body recognition in the mirror, even though they fail to recognise their body in direct view and update their body ownership more generally.

Rubber hand ownership was greatest when spatial attention was focused on the rubber hand, whereas focusing attention on mirror space did not have a differential effect on rubber hand ownership, and shifting attention to one's own hand reduced the strength of the illusion. This latter finding further suggests that focusing attention in peripersonal space might enhance one's first-person representation of the body. In healthy individuals, this manipulation reduces ownership of a foreign body part (i.e. the rubber hand), whilst in patients with somatoparaphrenia this same enhancement of the (impaired) body representation increases disownership. An alternative, but not incompatible explanation, might be that focusing attention on one's own arm reinforces the current ownership status (i.e. disownership in GR and ownership in controls), while shifting focus away from the body allows a change in ownership status to occur (i.e. re-ownership in GR and ownership of the rubber hand in controls). Further research is needed to explore these possibilities, and the mechanisms that underlie differences in body ownership when attention is shifted to multisensory integration occurring in different locations near to the body (e.g. focusing attention on the rubber hand vs. the real hand).

6.4. *Neural mechanisms of body ownership and attention in somatoparaphrenia*

Our small sample size did not warrant a statistical comparison of the lesions found in GR and our control patients; however, our subtraction of shared lesion voxels revealed more unique damage to GR compared with controls in limbic areas, inferior frontal regions, and associated white matter. Our findings of increased damage in the amygdala, hippocampus, opercular part of the inferior frontal lobe, and white matter connections between these areas (i.e. fornix, terminal stria, and uncinate fasciculus) are consistent with recent anatomical accounts of somatoparaphrenia (Gandola et al., 2012; Invernizzi et al., 2013). However, these findings are not consistent with the predicted damage to dorsal areas responsible for egocentric and near space processing (e.g. superior parietal lobe), and relative sparing of areas subserving allocentric and extrapersonal space processing (e.g. the hippocampus). This unexpected neuroanatomical finding requires further examination in future studies, since it highlights ongoing debates in the literature regarding the neural bases of, and interactions between, allocentric and egocentric processes (see Chen et al., 2012; Neggers et al., 2006), and first- and third-person perspectives (Vogeley & Fink, 2003).

GR's lesion to the anterior insula is consistent with idea that the insula plays an important role in body ownership (Baier & Karnath, 2008; Karnath, Baier & Nägele, 2005). Nevertheless, the co-occurrence of insula damage in our control patients is also consistent with recent work suggesting that damage to this area is not sufficient to produce somatoparaphrenia (Gandola et al., 2012). By contrast, our study did not support the recent findings of Feinberg et al. (2010), linking somatoparaphrenic delusions with lesions to the orbitofrontal cortex. Although GR's lesion extends to the posterior parts of the inferior frontal gyrus, orbitofrontal areas were unaffected (see Gandola et al., 2012, for similar findings). As such, damage to the orbitofrontal cortex may not directly lead to somatoparaphrenia, but might instead be linked to the fact that more conceptual aspects of perspective-taking and mentalising have been associated with ventromedial prefrontal and orbitofrontal cortex involvement (Qureshi, Apperly, & Samson, 2010; Samson, Apperly, Kathirgamanathan, & Humphreys, 2005; Vogeley et al., 2001)

The current study also demonstrated for the first time how attention could modulate body ownership in somatoparaphrenia. Our limited lesion-mapping investigation makes it impossible to provide a definitive account of the neuroanatomical mechanisms underlying this effect; however, our findings may be successfully related to an existing neuroanatomical model of attentional control. Corbetta and Shulman (2002) suggest that partially segregated frontoparietal networks carry out different attentional functions: a bilateral dorsal system comprising parts of the superior frontal cortex (fontal eye field) and dorsal parietal lobe (intraparietal sulcus/superior parietal lobule) is thought to be specialised for goal-directed (top-down) selecting and responding to visual stimuli, while a right-lateralised ventral system that includes inferior frontal cortex (inferior and middle frontal gyri) and the temporoparietal junction (TPJ) (inferior parietal lobule/superior temporal gyrus) is involved in stimulus-driven (bottom-up) detection of behaviourally relevant stimuli (note however that some discrepancies exist between functional neuroimaging studies of spatial attention in healthy controls and lesion-mapping studies of neglect; see Corbetta, Kincade & Shulman, 2002).

Lesions in our somatoparaphrenic patient were restricted to the right-hemisphere, involved the TPJ, and were more extensive than controls in the inferior frontal gyrus and white matter tract (i.e. uncinate fasciculus) connecting the limbic system and frontal cortex. Thus, the areas damaged in GR best match those of the stimulus-driven ventral attentional network, while the goal-directed dorsal network appears to be relatively intact. As such, we speculate that the attention-based modulation of limb ownership in GR may be the result of either: (i) our facilitating the goal-directed (dorsal) network to direct attention to relevant, third-person information about the body, or alternatively, (ii) our manipulation serving to enhance neural activity in residual parts of the defective ventral network, which disengages current actions in favour of new, behavioural responses (Corbetta & Shulman, 2002). Future functional imaging studies are needed in order to assess this hypothesis.

Finally, our study shows that it is only when a right-hemisphere lesion impairs the subjective perception of body-part ownership from an egocentric/first-person perspective, as detailed above in our somatoparaphrenic patient, that a shift in attention causes changes in body ownership. Contrastingly, when right-hemisphere damage does not produce disownership, or changes in limb ownership are not the consequence of such damage (such as in our control patients and rubber hand experiment with healthy controls), this shift of attention does not change the sense of body ownership. Thus, the beneficial effect of spatial attention demonstrated in our patient depends specifically on her right hemisphere lesion and impaired first-person body representation.

6.5. Limitations

We also acknowledge some final limitations of our single case report. Collecting systematic data on somatoparaphrenic patients presents several difficulties; for example, the quantification and characterisation of delusional claims are especially problematic given variability in behaviour within and between patients. Neuroanatomical conclusions drawn from single cases must also be done so with caution. Nevertheless, detailed descriptions of specific somatoparaphrenic cases, combined with carefully controlled and repeated experimental manipulations, remain important for characterising the clinical variability of the syndrome, and understanding the subjective and neural mechanisms of body ownership. Thus, although the present study involved only a single case of somatoparaphrenia, we still considered this to be of particular value given the rarity of the condition and dearth of existing experimental studies.

Unfortunately, we also did not assess whether GR's limb ownership changed when she viewed her arm directly and focused attention in extrapersonal space. On the basis of our previous findings, we expected that re-ownership would occur only when GR was provided with a third-person visual perspective. However, formal testing of this manipulation would be interesting to include in future research. To our knowledge, there has never been a reported case of improved body ownership in such conditions, and we have not observed clinically an improvement in ownership when a patient's attention is 'distracted' during direct view of their affected limb.

6.6. Conclusions

The present study confirms our previous finding that somatoparaphrenic patients who deny the ownership of their own left hand in direct view, are able to recognise it as their own in the mirror (see Fotopoulou et al., 2011), and extends our previous study in showing that this temporary reinstatement is significantly enhanced when attention is drawn to extrapersonal, mirror space. These manipulations suggest that body recognition can be improved by visual feedback from a third-person perspective, but self-recognition even in this perspective deteriorates when spatial attention is directed to the first-person representation of the body in peripersonal space. The temporary nature of this effect indicates that patients with somatoparaphrenia may be unable to integrate information from first- and third-person perspectives into a stable body representation, and instead they remain delusional about their own bodies despite momentary self-recognition.

When we manipulated vision and attention in the same way in healthy controls undertaking the Rubber Hand Illusion, we found that ownership of the rubber hand occurred in both direct and mirror view, but shifting attention between peripersonal and extrapersonal space had no effect on rubber-hand ownership. This indicates that the effect of third-person visual feedback and attention on body ownership depends on damage to a network of right-hemisphere structures including the limbic system, inferior frontal lobe, and white matter connections, which may subserve a first-person representation of the body. Thus, isolation of visual perspectives on the body, and the division of attention between two different locations, is not sufficient to affect body ownership in healthy individuals and right hemisphere controls with intact body representations.

Finally, our qualitative lesion analysis supported some previous group findings on the neural basis of somatoparaphrenia, including critical cortical and subcortical lesion sites, but further suggested that the sparing of some dorsal frontal areas may be linked with the dynamic changes of ownership observed in this study.

Acknowledgements

The authors would like to thank the patients and their families for their participation. We are also grateful to senior physiotherapist Sandra Chambers and the staff at Mark Ward, St Thomas's Hospital, for their assistance with this study. Finally, the authors thank Simone Pernigo and Valentina Moro for their support with lesion identification and representation, and Tanya Adams for her illustrations.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2013.03.029.

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