

Visual body recognition in a prosopagnosic patient

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ABSTRACT

Conspicuous deficits in face recognition characterize prosopagnosia. Information on whether agnostic deficits may extend to non-facial body parts is lacking. Here we report the neuropsychological description of FM, a patient affected by a complete deficit in face recognition in the presence of mild clinical signs of visual object agnosia. His deficit involves both overt and covert recognition of faces (i.e. recognition of familiar faces, but also categorization of faces for gender or age) as well as the visual mental imagery of faces. By means of a series of matching-to-sample tasks we investigated: (i) a possible association between prosopagnosia and disorders in visual body perception; (ii) the effect of the emotional content of stimuli on the visual discrimination of faces, bodies and objects; (iii) the existence of a dissociation between identity recognition and the emotional discrimination of faces and bodies. Our results document, for the first time, the co-occurrence of body agnosia, i.e. the visual inability to discriminate body forms and body actions, and prosopagnosia. Moreover, the results show better performance in the discrimination of emotional face and body expressions with respect to body identity and neutral actions. Since FM's lesions involve bilateral fusiform areas, it is unlikely that the amygdala-temporal projections explain the relative sparing of emotion discrimination performance. Indeed, the emotional content of the stimuli did not improve the discrimination of their identity. The results hint at the existence of two segregated brain networks involved in identity and emotional discrimination that are at least partially shared by face and body processing.

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1. Introduction

Prosopagnosia is a relatively rare neuropsychological disorder characterized by the inability to identify human faces, including one's own face, in terms of both configural processing and/or the processing of features. The ability to recognize faces relies on processing not only the shapes of individual features but also the relationships between them (Maurer, Le Grand, & Mondloch, 2002). Since prosopagnosic subjects can easily identify individuals on the basis of their voice or verbal descriptions, prosopagnosia cannot be considered as a general incapacity to identify people, but rather as a specific deficit regarding the visual recognition of faces. This deficit occurs despite intact intellectual and cognitive functions and comparatively preserved low-level visual processing.

Prosopagnosia usually occurs following bilateral brain damage involving the ventral occipito-temporal cortex (Damasio, Damasio, & Von Hoesen, 1982; Rossion et al., 2003), although many prosopagnosic patients with right unilateral lesions have

been reported (Barton, Press, Keenan, & O'Connor, 2002; Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010; De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994; Uttner, Bliem, & Danek, 2002). Furthermore, developmental forms of prosopagnosia have also been described (Behrmann & Avidan, 2005; Duchaine, Yovel, Butterworth, & Nakayama, 2006).

Prosopagnosia may or may not be accompanied by object recognition deficits; however, it is worth noting that some of the patients reported as being affected by pure prosopagnosic deficits (Bukach, Bub, Gauthier, & Tarr, 2006; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008; Wada & Yamamoto, 2001) have not been tested with a degree of detail that allows excluding the presence of minor object recognition deficits (Busigny, Graf, Mayer, & Rossion, 2010).

Neuroimaging studies have revealed that face perception selectively activates specific visual system areas including the bilateral fusiform face area (FFA) in the middle inferior temporal cortex (Kanwisher & Yovel, 2006; Kanwisher, McDermott, & Chun, 1997; Sergent, Otha, & MacDonald, 1992) and the occipital face area (OFA) in the inferior lateral occipital gyrus (Gauthier et al., 2000; Peelen & Downing, 2007; Pitcher, Walsh, & Duchaine, 2011; Weiner & Grill-Spector, 2010). These regions are fundamentally involved in the

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visual analysis required for face identification and, crucially, are damaged in prosopagnosic patients (Rossion et al., 2003; Sorger, Goebel, Schiltz, & Rossion, 2007; Steeves et al., 2009). Other face-sensitive brain regions, in particular the superior temporal sulcus (STS), seem to be mainly involved in the representation of changing facial features, such as emotional expressions, rather than in the discrimination of stable features such as facial identity (Haxby, Hoffman, & Gobbini, 2000; Kanwisher & Yovel, 2006).

In recent years, knowledge of the neural mechanisms of face perception has been expanded by research on the neural substrates for the processing of emotional facial expressions (Morris et al., 1998; Vuilleumier, Armony, Driver, & Dolan, 2003; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). Several studies have provided evidence, both in healthy subjects and in neurological patients (de Gelder, Frissen, Barton, & Hadjikhani, 2003; de Gelder et al., 2010), that the emotional content of facial expressions strongly influences face perception (Vuilleumier & Schwartz, 2001; Vuilleumier, 2005). Patients with lesions in the striate visual cortex (V1) are able to guess above chance level the affective valence of facial expressions presented in their blind fields despite having no conscious perception of the stimuli (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999; De Gelder, Morris, & Dolan, 2005). In a similar vein, a modulation of visual extinction according to the emotional content of facial expressions has been shown in patients with hemispatial neglect, as emotional facial expressions presented to their contralesional visual hemifield tend to call for attention and are detected more accurately than neutral faces or objects (Vuilleumier et al., 2002). Emotionally expressive faces also guide attention in individuals with acquired or developmental prosopagnosia, who show enhanced activation of face-selective visual areas, such as the FFA, in response to faces expressing emotions (Peelen, Lucas, Mayer, & Vuilleumier, 2009; Van den Stock, Van de Riet, Righart, & de Gelder, 2008). This emotional modulation is thought to be based on the direct modulatory influences of the amygdala that promotes the processing of emotionally salient events (Amaral & Price, 1984; Morris et al., 1998; Rotshtein, Malach, Hadar, Graif, & Hendler, 2001; Sah, Faber, Lopez de Armentia, & Power, 2003; Vuilleumier et al., 2004).

Important information about the identity and emotional state of co-specifics, however, is not solely conveyed by faces, but also by non-facial body parts (de Gelder et al., 2010).

Recent studies have shown that non-facial body parts, in the same way as faces, represent a special perceptual category. Indeed, the cognitive processing and the neural representations of both faces and bodies seem to be at least partially segregated from those of non-corporeal objects and share some anatomic-functional similarities (Downing, Jiang, Shuman, & Kanwisher, 2001; Moro et al., 2008; Orlov, Makin, & Zohari, 2010; Urgesi, Berlucchi, & Aglioti, 2004; Urgesi, Candidi, Ionta, & Aglioti, 2007; Weiner & Grill-Spector, 2010).

Recent behavioral studies have shown similarities in the cognitive processes involved in face and body perception. One example is the so-called inversion effect that refers to the decrease of performance in the recognition of inverted as compared to upright stimuli. The inversion effect is reliably measured for faces and bodies but is weaker or absent for other stimulus categories (Minnebusch, Keune, Suchan, & Daum, 2010; Reed, Stone, Bozova, & Tanaka, 2003; Yin, 1969).

Consistently, the brain areas specifically dedicated to the processing of faces (FFA and OFA) are in close proximity to the regions involved in body perception. The extrastriate body area (EBA) is localized in the postero-inferior temporal cortex, very close to the OFA, while the fusiform body area (FBA) is localized in the fusiform gyrus in the middle temporal cortex, partially overlapping the FFA (Peelen & Downing, 2007). In a similar vein, by combining psychophysical studies with lesion-mapping techniques, a recent

neuropsychological study has shown that lesions involving the EBA are causatively associated with exclusive impaired recognition of the body, while lesions of ventro-medial occipito-temporal areas induce deficits in both face and body recognition (Moro et al., 2008).

Furthermore, non-conscious processing of emotions has also been documented for faces as well as for bodies, indicating the possibility that these two types of stimuli share a common, subcortical representation, probably involving subcortical structures as the amygdala and superior colliculus (de Gelder et al., 2010; Tamietto & de Gelder, 2010; Van de Riet, Grezes, & de Gelder, 2009; but see also Pessoa & Adolphs, 2010). Indeed, visual presentation of both facial and bodily emotional expressions induces faster facial mimicry responses and greater pupil dilation (indicative of autonomic arousal) when they are non-consciously perceived as compared to when they are consciously perceived (Tamietto et al., 2009).

Considering the substantial overlap between face and body processing, a few studies have addressed the issue of whether and how body perception is affected in prosopagnosia. A first study investigated visual perception of the body in a single case of developmental prosopagnosia (Duchaine et al., 2006). In a matching-to-sample task, the authors assessed the patient's performance in the recognition of faces as compared to bodies and found a clear dissociation between impaired face and spared body perception abilities. The dissociation between face and body processing seems to be confirmed by the results of another study (Van den Stock et al., 2008) showing that developmental prosopagnosics present anomalous neuro-functional representations of neutral faces but not of bodies and bodily expressions. This study also revealed a weaker category-selective organization of body and face representations in developmental prosopagnosic patients, with higher activation of the EBA during the perception of neutral faces and greater activation of the inferior occipito-temporal cortex during the perception of bodies.

Moreover, electroencephalographic recordings showed that the N170 component of event-related potentials (ERP) was not modulated by the inversion of face and body stimuli in three out of four developmental prosopagnosics, suggesting a disorder in the development of configuration-based perceptuo-visual strategies which may affect both face and body processing (Righart & de Gelder, 2007).

So far, the only study that has investigated body perception in an acquired prosopagnosic patient did not report any difficulties in recognizing bodies. In addition, as in the case of healthy subjects, this patient showed strong activation in both rFFA and rFBA and preserved functional modulations induced by emotional body expressions (Peelen et al., 2009).

Due to the low number of patients affected by acquired prosopagnosia and the enormous heterogeneity in terms of the site and size of lesions, to date a possible link between body and face perception remains unclear and the question concerning the visual perception of bodies in prosopagnosia is still under debate (Minnebusch & Daum, 2009).

Here we report the case of a young man (FM) who became prosopagnosic after cerebral damage involving the bilateral posterior occipito-temporal regions. In a series of matching-to-sample tasks, we investigated his ability to discriminate faces and bodies with respect to objects. Moreover, we explored the possible modulation of body and face perception by the emotional content of the stimuli, and controlled for perceptual and emotional selectivity by using dogs' faces and knives. We also tested whether the deficits in discriminating human face and body identity may be dissociated from the ability to discriminate face and body emotional expressions. Finally, in a control experiment, we also studied the dissociation between FM's abilities to discriminate body identity and body actions (Moro et al., 2008).

2. Method

2.1. Case report

FM is a right-handed man with a relatively high standard of education (17 years of schooling) who works as a clerk. He exhibited face recognition deficits after a stroke following a cardiological surgical operation in October 2009, when he was 35 years old. After the operation, he did not regain consciousness immediately, appeared agitated and did not respond to stimuli. An anatomical MRI scan revealed bilateral ischemic cerebral lesions in the temporo-occipito-parietal cortex, involving the calcarine, fusiform and inferior temporal areas and the left thalamus.

At the first neuropsychological examination, three months after the onset of the neurological condition, he did not show motor or somato-sensorial deficits. He had regained consciousness but was not well oriented in time and was not fully aware of his condition. The stroke had left FM with profound difficulties in recognizing objects as well as familiar and unfamiliar faces, both in everyday life and in formal clinical and laboratory tests. Moreover, he showed alexia but not agraphia and had no problems with colour perception. His use of language was fluent but with frequent anomies and semantic paraphasias.

2.2. Neuropsychological assessment

Six months after the onset of cerebral damage, FM underwent an extensive neuropsychological examination. At that time he and his relatives complained about his total inability to discriminate human faces, but reported that his perception of everyday objects had recovered. However, when specifically asked about any residual deficits, FM conceded that he occasionally mixed up various items belonging to the same semantic category (e.g. fruits or tools) or failed to remember their names.

General cognitive and language deficits largely improved, as shown by his scores in the Verbal Subtests of the Wechsler Adult Intelligence Scale-Revised (VIQ, score = 113; *Weschler, 1997*), the Cognitive Estimation Task (score = 16 – cut-off ≤ 19; *Della Sala, Mac Pherson, Phillips, Sacco, & Spinnler, 2003*), the Attentional Matrices (score = 54 – Equivalent Score (ES) = 3; *Spinnler & Tognoni, 1987*) and the Aachen Aphasia Test (token test = 0 errors; repetition = 0 errors; reading = 30/30; writing = 60/60; denomination: objects = 30/30; colours = 30/30; composed names = 24/30; oral comprehension = 54/60; written comprehension = 49/60; *Luzzatti et al., 1991* – in these latter tasks, he complained that he was not able to see the whole scene of complex images). Standard tests were used to assess verbal and visual memory (Word span, Verbal Supra-span, Story recall, Spatial span, Long-term spatial memory) (*Spinnler & Tognoni, 1987*) and verbal working memory (Listening Span Test-BAC, *De Beni & Borella, 2008*). These tests revealed deficits in verbal and spatial short term memory (Word and Spatial span = 4 – ES = 1) and in verbal fluency (score = 10; ES = 0; *Novelli et al., 1986*), but normal scores in all the tasks concerning learning, long-term memory and working memory (Verbal supra-span = 106 – ES = 3; Delayed repetition = 9 – ES = 4; Long-term spatial memory = 20.16 – ES = 2; Story recall = 13.25 – ES = 4; Listening span test = 24/40 – cut-off ≤ 19.06).

Low-level visual processing was not completely preserved in FM. A computerized campimetric examination showed “a generalized deficit of visual field, with many patches of reduced sensitivity, which had a greater extent in the lower hemifield”. In addition the patient showed a bilateral deficit in visual acuity.

When shown a picture, FM declared: “It is not that I see an object and I do not know what it is . . . My problem is that I see badly, out of focus, indistinctly . . . and I try and guess. When I see it, I know what the object is . . .”. And also: “If I see the upper part of the image I cannot see the lower part. If I look at the lower part, I see something in the upper part too”. Nevertheless, when asked to decide if the mouth of the person in front of him was open or closed he replied: “I can't see a mouth in a face (or a nose or the eyes. . .). I see a black hole and I think it should be the mouth”.

Testing for optic ataxia (i.e. the patient's difficulty in reaching when pointing or grasping) revealed no such deficit. This was assessed by two investigators, one sitting in front of the patient and the other standing behind him. FM looked fixedly at the nose of the investigator sitting in front of him and grasped an object that was presented by the second investigator at various locations in either the left or right visual half field. Ten reaches were tested for both hands separately and no misreaches were observed (*Karnath, Rüter, Mandler, & Himmelbach, 2009*).

2.3. Visuo-perception and visual mental imagery abilities

A clinical assessment confirmed the patient's ability to recognize real life objects (score = 24/24) and colours (score = 12/12). Spatial orienting and navigation skills, recall of routes in familiar environments and the ability to imagine new routes following the examiner's indications were all preserved.

Perceptual abilities were investigated by means of the Birmingham Object Recognition Battery (*Riddoch & Humphreys, 1993*). The very long response times in FM's performance indicated the presence of signs of object recognition difficulties. Nevertheless, his scores in the BORB subtests for pre-categorical visual processing (i.e. encoding of basic dimensions, linking together of features and segmentation of an object from its background and encoding of the properties of objects that remain invariant across changes of view) were in the normal range (*Table 1*). He also had normal scores in the Constructional Apraxia Test (score 14/14 – ES = 4; *Spinnler &*

Table 1

FM's performance in Object Recognition tasks (subtest for apperceptive agnosia in upper part and subtest for associative agnosia in lower part), Constructional apraxia (*Spinnler & Tognoni, 1987*) and Visual Imagery tasks (*Policardi et al., 1996*). In bold the scores under cut-off. Mean and SD scores, as reported in the Birmingham Object Recognition Battery (*Riddoch & Humphreys, 1993*) and *Policardi et al. (1996)* are indicated in the third column.

BORB	Score	Cut-off	Mean (SD)
Copying (n. 9)	9	9	–
Length match (n. 30)	28	24	26.9 (1.6)
Size match (n. 30)	24	23	27.3 (2.4)
Orientation match (n. 30)	20	20	24.8 (2.6)
Position of gap (n. 40)	34	27	35.1 (4)
Letters (n. 36)	34	–	–
Overlapping letters (n. 36)	36	–	–
Geometric shape (n. 36)	29	–	–
Minimal feature match (n. 25)	19	19	23.3 (2)
Foreshortened view (n. 25)	19	16	21.6 (2.6)
Drawing from memory (6)	6	6	–
Object decision task: hard (32)	16	23	27 (2.2)
Object decision task: easy (32)	24	24	28.9 (2.4)
Item match task	29	26	30 (2.2)
Associative match task	27	22	27.5 (2.4)
Picture naming	10	8	12.7 (2.2)
Constructional Apraxia Test	14	11.25	–
Street Completion Test	0	5.25	–
Visual Imagery Questionnaire	–	–	–
Comparison of similar letters (n = 14)	14	–	14 (0)
Comparison of paired animals (n = 30)	30	–	29.3 (0.64)
Animal ears (n = 20)	17	–	18 (1.18)
Animal legs (n = 30)	29	–	29.1 (0.94)
Animal tails (n = 20)	16	–	18.7 (1.10)
Thickness of object judgment (n = 30)	29	–	29.6 (0.66)

Tognoni, 1987). As compared to the BORB cut-offs (2 standard deviations from the mean score in a healthy group of 30–39 people; *Riddoch & Humphreys, 1993*), FM's accuracy fell in the normal range in associative tasks that require accessing stored knowledge about particular observed objects, except in the Object decision task (score: 16/32, cut-off: 23). In this task the subject was presented with line drawings of real or unreal chimeric animals or tools and asked to determine whether or not the depicted objects exist in real life. FM was also totally unable to carry out the Street Completion Test (score 0/14 – ES = 0; *Spinnler & Tognoni, 1987*), a task requiring the mental integration of separate parts of an image. In this test, each trial presents several ink stains and broken outlines that only represent a whole image if perceived together (e.g. a dog, a baby). FM's inability to carry out these tasks may be due, at least in part, to a specific deficit in the process of integrating single features of the stimulus but also to visual deficits. In fact, during the tasks he often reported that he needed to move his head and eyes to see all the parts of the image.

To assess whether any concomitant disorder of visual mental imagery might have influenced the patient's performance, six subtests of the *Policardi* and colleagues' Visual Imagery Questionnaire (*Moro, Berlucchi, & Aglioti, 2008; Policardi et al., 1996*) were used. As shown in *Table 1*, the overall performance of FM in visual imagery tasks was normal for both living stimuli (comparison of paired animals; animals' ears, legs and tails) and non-living stimuli (comparison of similar letters; judgment of the thickness of an object).

2.4. Face recognition performance

To confirm that FM's face processing ability was impaired, the Benton Facial Recognition Test (*Benton, Sivan, Hamsher, Varney, & Spreen, 1983*) was administered. As shown in *Table 2*, the patient's performance was below the cut-off value. In order to investigate the presence of residual abilities in the discrimination of faces, FM was presented with further clinical tasks. Where relevant, his performance in the various tasks was compared with that of age-, gender- and education-matched control subjects with no history of neurological or psychiatric illness (see below).

2.4.1. Famous and non-famous faces

FM's ability to recognize famous faces was assessed by means of 12 gray-scale photographs of Italian male celebrities from the political arena and the entertainment industry. All images were taken from the Internet and the faces were presented in a free viewing condition with unlimited time to respond. Providing either the name of the individual (e.g. Gerry Scotti) or any contextual information associated with the person (e.g. a showman) was counted as a correct response (Famous face recognition task in *Table 2*). Since this task was impossible for FM, the same photographs of famous faces were presented randomly intermingled with 12 images of anonymous faces, all showing male subjects. FM was requested to indicate whether these faces represented a famous or a non-famous individual (familiar/unfamiliar discrimination in *Table 2*). Finally, with the aim of establishing whether some covert

Table 2

FM's performance in tasks concerning recognition of faces. Visual imagery of faces is compared with imagery of bodies and dogs' faces. Where possible FM's scores have been compared with Italian normative data (Benton Facial Recognition – Benton et al., 1983; Facial Expression – Meneghini, 2005). Since the other tasks are to be considered trivial for normal controls, an errorless performance is expected. Thus, any score different from the number of items can be considered as an index of disorders in face recognition. The scores under the cut-off value are in bold.

	Score	Cent/cut-off
Face recognition		
Benton Facial Recognition (n. 27)	17	10 ^o cent
Famous face recognition (n. 12)	0	12
Familiar/unfamiliar (n. 24)	0	24
Forced choice (n. 12)	7	12
Sex classification (n. 32)	20	32
Facial expression (n. 36)	12	≤18.77
Face visual imagery		
Face (n. 15)	8	13.33 (0.65)
Body (n. 15)	14	13.17 (0.72)
Dog (n. 15)	13	12.83 (1.03)

implicit recognition was preserved, FM was told the name of a celebrity and was asked to indicate which of two pictures of famous faces matched the identity of the person named. As shown in Table 2 (Forced choice = 7/12), in this last condition, FM's performance was due to chance. A healthy control subject, matched for age, gender and education carried out these tasks without errors.

2.4.2. Male and female faces

FM's ability to classify the sex of faces was assessed using the neutral images from the Ekman and Friesen (1976) set, which has been widely used in previous brain lesion patient studies (Calder, Keane, Cole, Campbell, & Young, 2000; Humphreys, Avidan, & Behrmann, 2007). Since both the hair and external features are removed, classification decisions can be based solely on the analysis of internal facial features of the stimuli. A total of 32 images (16 female and 16 male) were presented one at a time on a computer screen for an unlimited time and a decision about the sex of the individual shown in the image was requested. While the control subject executed the task without errors, FM also showed a marked deficit in this task (score = 20/32).

2.4.3. Recognition of facial expressions

To evaluate the recognition of facial expressions, we used an Italian modified computerized version (Meneghini, 2005) of the Reading the Mind in the Eyes Test, which assesses the attribution of emotions (Baron-Cohen, Jolliffe, Mortimore, & Robertson, 1997; Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001). 36 photographs of faces that show only the eye region are presented one at a time along with four terms describing different emotional states. Participants have an unlimited amount of time to decide which adjective best describes the emotional state of the model. An experimenter records patients' answers. Comparison of FM's score with the score of 30 male Italian control subjects (Meneghini, 2005) demonstrated a clear impairment.

2.4.4. Visual imagery

The presence of visual imagery disorders was investigated by means of a questionnaire that asks for a comparison of the facial appearance of two celebrities from the past and present time: the questions may regard the features (mouth, nose, eyes etc.) or the overall facial shape or configuration (round, angular etc.) of the faces. Examples include: "Who had the bigger moustache: Adolph Hitler or Josef Stalin? (Expected response: Stalin)", "Who has an angular face: Fassino or Di Pietro? (Expected response: Fassino)". The questionnaire was modeled on that of a previous study on face imagery (Barton and Cherkasova, 2003), but was compared to two other questionnaires, one assessing imagery abilities concerning celebrities' bodies and the other assessing imagery of dogs' faces. Examples of these questions include: "Who was fatter: Churchill or Mazzini? (Expected response: Churchill)", "Who has very slim legs?: Alessia Marcuzzi or Valeria Marini? (Expected response: Marcuzzi)", "Who has a square face: a fox-terrier or a collie? (Expected response: the fox-terrier)". 15 items were presented in each questionnaire. FM's scores were compared with those of twelve control subjects matched for age and education (Table 2). The Crawford's *t*-test (Crawford & Garthwaite, 2007) showed a significant deficit in the imagery of faces (Crawford's *t* = 7.87, *p* < 0.01), but not in the imagery of bodies (Crawford's *t* = 1.12, *p* = 0.288) and dogs' faces (Crawford's *t* = 0.16, *p* = 0.879). To sum up, the neuropsychological assessment confirmed the deficits of FM in face visual perception and imagery, but also showed signs of disorders in object perception and normal performance in non-facial visual imagery.

2.5. General procedure of the experimental part of the study

The experimental part of this study aimed to investigate whether, besides face processing, body visual perception abilities may also be impaired in the present case

of prosopagnosia (Experiment 1). Moreover, the study aimed to highlight the possible effect of the emotional content of the stimuli on face, body and object visual discrimination. To this aim, we compared the visual discrimination of emotional and neutral face and body pictures with the visual discrimination of images of emotional and neutral living and non-living objects, namely dogs and knives (Experiment 2). Finally, Experiment 3 investigated the possibility that the modulation of face perception by the emotional content of the stimuli could be ascribed to the discrimination of the action implied in the emotional postures rather than to emotional perception *per se*. To this end, we compared FM's abilities in the discrimination of body form and body actions. An age-, gender and education-matched subject served as control. In each experiment, accuracy of responses was automatically recorded and stored for analysis. Individual percentages of correct responses were calculated for each condition and the analyses were performed by means of SPSS (SPSS 13 Inc., Chicago, IL, USA). A two-tailed alpha level of 0.05 was set as the significance threshold for all statistical analyses.

All the experiments reported in this study were carried out in accordance with the principles of the 1964 Declaration of Helsinki and the Local Ethical Committee approved the procedures. All participants provided written informed consent.

2.6. Anatomy

The precise neuroanatomic delineation of FM's lesions was accomplished by means of a three-dimensional reconstruction of his lesion superimposed on the T1-weighted template MRI scan from the Montreal Neurological Institute (MNI). One blind examiner who did not know the clinical deficits of the patient mapped the lesion using the MRICro software (Rorden & Brett, 2000). By superimposing the lesion on the Automatic Anatomical Label template provided by MRICro, we calculated the number and percentage of lesioned voxels, the mm³ and the centre of gravity (centre of mass) in each area of lesion.

Major lesions were located in the bilateral medial and posterior occipital cortex (right: mm³ = 28,883, centre of gravity: *x* = 17, *y* = -86, *z* = 7; left: mm³ = 36,235, centre of gravity: *x* = -21, *y* = -86, *z* = 3). Two additional lesions were situated more anteriorly in the inferior right and left medial temporal areas (right: mm³ = 9134, centre of gravity: *x* = 42, *y* = -24, *z* = -28; left: mm³ = 9620, centre of gravity: *x* = -43, *y* = -30, *z* = -23), partially damaging the lingual and posterior fusiform and mid-fusiform gyri, but sparing the parahippocampal and the anterior-mid-fusiform gyri. Finally, the anatomical images also demonstrated two small lesions in the left thalamus (mm³ = 1926, centre of gravity: *x* = -5, *y* = -18, *z* = 10) and right cerebellar hemisphere (mm³ = 4453, centre of gravity: *x* = 46, *y* = -75, *z* = -35) (see Fig. 1).

3. Experiment 1: recognition of face, body and object parts

3.1. Stimuli and procedure

In this study we investigated the possibility that, in addition to his disorder in face perception, FM may show a deficit in body form discrimination. The task assessed the ability to discriminate body parts, face parts and object parts. The task and stimuli were those used in an rTMS study in healthy individuals (Urgesi et al., 2004), in a modified version which had been previously used in a study with patients affected by cerebral stroke (Moro et al., 2008). The stimuli were colour pictures taken using a digital camera representing face parts, upper-limb parts and motorcycle parts. The upper-limb stimuli included dorsum- and palm-views of hands, entire arms and forearms of different individuals. The face part stimuli included frontal and side views of the noses, lips, eyes and ears of different individuals. The motorcycle part stimuli included frontal and side views of handlebars with rear-view mirrors, front wheels with a front lamp, back wheels with a muffler, saddles, and tanks of various types of motorcycles (Urgesi et al., 2004). FM was given a delayed matching-to-sample task, in which he had to decide which one of two different probe images matched a previously presented sample stimulus.

In each pair of probe stimuli, the non-facial body and facial stimuli were pictures of two different models assuming the same posture or facial expression. Each set was balanced for laterality. In each experimental section, sixteen pairs of stimuli for each category were used and each stimulus was presented twice for a total of 32 stimuli per category, in two different 48-trial blocks. In each block, each stimulus set was presented separately with a block design and a short rest was allowed before proceeding to a different stimulus category. The experiment was repeated in three consecutive

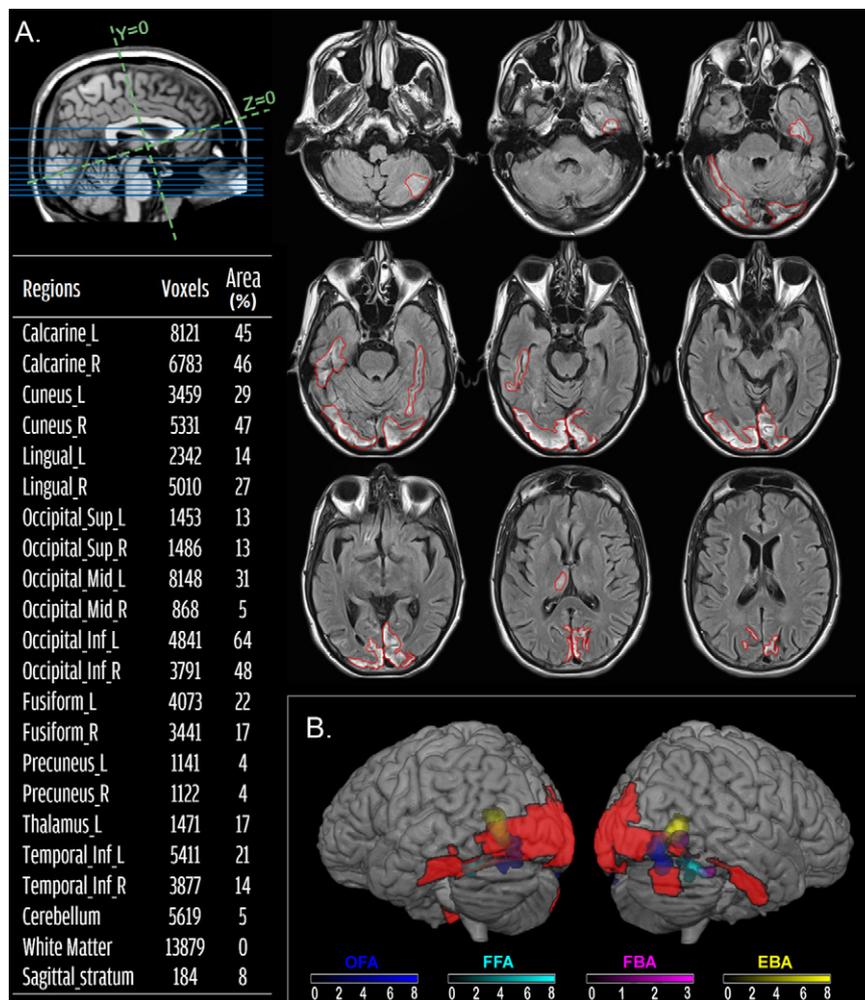


Fig. 1. (A) FM's MRI scan carried out four months after the brain damage. The right hemisphere is on the right. The lesions involve the bilateral occipital cortex, the bilateral medial temporal areas, the left thalamus and the right cerebellar hemisphere. The table shows the number of lesioned voxels and the percentage of lesioned tissue for each area. (B) Cortical renderings of FM's lesions (red) with the areas of body and face selective activations in previous fMRI studies. In keeping with Moro et al. (2008), we created 6-mm-radius ROIs around the coordinates reported in the fMRI studies that localized the extrastriate body area (EBA), the fusiform body area (FBA), the occipital face area (OFA), and the fusiform face area (FFA). The map for each functional area represents the number of fMRI studies that localized the category-selective activations in each voxel. Only voxels activated in at least two studies are reported. See Moro et al. (2008; Supplemental Material and Table S1) for details on selection of fMRI studies. Left hemisphere (LH) is on the left, and right hemisphere (RH) is on the right.

sessions spaced out over three weeks. A total of 96 stimuli per category were presented during the three sessions. Before each experimental session, FM was shown a printed example of the stimuli and completed a six-trial practice block.

Stimulus presentation timing and randomization were controlled using E-prime V1.1 software (Psychology Software Tools Inc., Pittsburgh, PA). FM and the control subject sat 57 cm away from a 15 inch LCD monitor (resolution, 1024 × 768 pixels; refresh frequency, 60 Hz) where stimuli appeared on a white background and subtended a 10.6° × 10.6° square region around the fovea. The trial started with the presentation of a central fixation point lasting 1000 ms. A sample stimulus was presented for 3000 ms at the centre of the monitor. Image persistence was limited by presenting a random-dot-mask (10.6° × 10.6° in size; duration, 1000 ms) obtained by scrambling the corresponding sample stimulus by means of a custom-made image segmentation software. Immediately after the disappearance of the mask, the two probe stimuli appeared and remained on the screen until a response was made. They were presented vertically at the centre of the screen and the position of the matching stimulus was randomized between the upper and lower location. Subjects were asked to indicate verbally which of the two probe stimuli matched the sample stimulus. The trial event timeline is provided in Fig. 2A. The examiner recorded

the subjects' responses, pressing one of the two mouse keys that corresponded to one of the two positions on the screen where the probe stimuli were presented. When the subjects were fixating the centre of the screen, the examiner pressed a key on the keyboard to proceed to the next trial.

3.2. Results

Unsurprisingly the control subject performed the task without errors since the exposure time for the sample stimulus was very long (3000 ms) and allowed accurate observation of the stimuli details. This long exposure time was necessary due to FM's difficulties in visual field exploration, as a result of patches of reduced sensitivity in his visual field.

FM's performance (Fig. 2B) showed a significant difference between face and motorcycle discrimination (face: 71/96, motorcycle: 83/96; $\chi^2(1, N=192)=4.72, p=0.030$) and also between body and motorcycle stimuli (body: 68/96; $\chi^2(1, N=192)=6.98, p=0.008$), while there was no difference between the face and body categories ($\chi^2(1, N=192)=0.23, p>0.05$). Although the control subject's performance was at ceiling for all categories and did not provide information regarding their relative difficulty, previous data of our group (Moro et al., 2008; Urgesi

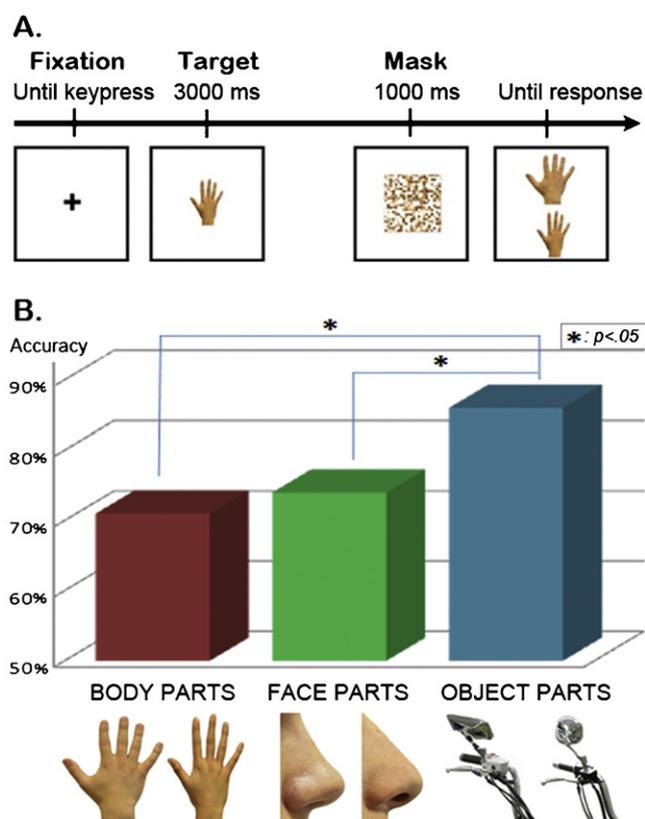


Fig. 2. Body, face and object part discrimination. (A) Schematic representation of a typical trial event. FM was requested to decide which of the two probe stimuli presented in free-viewing conditions matched the sample stimulus previously presented for 3000 ms. (B) Accuracy of FM's responses for the three categories of stimuli. His scores were significantly lower for face and body parts with respect to the discrimination of object parts.

et al., 2004) allow us to exclude the possibility that matching face or body stimuli was more difficult than matching motorcycle parts. Note that the performance of control subjects ($N = 14$, 5 females, mean age = 66.1 years, range = 54–78 years) tested with exactly the same stimuli and procedure but with a presentation time of 1500 ms (Moro et al., 2008), was comparable for the different stimulus categories for both accuracy (bodies: $M = 92.86\%$, $SE = 1.68\%$; faces: $M = 90.18\%$, $SE = 2.7\%$; objects: $M = 93.97\%$, $SE = 1.29\%$; one way ANOVA: $F_{(2,26)} = 1.91$, $p = 0.169$) and reaction times (bodies: $M = 1302.52$ ms, $SE = 129.36$ ms; faces: $M = 1428.94$ ms, $SE = 148.87$ ms; objects: $M = 1334.83$ ms, $SE = 109.32$ ms; one way ANOVA: $F_{(2,26)} = 1.94$, $p = 0.164$).

Thus, these results confirm the presence of face discrimination disorders in FM, but also indicate a deficit in body part discrimination which is significantly greater than the deficit in object part recognition.

Experiment 2 investigated the possible modulation of the emotional content of the stimuli in the visual discrimination of faces, bodies, and objects.

4. Experiment 2: influence of emotional expressions on the recognition of faces and bodies

4.1. Stimuli and procedure

Previous studies with patients affected by hemianopsia (De Gelder & Tamietto, 2007), visual neglect (Tamietto, Geminiani, Genero, & de Gelder, 2007) and prosopagnosia (Peelen et al., 2009) have shown that visual perception of faces may be modulated by

their emotional expressions. In Experiment 2 we explored whether emotional body expressions may modulate the ability to recognize body postures. Furthermore, we tested whether the ability to discriminate face and body identities was dissociated from the ability to discriminate between emotional expressions in faces and bodies. We compared four categories of stimuli: faces, bodies, dog faces and knives. The choice of the stimulus categories was motivated by the necessity to compare neutral exemplars to those that might elicit or depict an emotion of fear within each category. Face stimuli were selected from the neutral and fearful facial expressions of the Ekman and Friesen (1976) set. Body stimuli were black and white pictures taken using a digital camera and representing two male subjects in neutral positions or in a defensive posture indicating fear. The images of dogs and knives were taken from the Internet and were modified with the Adobe Photoshop software (Adobe System Incorporate, San Jose, CA). The images of dogs showed the same animal in neutral positions or in the act of growling. For the knives, the handle remained the same while the blade was modified to emphasize the emotional component (e.g. a knife for a cake or a butcher's knife). For each category, we used 8 emotional stimuli and 8 neutral stimuli. Examples of the stimuli are shown in Fig. 3.

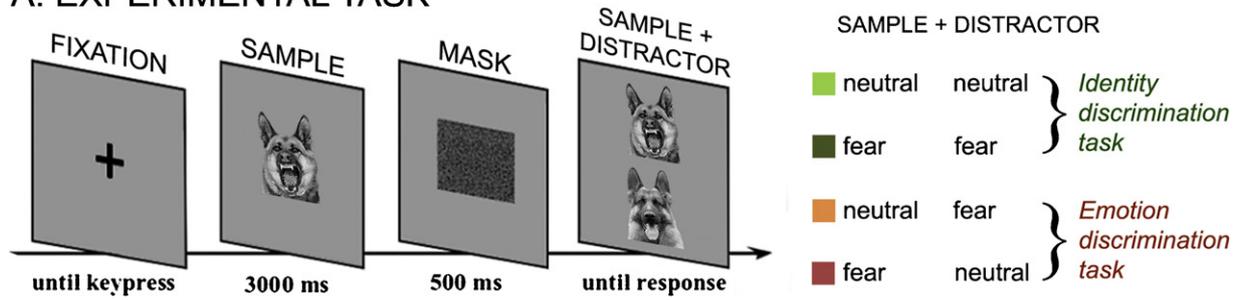
The method and procedure used were similar to those of Experiment 1. FM and the control subject were given a delayed matching-to-sample task in which they had to decide which of two different probe images matched a previously presented sample stimulus (the target stimulus). However, in this second Experiment, two different tasks were randomly used in each block, the *identity discrimination task* and the *emotional discrimination task*. In the identity discrimination task, the matching and non-matching stimuli differed for the morphology of the stimuli (the pictures showed two different individuals, breeds of dog or models of knives) but presented the same emotion (neutral or fearful). In the emotional discrimination task, each probe stimuli depicted two different emotions (neutral or fearful) expressed by the same model. Thus, during these tasks a sample stimulus of fear might be followed by two probe stimuli for fear (depicting two different models, identity discrimination) or one fearful and one neutral probe stimulus (depicting the same model, emotional discrimination). In a similar vein, a sample neutral stimulus might be followed by two neutral stimuli or by a neutral and an emotional posture expressed by two different models.

Forty trials for each category were presented in three sessions. In the first two sessions, eight pairs of stimuli for each category were randomly presented and each stimulus was presented twice for a total of 16 stimuli per category, in two different 32-trial blocks. In the third session only one block was carried out.

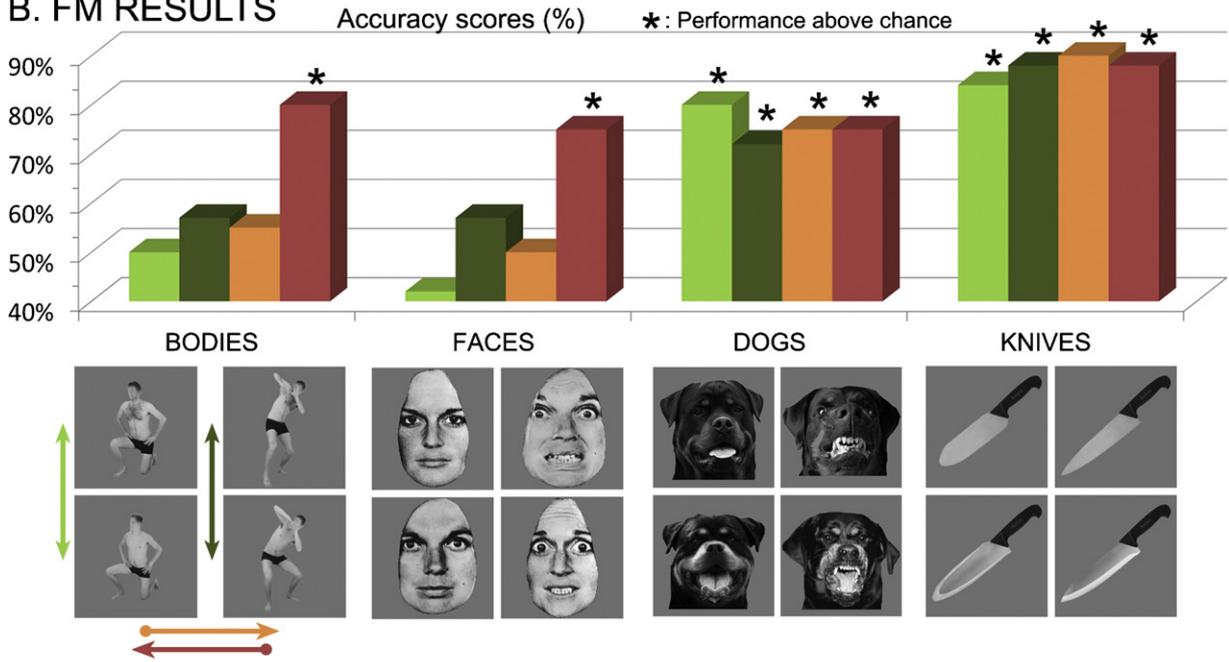
In a preliminary rating experiment, we tested whether the emotional valence and the implied motion of the stimuli may differently affect the discrimination of body, face, dog and knife stimuli. All the stimuli were presented to 15 healthy individuals (age: $M = 26.5$ years; $SD = 3.2$) who were asked to make judgements using a visual analogical scale (VAS, score 0–100 mm) regarding the degree of emotion (“How much does this picture stir up emotions?”) and the degree of movement (“How much does this picture convey motion to you?”) elicited by each stimulus. For each stimulus category and each task, we compared the mean ratings provided by the participants on the emotion and the movement implied in the matching and non-matching probes of each pair (e.g., angry dog vs neutral dog for the emotional discrimination task).

For the emotional discrimination task, we found that the two stimuli in all the pairs differed from each other for both the elicited emotion and their implied movement (paired t -test, all $t_{(14)} > 2.15$, $p < 0.05$). On the contrary, in the identity discrimination task, the two stimuli of each pair did not differ from one another either for the elicited emotion or for their implied movement (paired t -test, all $t_{(14)} < 2.15$, $p > 0.05$). We then

A. EXPERIMENTAL TASK



B. FM RESULTS



C. CONTROLS RESULTS

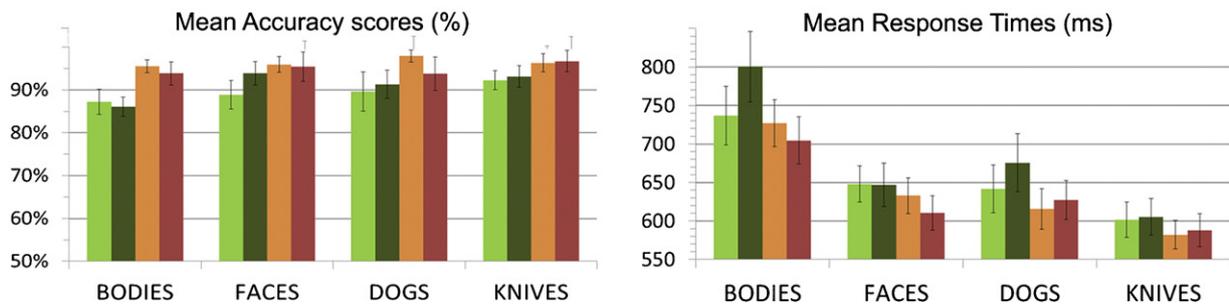


Fig. 3. Discrimination of emotional expressions. (A) Schematic representation of the trial events. (B) Accuracy of FM's responses for the four categories of stimuli, in the conditions of identity (fearful versus fearful and neutral versus neutral) and the discrimination of emotional expressions (fearful versus neutral and neutral versus fearful). For bodies and faces, only in the condition fearful versus neutral was FM's performance above chance. For details of results see Table 3). (C) Mean accuracy and reaction times of controls' responses. Error bars represent standard errors. For details of results see text.

investigated whether the difference between the matching and non-matching probes was consistent across the emotional and motion judgments and across the four stimuli categories. The difference in scores between the two probes of each pair was entered into two repeated measures 2×4 ANOVAs, one for the identity and one for the emotional discrimination task, with the type of judgment (movement, emotion) and the stimuli categories (faces, bodies, dogs, knives) as factors. Non-significant main effects were obtained for the identity discrimination task (all $F_s < 1$), while a significant two way interaction was obtained for the emotional

discrimination task ($F_{(3,42)} = 10, p < 0.001$). Pair-wise comparisons showed that for the emotional discrimination task, the dog probes differed more in implied movement than emotion (mean difference = 1.26, $SE = 0.42, t_{(14)} = 3.02, p = 0.009$), while the faces showed an opposite pattern and differed more in emotion than movement (mean difference = -1.53, $SE = 0.4, t_{(14)} = 3.23, p = 0.006$). Non-significant differences were observed between the emotion and motion judgments for knives (mean difference = -0.31, $SE = 0.21$) and bodies (mean difference = -0.10, $SE = 0.39$). Comparing each judgment type between the four categories of stimuli

showed that the face probes were judged to be more different in emotional value ($M=3.01$, $SE=0.51$) as compared to bodies ($M=1.83$, $SE=0.49$, $t_{(14)}=2.88$, $p=0.012$). Importantly, for faces and bodies, the difference in the emotion ratings of the two probes of each pair did not differ from that for knives ($M=1.93$, $SE=0.39$) and dogs ($M=2.89$, $SE=0.5$). As for implied motion ratings, the dog probes ($M=4.15$, $SE=0.5$) differed more than the body ($M=1.72$, $SE=0.25$, $t_{(14)}=4.76$, $p<0.001$), knife ($M=1.62$, $SE=0.34$, $t_{(14)}=6.28$, $p<0.001$), and face probes ($M=1.48$, $SE=0.25$, $t_{(14)}=4.89$, $p<0.001$). Thus, any differential effect of the emotional content for faces and bodies as compared to knives and dogs cannot be ascribed to different intensities of emotion or motion perception in human as compared to non-human stimuli.

4.2. Results

The control subject carried out the tasks without errors. In contrast, the binomial test indicates that FM's accuracy was different for the four categories of stimuli (Table 3 and Fig. 3). Indeed, FM's performance for dogs and knives was always above chance, both for the identity and the emotional discrimination task (binomial test, all $z>2.8$, all $p<0.005$).

In the case of body and face stimuli, the patient was not able to discriminate the identity but performed better than chance in the emotional discrimination task, particularly when the fearful picture was presented first. In fact, in the body and face identity tasks (i.e. a fear stimulus followed by two fear stimuli or a neutral stimulus followed by two neutral stimuli) FM's performance was at chance (binomial test, all $z<1$, all $p>0.34$). In contrast, in the emotional task (i.e. two images showing the same model expressing two different emotional states), and specifically in the condition in which the sample stimulus represented fear and not when it represented a neutral expression, his performance dramatically improved, rising above chance (binomial test, bodies: $M=80\%$, $z=3.8$, $p<0.001$; faces: $M=75\%$, $z=3.2$, $p=0.002$; see Table 3 and Fig. 3).

Thus, his performance in the emotional body task when the sample depicted an emotional posture ($M=80\%$) was significantly better with respect to when, in the same task, the sample depicted a neutral posture ($M=55\%$, $\chi^2(1, N=80)=5.7$, $p=0.015$). In addition, his performance when the sample stimulus represented a fearful stimulus was better with respect to the identity task, either for neutral postures ($M=50\%$, $\chi^2(1, N=80)=7.91$, $p=0.005$) and for emotional postures ($M=57\%$, $\chi^2(1, N=80)=4.71$, $p=0.026$).

In a similar vein, during face discrimination FM's performance in the emotional task was significantly better when the sample stimulus was emotional ($M=75\%$) as compared to when it was neutral ($M=50\%$, $\chi^2(1, N=80)=5.33$, $p=0.018$). In addition, his performance in the discrimination task for facial emotions with an emotional sample was better with respect to the identity discrimination task between neutral stimuli ($M=42\%$, $\chi^2(1, N=80)=8.72$, $p=0.003$), while it did not differ from his performance in the identity discrimination task between emotional stimuli ($M=57\%$, $\chi^2(1, N=80)=2.74$, $p=0.078$).

Comparing the four categories of stimuli, FM performed better with the knives ($M=87.75\%$) than with the dogs ($M=75\%$), faces ($M=56\%$), or bodies ($M=60.5\%$) (for all comparisons: $\chi^2(1, N=320)>6.49$, $p<0.01$) and with the dogs with respect to faces and bodies (for all comparisons: $\chi^2(1, N=320)>8.29$, $p<0.01$). There was no significant difference between faces and bodies ($\chi^2(1, N=320)=0.63$, $p=0.25$).

The presentation time of the stimuli in this experiment (3000 ms) was long enough to allow control subjects to perform at ceiling thus eliminating any stimulus category related differential effect on performance. Therefore, we administered to a group of healthy individuals ($N=15$, mean age = 24.5 years, range = 21–29 years), a task which was identical to the one performed by FM

with the only difference being that the exposure time of the stimuli was 250 ms. Accuracy and response times (RTs) were entered into two separated repeated-measures ANOVAs with category (bodies, faces, dogs, knives) and task (identity, emotion) as factors. The main effect of category was significant for both accuracy ($F_{(3,42)}=2.96$, $p=0.043$) and RTs ($F_{(3,42)}=25.25$, $p<0.001$). Planned pair-wise comparisons showed that accuracy in discriminating bodies ($M=91\%$; $SE=1.8\%$) was comparable to that in discriminating knives ($M=93.2\%$; $SE=3\%$, $F_{(1,14)}=1.96$, $p=0.18$), but worse than in discriminating faces ($M=93.5\%$; $SE=2.1\%$, $F_{(1,14)}=9$, $p<0.01$) and dogs ($M=94.6\%$; $SE=2.1\%$, $F_{(1,14)}=8.56$, $p<0.05$).

No differences were observed between the visual discrimination of faces, knives and dogs (all $F_{(1,14)}<1$). Coherently, RTs were slower for the visual discrimination of bodies ($M=742$ ms; $SE=36$ ms) with respect to faces ($M=634$ ms; $SE=25$ ms, $F_{(1,14)}=45$, $p<0.001$), dogs ($M=594$ ms; $SE=22$ ms, $F_{(1,14)}=50$, $p<0.001$), and knives ($M=640$ ms; $SE=33$ ms, $F_{(1,14)}=46$, $p<0.001$). Furthermore, RTs were slower for the visual discrimination of faces with respect to dogs ($F_{(1,14)}=11$, $p<0.01$) and showed a tendency to be slower for knives with respect to dogs ($F_{(1,14)}=4.3$, $p=0.056$). No difference was found between the RTs in the visual discrimination of faces and knives ($F_{(1,14)}<1$). To sum up, healthy individuals' overall performance was lower for body and better for dog stimuli as compared to the other categories, while no difference was observed between faces and knives.

The main effect of task was significant for both accuracy ($F_{(1,14)}=25$, $p<0.001$) and RTs ($F_{(1,14)}=15$, $p<0.001$), showing a worse and slower performance in the identity than in the emotional discrimination task. The non-significant effect of the interaction between category and task (Accuracy: $F_{(3,42)}=1.88$, $p=0.147$; RTs: $F_{(3,42)}=1.59$, $p=0.205$) indicates that the better performance in the emotion vs. the identity discrimination task was comparable across the four stimulus categories.

To explore the source of modulation due to emotional content in healthy individuals as compared to FM, we further analyzed accuracy and RTs in the emotional discrimination task by comparing the trials with neutral and fearful samples. Accuracy and RT values for the emotional discrimination task were entered into separate repeated-measure ANOVAs with category (bodies, faces, dogs, knives) and sample type (neutral, emotional) as factors. The main effect of category was significant for RTs ($F_{(3,42)}=22.16$, $p<0.001$) but not for accuracy ($F_{(3,42)}=1$, $p=0.4$). Thus, different speeds in discriminating the four categories were also observed in the identity discrimination task. Overall, the performance of healthy individuals did not show any difference between the emotional discrimination tasks with a neutral or an emotional sample for either accuracy (neutral sample: $M=96.4\%$, $SE=1.3\%$; emotional sample: $M=95\%$, $SE=2.9$; $F_{(1,14)}<1$) or RTs (neutral sample: $M=639$ ms, $SE=24$ ms; emotional sample: $M=633$ ms, $SE=24$ ms, $F_{(1,14)}=2.44$, $p=0.14$). Significantly, the interaction between category and sample type for accuracy ($F_{(3,42)}=1.16$, $p=0.334$) and RTs ($F_{(3,42)}=1.53$, $p=0.22$) turned out to be non-significant, suggesting that, although healthy individuals showed an advantage in the emotional as compared to the identity discrimination task for all categories, they did not show any difference between trials with a fearful and a neutral sample for any category.

These results confirm the specificity of FM's better performance in the body and face emotional discrimination tasks when he was required to recognize a fearful stimulus. Indeed, unlike the controls, FM improved his performance in a very specific way, i.e. only for the body and face stimuli and exclusively when the stimulus sample was an emotional stimulus to be compared to a neutral one, but not vice versa. Although the difficulty of the four categories of stimuli was not perfectly balanced, it is unlikely that this explains the body and face selective emotional modulation found in FM for at least three reasons. First, the performance of control

Table 3
FM's percentage of accuracy in the task for the discrimination of identity and emotional expressions. The table shows the results of the binomial tests (In bold the significant z and p values).

Target	Probe	Face		Body		Dog		Knife	
		z	p	z	p	z	p	z	p
F	F	1	0.34	1	0.34	2.8	0.004	4.2	<0.001
N	N	-1	-0.34	0	1	3.8	0.000	3.8	<0.001
F	N	3.2	0.002	3.8	0.000	3.2	0.002	4.2	<0.001
N	F	1	0	0.6	0.53	3.2	0.002	4.6	<0.001

individuals when fast stimulus exposure eliminated ceiling effects was comparable for faces and knives, worse for bodies and better for dogs. Second, FM's performance for dog and knife stimuli was far from ceiling (dogs: $\chi^2(1, N=80)=11.43, p < 0.001$; knives: $\chi^2(1, N=80)=5.33, p < 0.05$), thus ruling out the masking influence of any low task sensitivity on the emotion- and category-specific related improvement of his performance. Third, while the performance of healthy individuals in the emotion discrimination task was not modulated by whether the sample was a neutral or an emotional stimulus, FM's performance improved only when the sample was an emotional stimulus. Thus, the emotion-related modulation of FM's discrimination of body and face stimuli was qualitatively different from the modulation seen in control subjects, suggesting that different cognitive processes and different neural structures may underlie FM's and healthy subjects' performance.

The emotional modulation of face and body recognition in FM would support the notion that the systems involved in the recognition of emotional facial expressions can be relatively spared in subjects with acquired prosopagnosia and can be dissociated from those systems involved in face identification. Moreover, our data support previous evidence by showing that the recognition of human body identities in prosopagnosic patients may be dissociated from the recognition of emotional body expressions.

It has been demonstrated that facial motion facilitates face recognition (de Gelder et al., 2003; O'Toole, Rozik, & Abdi, 2002; Pilz, Thornton, & Bulthoff, 2006) and that discrimination of body actions can be spared in the presence of a deficit in body identity recognition (Moro et al., 2008). Thus, it is possible that the better performance in the tasks involving discrimination of emotional faces and bodies might be due to a facilitation induced by FM's ability to recognize facial and body implied movements. Even though this seems less likely since the emotion-related facilitation only occurred with emotional samples and not with neutral samples, we carried out a third experiment in order to compare FM's abilities in the discrimination of body forms and actions.

5. Experiment 3: discrimination of body forms and body actions

5.1. Stimuli and procedure

The fact that processing body form and implied body action (Urgesi, Moro, Candidi, & Aglioti, 2006) relies on distinct neural substrates has been previously demonstrated in healthy subjects (Urgesi, Candidi, et al., 2007; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007b) as well as in neurological patients (Moro et al., 2008). Specifically, lesions of ventromedial occipito-temporal areas induce deficits in face and body recognition while lesions involving the ventral premotor cortex seem to be associated with impaired recognition of body actions. Since FM's brain damage involves the occipito-temporal cortex, it is possible that his advantage in discriminating emotional faces and bodies is due to a facilitation induced by the recognition of implied actions.

All the procedures of Experiment 3 were similar to those of Experiment 2 with the exception of the stimuli. FM and the control

subject were given two delayed matching-to-sample tasks where they had to decide which of two different probe images matched a previously presented sample stimulus. The stimuli were static snapshots depicting the middle phase of specific actions performed by two models. Both models performed all actions and the posture of each model was matched with that of the other model. Four pairs of different actions were used. Each pair was composed of two slightly different actions performed using the same limb. Using the mirror image of each stimulus allowed us to balance the laterality of the stimulus set. Thus, 32 stimuli were presented, i.e. eight right- and eight left-limb stimuli per model for each task. The two tasks were presented in two separate 32-trial blocks and, as in the original experiment (Urgesi, Candidi, et al., 2007), the same set of stimuli was used in the two tasks. In the action discrimination task each target image was paired with an image representing a different action performed by the same model. In the form discrimination task the target image was paired with an image representing the same action executed by a different model. Before the experimental session, the subjects inspected printed examples of stimuli and completed a six-trial practice block (see Fig. 4).

5.2. Results

In this task, as in the previous experiments, the control subject performed without errors, while FM's scores were at chance (binomial, $p > 0.05$) and nearly identical in the form (score 19/32, 59.37%) and action (score 20/32, 62.5%, $\chi^2 = 0.066, p = 0.8$) tasks. Thus, it is possible to exclude the hypothesis that the increased accuracy in the emotional discrimination was an effect of a more general ability to recognize the action implied by body or face stimuli. Although FM's lesions do not seem to involve the ventral premotor cortex, his performance did not improve when he was asked to discriminate between two different actions as compared to when he was asked to discriminate between two different models. It is possible, therefore, to conclude that FM presents an evident deficit not only in the recognition of faces but also bodies. This deficit becomes less evident when the stimuli convey an emotional value (fear) while it is unaffected by changes in non-emotional action content.

6. Discussion

In the present study we examined face, body and object perception in a case of acquired prosopagnosia. We found three main results. First, we provide an accurate neuropsychological description of a new case of prosopagnosia and provide detailed information on the underlying lesion. Second, we document serious body perception deficits (body agnosia) in a case of acquired prosopagnosia. Third, we show that discrimination of emotional face and body expressions can be relatively spared in the context of notable deficits in the discrimination of face and body identities and of neutral body actions.

6.1. Lesion correlates of FM's prosopagnosia

FM reported serious deficits in the recognition of face stimuli with comparatively minor disorders in object identification.

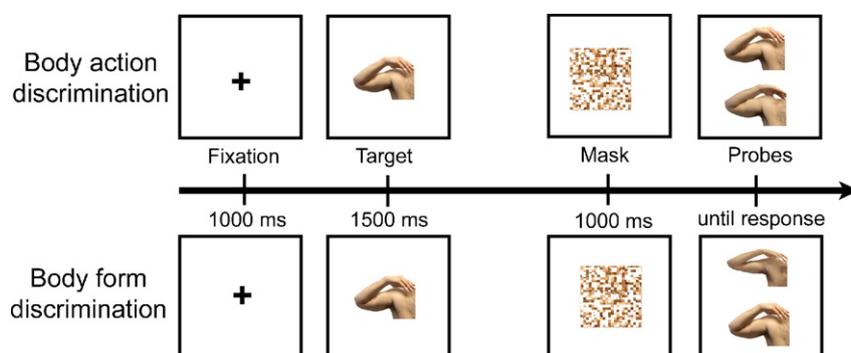


Fig. 4. Discrimination of body forms and body actions: representation of typical trial events in Experiment 3.

Indeed, the only symptom the patient complained of was being unable to recognize faces and he did not report any difficulties in recognizing real objects in his daily life at the time of testing. The extensive neuropsychological evaluation confirmed that, in spite of serious deficits in all face recognition tests, FM's scores in the BORB and other tests that investigated his ability to recognize objects were within the normal range, although he required a great deal of time to perform the tests. Thus, the dissociation between face and object recognition was not complete. This is supported by his performance in all of our tasks, in which FM was slower and less accurate than the controls. In addition, FM's general perceptual deficits may be at least in part aggravated by his residual campimetric deficits, which may have slowed down his recognition performance and prevented a full recognition of all stimuli.

Crucially, however, face recognition abilities were seriously impaired with respect to the recognition of other objects as measured through standard neuropsychological tests. Thus, the neuropsychological description of FM provides a new case of prosopagnosia. In addition, our patient shows specific disorders in the visual mental imagery of human faces, but not in the visual imagery of bodies or dog's faces. The possibility that our questionnaire may be more difficult for faces than other categories of stimuli can be excluded as the mean scores of the control group do not differ between categories.

Brain regions thought to be crucial in face perception are located in the lingual, fusiform and parahippocampal gyri, with a right hemisphere dominance. However, the variability of the location and extent of the lesions in patients affected by prosopagnosia are considerable. For example PS, a well documented female prosopagnosic patient (Rossion et al., 2003), showed lesions in the left fusiform gyrus and in the right occipital face area with the sparing of the right fusiform face area (Peelen et al., 2009; Sorger et al., 2007). DF, the well known patient affected by visual agnosia studied by Goodale and colleagues (Goodale et al., 1994; Steeves et al., 2009), presented impairments in face identity recognition and damage in the right OFA, with a normal range of sensitivity to faces in the right fusiform gyrus area (Steeves et al., 2009). These data, thus, suggest that the right OFA plays a central role in the processing of face identity, although it is probably part of a wider face recognition neural network.

The anatomical localization of FM's lesions involves the right and left ventral middle occipito-temporal cortex, i.e. the fusiform gyrus where the FFA is located (Chao, Haxby, & Martin, 1999; Kanwisher et al., 1997; Peelen & Downing, 2005; Summerfield, Trittschuh, Monti, Mesulam, & Egnér, 2008) and the left lateral occipital cortex, where the OFA is located (Gauthier et al., 2000; Pitcher et al., 2011). The lesion in the right lateral occipital cortex has a smaller extension as compared to the left hemisphere lesion and only marginally includes the region where the right OFA

is typically located (Rossion et al., 2003; see Fig. 1B). However, since the spatial location and extent of category selective regions in the occipito-temporal cortex may vary greatly between individuals, we cannot exclude the possibility that the lesion also involves the right OFA. Furthermore, since brain regions that appear to be structurally intact in a patient may be functionally depressed because of lesioned regions nearby, the right OFA may be functionally, if not structurally, lesioned in FM.

FM's bilateral lesions do not provide an answer to the unresolved question concerning whether a right hemisphere lesion alone is enough to cause prosopagnosia or whether there must always be a bilateral lesion (Sorger et al., 2007). However, the fact that FM's lesion may involve both the left and right FFA and the left OFA, may explain some of the differences between his deficits and those of PS and DF.

Firstly, DF is able to categorize faces even though she cannot recognize them (Steeves et al., 2006) and PS is still able to detect faces and categorize them according to their gender, age and expression (Rossion et al., 2003). These tasks are absolutely impossible for FM who fails in the discrimination of famous versus non-famous faces and of female versus male faces.

Moreover it is noteworthy that FM displays a total absence of signs of covert recognition (Barton, Cherkasova, & Hefter, 2004).

In conclusion, although damage to the right occipital inferior area may be critical for prosopagnosia to occur, as demonstrated by the patient PS (Sorger et al., 2007), our data support the notion of a distributed network for face processing in the human brain (Haxby et al., 2000) where different nodes are involved in the processing of the stimuli for facial features of face stimuli besides identity discrimination (Sorger et al., 2007). This hypothesis is also confirmed by a study of four patients whose lesions included the right fusiform area and who showed impaired perception of facial configuration. These patients were unable to discriminate changes in the spatial position of facial features, while their performance was normal for changes in eye colour (Barton et al., 2004).

6.2. Body processing in prosopagnosia

Although it is generally accepted (Haxby et al., 2000) that the human face and body represent special perceptual categories which are processed by specialized cortical mechanisms, the pattern of similarities and differences between face and body processing remains to be fully determined (Minnebusch & Daum, 2009).

Recent models of body perception (Minnebusch & Daum, 2009; Taylor, Wiggett, & Downing, 2007) emphasize the similarities in face and body processing and in the functional neuroanatomy of face and body selective areas in the lateral (OFA and EBA) and medial (FFA and FBA) occipito-temporal areas. Both the FFA and the FBA show more pronounced activation for whole face and

body stimuli, respectively, as compared to single face or body parts (Benussi et al., 2007; Taylor et al., 2007). Thus, the EBA may be involved in the basic analysis of body features, similar to the involvement of the OFA in face processing, whereas the FBA, like the FFA, may be implicated in the processing of the configuration of the body as a whole (Minnebusch & Daum, 2009).

Another model (Urgesi, Calvo-Merino, et al., 2007) suggests the existence of two dissociable and partially independent routes for the processing of the human body. The first route, relying more on ventral cortices and encompassing EBA, may be involved in the processing of body form and individual body parts. The second one, relying considerably more on the dorsal stream, may process the whole body in a configural manner and map postures onto the observer's sensorimotor representation. Finally, Hodzic proposed the existence of distinct occipito-parietal and fronto-parietal networks, respectively for body detection and body identification (Hodzic, Muckli, Singer, & Stirn, 2009). These three models lead us to hypothesize that intact body perception abilities require a functional interconnection between ventro-medial and lateral occipito-temporal and fronto-parietal areas belonging to a distributed system for body perception.

In line with the assumption of similarities between face and body processing, Righart and de Gelder (2007) reported an abnormal inversion effect for both face and body stimuli in three out of four developmental prosopagnosics. Since the N170 ERP component may reflect a configuration-based analysis of visual stimuli, which is stronger for body and face stimuli, the authors suggested an association between face and body recognition deficits in prosopagnosia. However, they did not carry out behavioral tests for body perception abilities in their patients. Furthermore, Peelen et al. (2009) reported that the face perception deficits of a prosopagnosic patient did not extend to body perception. Thus, to the best of our knowledge, FM represents the first reported case of acquired prosopagnosia associated with a specific deficit in visual body discrimination.

The anatomical localization of FM's lesions encompasses the left EBA (Astafiev, Stanley, Shulman, & Corbetta, 2004; Chan, Peelen, & Downing, 2004; Downing, Peelen, Wiggett, & Tew, 2006; Hodzic et al., 2009; Peelen & Downing, 2005; Peelen & Downing, 2005) and the right FBA (Peelen & Downing, 2005) and falls in close proximity to the right EBA (Downing et al., 2006; Peelen & Downing, 2005). His disorders in the body discrimination tasks may thus be due to the localization of damage that involves both face and body processing areas. However, two issues are worth discussion. The first concerns the fact that FM does not complain of any difficulty in body recognition, but only in face discrimination. It is possible that the deficit in body processing is masked by a more evident and distressing inability to recognize faces. Finally, FM may be able to compensate in everyday life for the body deficit by identifying specific details in people's clothes and mannerisms, while his body perception deficits become apparent only in laboratory tests where other cues are eliminated.

The other issue concerns the unexpected result indicating a deficit not only in body form but also in body action discrimination (Experiment 3). Our previous studies (Urgesi, Candidi, et al., 2007; Urgesi, Calvo-Merino, et al., 2007; Moro et al., 2008) suggested that the visual analysis of human body stimuli is based on the division of labor into two cortical systems, with the EBA and FBA representing the actors' identity and vPMC mapping the action observed in a neutral format with respect to the identity of the acting bodies. Since the dorsal stream and vPMC are spared in FM's lesions, we expected normal performance in the action task. We cannot exclude, however, that the lesions in early visual areas and in the thalamus may also induce dysfunctional processing of body actions in fronto-parietal areas.

6.3. Dissociation between identity and emotion discrimination for body and face

A further aim of this study was to verify whether or not the emotional content of the perceived face and body postures might affect the discrimination of face and body identities. In addition, we tested whether discrimination of emotional face and body expressions may be spared in a prosopagnosic patient with serious face and body recognition deficits. Although previous studies in prosopagnosic patients have documented that the activity of face selective regions is modulated by emotion (Peelen et al., 2009; Van den Stock et al., 2008), no study has so far reported whether this modulation of neural activity is reflected in a behavioral advantage for prosopagnosic patients in recognizing the identity of faces and bodies expressing an emotion as compared to neutral faces and bodies. The results of Experiment 2 showed that when FM was requested to recognize the identity of neutral and fearful faces and bodies his performance was at chance. Thus, the emotional content of the expressions did not modulate his face and body identity recognition deficits. However, when the task involved the discrimination of face and body stimuli on the basis of their emotional content (fearful vs. neutral), FM's performance dramatically improved, thus suggesting a dissociation between identity recognition deficits and spared emotion discrimination abilities. Comparing the recognition of neutral and emotional face and body stimuli with living (but non-human) stimuli (i.e. dogs' faces) and inanimate stimuli (knives), suggested that FM's advantage in recognizing emotional expression was specific for faces and bodies. As expected, FM's performance in recognizing dogs and knives was better than for faces and bodies, but was not influenced by the emotional content of the images. This evidence rules out the possibility of a non-specific effect of the emotional value of the stimuli on FM's performance in discrimination tasks.

The spared emotion discrimination performance may not be due to the discrimination of the action implied in the stimuli, since FM was unable to recognize between two neutral actions implied by static images of human bodies.

The lesion of the patient examined by Peelen and colleagues (PS) was spared in the right fusiform gyrus, the activation of which was enhanced by emotionally expressive faces and bodies (Peelen et al., 2009).

An increase in right fusiform activation was also found in developmental prosopagnosics in response to fearful vs. neutral faces, whereas no difference was found between neutral and emotionally expressive bodies (Van den Stock et al., 2008). These data are consistent with the hypothesis of a subcortical pathway able to process facial expressions (the pulvinar-superior colliculus-amygdala route) which in turn may boost face representations in the cortical route in the temporal cortex, even when face representation in the temporal cortex is weak (Van den Stock et al., 2008). The absence of any modulation of FM's face and body identity recognition due to emotional content may seem to be in contrast to the view that spared projections from the intact amygdala to the fusiform cortex might boost face recognition abilities. However, FM's lesions encompass both the left and right fusiform face and the right fusiform body area and it is unlikely that these areas have residual activity since FM is impaired in both overt and covert face perception tasks. Thus, the extensive damage of left and right fusiform cortices may have prevented any influence due to emotional content on the neural activity of areas involved in the perception of face and body identity. That FM's ability to discriminate fearful from neutral faces and bodies was spared may be due to the activity of other areas that are involved in the discrimination of emotions and are at least partially independent from areas related to the recognition of identity. It is worth nothing that deficits in the recognition of expressions can occur in patients without prosopagnosia

(Vuilleumier & Pourtois, 2007). These deficits seem to be selective for some categories of emotion depending on the site of brain lesion, e.g. fear after amygdala lesions (Adolphs, Tranel, Damasio, & Damasio, 1995), disgust after insula damage (Calder, Keane, Manes, Antoun, & Young, 2000) or anger after ventral basal ganglia lesions (Calder, Young, Keane, & Dean, 2004). Moreover, the somatosensory cortex seems to play a role in the recognition of emotional facial expressions (Adolphs et al., 1995; Damasio, 1994; Pourtois et al., 2004). The activation of brain areas outside the occipito-temporal regions which process face identity may reflect the specific influence of the affective component present in faces and bodies (de Gelder et al., 2003; Van de Riet et al., 2009). These areas are the superior temporal sulcus, also known for its role in the perception of biological movement and in the processing of social information (Van de Riet et al., 2009), and the insula, a multimodal area with an important integrative role in social emotions and self-awareness (Craig, 2010). In addition, activity in the amygdala and the superior colliculus is reported in response to faces and bodies expressing fear but not happiness as compared to neutral expressions, whereas the periaqueductal gray seems to be involved for bodies expressing both fear and happiness. This activation is considered to be compatible with the reaction to bodies expressing fear, e.g. motor quiescence or freezing and flight reaction, but this area is also active in positive emotions (Van de Riet et al., 2009). In fact, other motor structures involved in body representation, such as the caudate nucleus, the orbitofrontal and the primary somatosensory cortices, might be implicated in bodily reactions to emotional stimuli expressing fear and happiness (de Gelder et al., 2010). Crucially, FM's posterior lesions do not extend to the superior temporal sulcus or to other areas involved in processing emotional expressions that may have mediated his residual emotion discrimination abilities in spite of serious face and body identity discrimination deficits. This is in keeping with the model that proposes the existence of two separate pathways which, after an initial stage of visual structural encoding, process body expressions regardless of identity and vice versa (Haxby, 2000). This model, however, has been questioned by Vuilleumier and Pourtois (2007) who suggest that identity and emotion processing functions are not entirely segregated in the brain. These authors claim that affective responses in the amygdala and the anterior limbic regions may enhance the activity in the areas processing face identity, and, conversely, affective responses in the amygdala can be modulated by the familiarity of faces (de Gelder et al., 2010; Vuilleumier & Pourtois, 2007). We cannot exclude the possibility that dysfunctional activity in the identity processing areas may have influenced the response of emotion processing areas in the case of our patient FM since his performance was still lower than that of the control subject even in discriminating emotional and neutral faces and bodies. However, our data suggest that processing the identity and the emotion of face and body stimuli might be at least partially segregated in the brain. Crucially, accurate recognition of face and body expressions only occurred when the sample stimulus depicted an emotional expression to be discriminated from a neutral stimulus. In contrast, when the sample stimulus was neutral, FM's performance in discriminating the neutral from an emotional stimulus was at chance. This last evidence suggests the intriguing, but speculative, hypothesis that the emotional content of the initially presented sample stimulus may determine whether the identity or emotion processing system is mainly called into play during a delayed matching to sample task. If the sample stimulus depicts an emotional expression, the emotion processing system is called into play and FM can solve the task; if the sample stimulus is a neutral stimulus, the identity processing system is involved, leaving FM unable to solve the task. Additional studies are needed to clarify further the relationships between the various different systems involved in processing the identity and the emotions of co-specifics. Our data provide an

important aid to the understanding of these systems by suggesting that the networks recruited in the processing of emotional body and face stimuli may at least partially overlap.

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