Once you feel it, you see it: insula and sensory-motor contribution to visual awareness for fearful bodies in parietal neglect

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a b s t r a c t

The interplay between the neural mechanisms of visual awareness and those involved in emotion processing and the mapping of related somatic changes remains unclear. To address this issue we studied one patient with visual extinction following right parietal damage, in a combined behavioral, psychophysiological and neuroimaging experiment. Patient M.P. was presented with neutral and fearful bodily expressions, either unilaterally in the left (LVF) or right visual field (RVF), or in both visual fields simultaneously. Fearful expressions presented in the left visual field simultaneously with neutral bodies in the RVF were detected more often than left-side neutral bodies. Signal detection analysis showed that the preferential access of fearful bodies to visual awareness is related to higher perceptual sensitivity for these stimuli during attentional competition. Pupil dilation, which indexes autonomic arousal, increased for fearful more than for neutral bodies. Moreover, dilation for extinguished fearful bodies was bigger than for consciously perceived fearful bodies. This decoupling between (increased) arousal and (lack of) conscious visual experience argues against a direct relationship between visual awareness of emotional signals and peripheral changes. Neuroimaging results showed that fearful bodies activated the left amygdala and extrastriate cortex when consciously perceived as well as when extinguished. Critically, however, conscious perception of fearful bodies was uniquely associated with activity in the anterior insula, somatosensory, motor and pre-motor cortex (PMC), and the cerebellum. This suggests that the integration between peripheral arousal and the moment-to-moment mapping at the central neural level of these bodily changes is critical for the conscious visual experience of emotional signals.

Keywords:
Visual awareness
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Attention
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Interoception

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1. Introduction

The interaction between emotion, physiological arousal, and perceptual awareness has been a central theme in neuroscience since the classic James-Lange theory, which proposed that the essence of emotion resides in the conscious perception of interoceptive (i.e., visceral) and sensory-motor changes in the body (James, 1884). Contemporary neuroimaging and lesion studies provide compelling evidence that the brain regions implicated in emotion perception partly overlap those mapping interoceptive bodily states (Critchley, 2005). For example, the amygdala, which plays a pivotal role in the perception of emotional stimuli, also engenders autonomic responses to threat stimuli (Phelps & LeDoux, 2005), and its activity correlates with the intensity in arousal changes induced by fearful expressions (Critchley, Mathias, & Dolan, 2002; Williams et al., 2001). On the other hand, damage to the insula or to somatosensory cortices, which are primary targets of interoceptive and musculoskeletal/skin afferents (Craig, 2009; Khalsa, Rudrauf, Feinstein, & Tranel, 2009), may impair emotion perception (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Calder, Keane, Manes, Antoun, & Young, 2000; Couto et al., 2013), although the behavioral consequences of insular damage vary considerably depending on lesion etiology or involvement of the underlying white matter (Ibanez, Gleichgerrcht, & Manes, 2010).

Currently, the interplay between the neural mechanisms of visual awareness and those involved in emotion processing and in the mapping of related somatic changes remains unclear. There is evidence that emotional stimuli are prioritized for attentional selection and may gain privileged access to visual awareness compared to emotionally neutral stimuli through a modulatory influence of the amygdala over areas along the ventral visual stream (Catani, Dell'acqua, & Thiebaut de Schotten, 2013; Critchley et al., 2002; de Gelder, Hortensius, & Tamietto, 2012; Morris, Friston, et al., 1998; Pessoa, Kastner, & Ungerleider, 2002; Rolls, 2014; Tamietto & de Gelder, 2010; Tamietto, Geminiani, Genero, & de Gelder, 2007; Tamietto et al., 2005; Vuilleumier, 2005; Vuilleumier et al., 2002; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). However, the possible role of physiological arousal and related cortical dynamics in lowering the threshold for stimulus awareness has never been directly investigated. In fact, autonomic or expressive changes and amygdala activity have both been reported during conscious as well as nonconscious visual perception of the eliciting stimulus, thereby suggesting that physiological arousal and activity in limbic areas may not be critical to shape the content of awareness (Anders et al., 2009; Critchley et al., 2002; Esteves, Dimberg, & Ohman, 1994; de Gelder, van Honk, & Tamietto, 2011; Glascher & Adolphs, 2003; Morris, Ohman, & Dolan, 1998; Tamietto et al., 2009; Tamietto & de Gelder, 2010; Whalen et al., 1998). This raises the intriguing, though largely unexplored possibility, that the moment-to-moment mapping at the central neural level of ongoing physiological changes, rather than these peripheral changes *per se*, may reflect the neural signature of conscious perception of emotional stimuli.

Aside from the emotion dimension, recent studies provide preliminary support to the putative role of interoception and sensory-motor representations in gating attentional selection and visual awareness. In fact, the mapping of interoceptive signals in the anterior insula has been associated with reorienting of attention to visual stimuli and seems selectively linked to visual awareness, as this activity is not reported during lapses of attention or when the stimulus goes undetected (Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Weissman, Roberts, Visscher, & Woldorff, 2006). Moreover, during observation of ambiguous and bistable stimuli, activity in the anterior insula has been related to spontaneous changes of conscious perception and occurred earlier than activity in extrastriate visual cortex (Sterzer & Kleinschmidt, 2007). This temporal precedence suggests that insula activity participates in initiating spontaneous shifts of conscious perception, rather than being the consequence of it. Lastly, the anterior insula anticipates impeding stimulus significance and prepares the body for the sensory and affective impact of incoming stimulation (Lovero, Simmons, Aron, & Paulus, 2009).

In this context, the study of neurological patients with deficits in attentional selection offers a unique opportunity to investigate, without changing any stimulus parameter or task demands, naturally occurring dynamics of visual awareness under conditions of multiple inputs competing for attention (Bartolomeo, 2007; Corbetta & Shulman, 2002). As it happens, patients with visual extinction following right temporo-parietal lesion that spares visual areas, consciously perceive a stimulus in either the left or right side, if it is presented singly (Driver & Mattingley, 1998). However, when two stimuli are presented simultaneously and bilaterally, thus competing for attentional selection, the left contralesional stimulus is often extinguished from awareness.

In a previous behavioral study with three such patients, we reported that during bilateral stimulation, pictures of fearful bodily expressions presented to the left side were consciously detected more often than pictures of neutral body actions (Tamietto et al., 2007), akin to what was previously shown with facial expressions (Vuilleumier et al., 2002; Vuilleumier & Schwartz, 2001; Williams & Mattingley, 2004). The use of bodily, instead of facial, expressions is particularly ripe for investigation of the neural bases of visual awareness and their possible coupling with mechanisms encompassing interoception and sensory-motor representation of bodily states. In fact, compared to facial expressions or to more complex emotional scenes, the perception of fearful bodily expressions primes the observer for action and evokes responses in areas related to the representation of body movement (motor and premotor cortex (PMC)), somatosensory perception, and interoception (insula) (Borgomaneri, Gazzola, & Avenanti, 2012; de Gelder, 2006; de Gelder et al., 2012; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Kret, Pichon, Grezes, & de Gelder, 2011; Kret, Stekelenburg, Roelofs, & de Gelder, 2013; Van den Stock et al., 2011).

Therefore, in the present single-case study we address two fundamental questions regarding the interaction between emotion processing, peripheral arousal and visual awareness

in a combined behavioral, psychophysiological and neuroimaging experiment. First, we investigate the influence of levels of perceptual awareness for neutral and fearful bodily expressions on autonomic arousal, as indexed by pupil dilation. Second, we examine how visual awareness and peripheral changes are coupled with brain activity when fearful and neutral bodies are displayed.

2. Methods

2.1. *Patient*

Patient M.P. is a right-handed 71-year-old male with 8 years education who suffered an ischemic lesion to the right hemisphere 5 months before the present study. The lesion is centered on the supramarginal gyrus in the inferior parietal lobule (IPL). It extends anteriorly and mainly subcortically, involving the superior longitudinal fasciculus, but also including the inferior part of the postcentral and precentral gyrus, as well as the posterior and inferior part of the insula. The posterior boundary of the lesion is along the borders with the angular gyrus, while it extends ventrally to the posterior part of the superior temporal gyrus, to the transverse temporal gyrus and reaches the posterior and superior margin of the middle temporal gyrus that, however, remains largely intact (see Fig. 1).

On neurological examination he showed reliable visual extinction of left stimuli, intact visual fields, and mild hemispatial neglect. The patient scored within the normal range (28/30) in the Mini Mental State Examination (MMSE) for the diagnosis of the general cognitive functions (Folstein, Folstein, & McHugh, 1975). Before the present experiment, visual field defects and visual extinction were formally assessed separately for the upper and lower quadrants with a computerized version of the visual perimetry and of the confrontation test, respectively (Bisiach, Cappa, & Vallar, 1983; Bisiach, Vallar, & Geminiani, 1989). In both tests, stimuli consisted of small white circles (1^0; stimulus luminance: 95 cd/m^2) presented well above luminance detection threshold, against a dark background (2 cd/m^2) and on a 21-in computer monitor. In the perimetry, the stimuli were presented singly for 300 msec at each of 64 different positions in random sequence (sixteen stimuli for each of the four visual quadrants). M.P. was required to keep steady fixation on a central cross and to report verbally when any stimulus change was detected. This procedure enabled us to map the patient's visual field within an ideal grid spanning 24^0 of horizontal and 20^0 of vertical eccentricity. M.P. testing showed intact visual fields, missing only four stimuli in the upper-left quadrant and two stimuli in the lower right quadrant.

During the confrontation test, the stimuli were presented randomly, either unilaterally in the patient's left (LVF) or right visual field (RVF), or to both visual fields simultaneously (bilateral simultaneous stimulation, BSS) at 8^0 of eccentricity along the horizontal meridian and at 5^0 along the vertical meridian. Score ranges from 0 (normal vision, if the patient misses less than six contralesional left stimuli out of twenty correctly detected ipsilesional right stimuli in BSS) to 3 (severe defect, if the patient misses more than twelve contralesional stimuli out of twenty correctly detected ipsilesional stimuli in BSS). In the upper quadrant, the patient extinguished eight

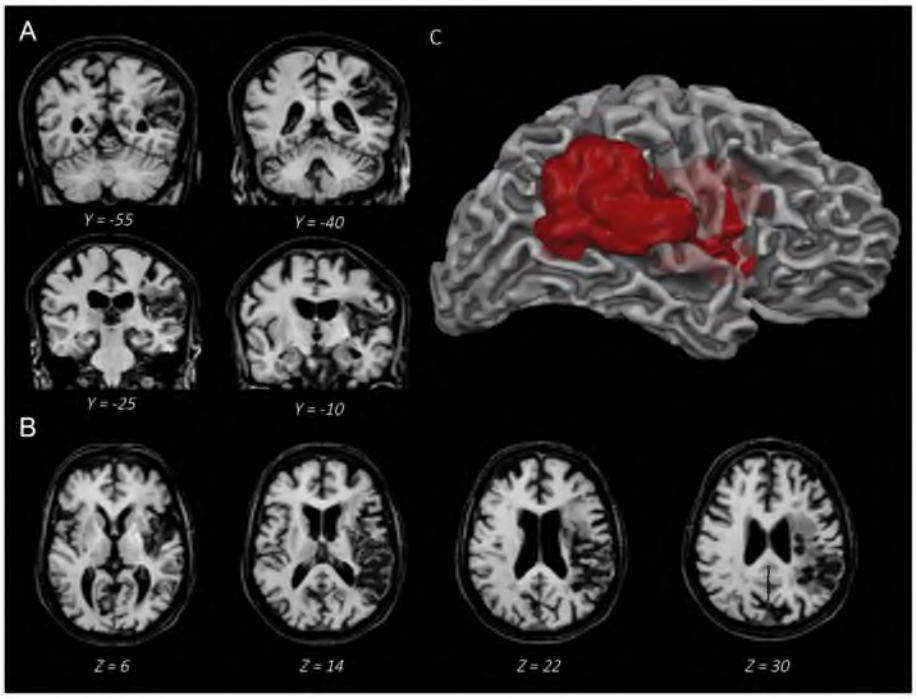

Fig. 1 e A) Coronal anatomical scans of patient M.P.'s brain. The lesion centered on the right parietal lobe is evident (Talairach coordinates are given); B) Transversal anatomical scans; C) 3-D cortical reconstruction of M.P.'s right hemisphere. Gyri are shown in light gray, sulci in dark gray, and the lesion is displayed in red.

contralesional stimuli out of twenty correctly detected ipsilesional stimuli in BSS, leading to a score of 1, which typically indicates visual extinction. Likewise, M.P. also scored 1 in the lower quadrant, missing nine contralesional stimuli in BSS. Hemispatial neglect was assessed by the Behavioral Inattention Test (BIT, conventional part), which includes the line crossing test, letter and shape cancellation tests, the line bisection test, copying of object drawings and geometrical shapes, and drawing from memory (Wilson, Cockburn, & Halligan, 1987). On this test the patient scored 128/146, indicative of mild neglect.

2.2. *Stimuli and apparatus*

Body stimuli were taken from the set developed and validated by Van den Stock and de Gelder (2011) in which facial information was removed from body images by blurring. The whole set used in the present study consisted of 30 gray-scale, whole-body posture images (half expressing fear and half displaying instrumentally neutral body actions) (see Fig. 2). All stimuli sustained a visual angle of 8^0 x 10.5^0 and had a mean luminance of 25 cd/m^2, thereby ruling-out any influence related to differences in low-level perceptual properties, such as brightness or size. Mean luminance of the dark background was 15 cd/m^2.

The stimuli were projected via the MR-compatible NordicNeuroLab's Visual System (refresh rate 85 Hz; FoV 30^0 horizontal, 23^0 vertical) connected to a standard PC that controlled stimulus presentation with E-Prime software. Eye movements and pupil diameter were monitored with an integrated eye-tracking camera that analyzed on-line monocular pupil and corneal reflection (sampling rate 60 Hz).

2.3. *Procedure*

Patient M.P. was tested within a standard extinction paradigm and a 2 x 2 factorial design with the factors Display Type (unilateral *vs* BSS) and Expression (neutral *vs* fearful), adapting for fMRI purposes our previous behavioral protocol (Tamietto et al., 2007). Each trial started with a central fixation cross that turned to red 1 sec before stimulus presentation to ensure steady fixation and attention to the task. Neutral or fearful bodily expressions were presented for 223.4 msec (i.e., 18 monitor refreshes) either unilaterally in the LVF or RVF, or to both visual fields (BSS). Stimulus duration was set during a practice phase with different stimuli to obtain reliable extinction on BSS trials (~50%), and good detection on unilateral LVF trials (~90%). The duration was then held constant throughout the experiment and for all stimulus conditions. There were four types of unilateral displays, each presented for 30 trials (a neutral or fearful bodily expression in the LVF; and a neutral or fearful bodily expression in the RVF); two types of BSS displays, each repeated for 60 trials (two neutral body images always showing two different neutral actions, or a fearful bodily expression in the LVF and a neutral expression in the RVF), and 20 catch trials where the fixation cross was not followed by any stimulus. The experiment was divided in five successive sessions (6 min each). Overall, 260 randomized trials were presented with a mean inter-stimulus interval (ISI) of 6.85 sec, randomly jittered between 4 and 10 sec.

The patient was asked to report verbally the location of the stimuli (i.e., "left", "right", "both" sides, or "none") without paying attention to the nature or the emotional content of the stimuli. Each response to this primary detection task was followed by a second rating task in which M.P. was required to indicate his confidence in the previous response on a 4-point scale (1 ¼ "least confident"; 4 ¼ "most confident"). An experimenter inside the scanner room recorded the responses on a score sheet. Notably, the choice of requiring a verbal, instead of motor, response ensures that recording of neural activity related to visual stimulation cannot be attributed to voluntary action execution, such as a button press. This is important because, based on previous neuroimaging studies of healthy subjects, we predicted enhanced activity in motor areas

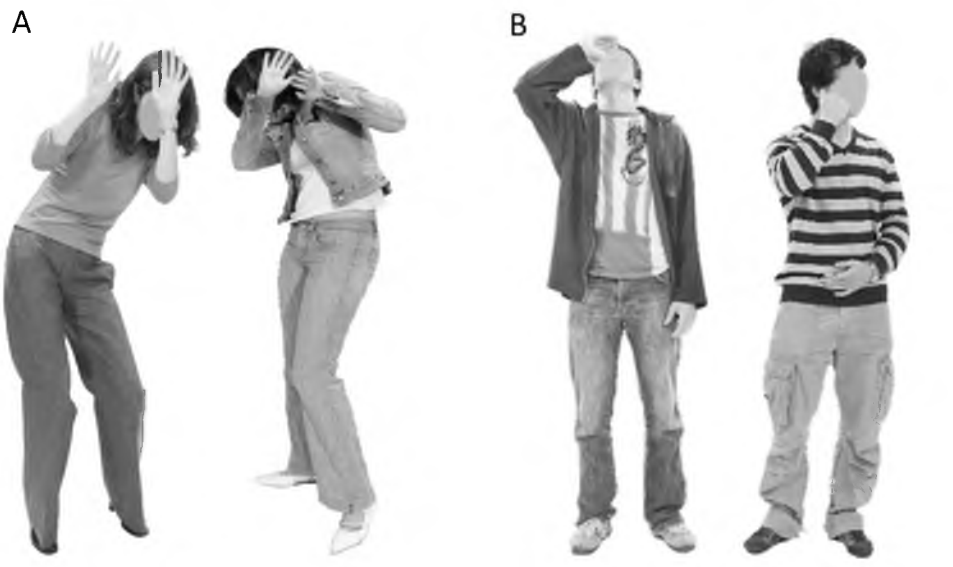

Fig. 2 e Examples of the bodily expressions used as stimuli. A) Fearful bodily expressions from two different actors; B) Neutral bodily expressions displaying two different instrumental actions (left image: drinking; right image: phone calling).

induced by passive exposure to fearful bodies (de Gelder et al., 2004).

2.4. fMRI acquisition

Data acquisition was performed on a 1.5 Tesla Intera scanner (Philips Medical Systems) with a SENSE high-field, high-resolution (MRIDC) head coil, optimized for functional imaging. Multi-slice T2-weighted fMRI images were acquired using an EPI sequence (TR/TE/flip angle ¼ 2000 msec/60 msec/90^0; FoV ¼ 256 mm; acquisition matrix ¼ 64 x 64; 19 contiguous 5 mm axial slices with no gap). For each of the five sessions, 182 volumes were acquired. Two scans were added at the beginning of the functional scanning (and the data discarded) to reach steady-state magnetization before acquisition of the experimental data.

Three-dimensional high-resolution T1-weighted structural images were acquired in the same session using a fast field echo sequence (TR/TE/flip angle ¼ 25 msec/2.4 msec/30^0; FoV ¼ 256 mm; acquisition matrix ¼ 256 x 256; 160 contiguous 1 mm sagittal slices, isotropic voxel size ¼ 1 x 1 x 1 mm).

2.5. Signal detection analysis

In addition to nonparametric statistical analyses on the rate of extinction, we also carried out signal detection theory analyses (SDT) to determine the perceptual sensitivity, d^0, and the response criterion, c, employed by patient M.P. when reporting contralesional left stimuli (Green & Swetz, 1966).

According to SDT, M.P.'s performance is fully described by four parameters: hits, misses, correct rejections and false alarms. Hits refer to correct detection of left-side stimuli in signal trials (i.e., in unilateral LVF or BSS trials), while misses refer to incorrect responses or extinction in the same trials. Correct rejections refer to lack of detection of left-side stimuli in noise trials (i.e., in unilateral RVF or catch trials), and false alarms refer to incorrect detection in the same trials. The rating task, requiring an additional graded response following the primary detection task, is typically used to measure sensitivity. Because each response in the primary detection task had four ratings associated with it, there were eight possible responses for each trial that can be graded ranging from the most confident absence of conscious perception to the most confident conscious detection of left-side stimuli (Azzopardi & Cowey, 1997; Evans & Azzopardi, 2007; Stanislaw & Todorov, 1999).

M.P.'s ratings were thus used to determine points on the Receiver Operating Characteristics (ROC) curve, which plots the hit rate as a function of false alarm rate, for all possible values of the criterion and for each stimulus condition independently. A rating task with 8 possible responses, as in the present case, determines 7 points on the ROC curve, and the area under the curve is a measure of sensitivity unaffected by response bias. The ROC area typically ranges from about .5, meaning that signal cannot be distinguished from noise, to 1, meaning perfect performance. The present design generated four ROC curves describing sensitivity for left-side neural and fearful bodily expressions in either unilateral or BSS displays. The 7 ROC points for each curve were then transformed to Z scores for each pair of hit and false alarm rates, and sensitivity was measured as d_a, a variant of d^0 that takes into account non-unit slopes of z-transformed ROCs and is appropriate in case of unequal variance between distributions, while being numerically equal to d' in the case of equal variance. Finally, differences between pairs of d_a values for each of the four conditions, expressed as normal deviates, Z_{da}, were compared to each other by a series of two-tailed paired-sample t-tests to assess statistically significant differences in sensitivity to left-side stimuli.

2.6. Pupillometric data reduction

Raw pupillary diameter data were first inspected for gross artifacts and discarded in case of major artifacts or excessive blinking. Minor artifacts and normal eye blinks that cause the loss of few data bins were corrected by linear interpolation. A five-point smoothing filter was then passed over the data. Artifact-free and smoothed pupillary response data were segmented into 4 sec epochs, including 1 sec of pre-stimulus period and 3 sec after stimulus onset for each condition separately. A baseline pupil diameter was calculated for each trial by averaging the pupillary diameter samples recorded during the 1 sec preceding stimulus onset. Data were then expressed as differences from baseline by subtracting the mean baseline pupillary diameter from all subsequent samples. A mean pupillary response-from-baseline waveform was then obtained for each condition by averaging the values at each time point across trials.

2.7. fMRI analysis

Brain Voyager QX was used for image processing and analysis (Brain Innovation©, The Netherlands). After standard preprocessing, functional volumes were spatially aligned to the first volume by a trilinear interpolation algorithm and smoothed by a 3-D Gaussian kernel with full width at half-maximum (FWHM) of 4 mm. Temporal smoothing with a 2 sec FWHM Gaussian kernel was also applied to improve the signal-to-noise ratio by removing high frequency fluctuations. Finally, functional scans were co-registered with their 3-D high-resolution structural scan and 3-D structural datasets were transformed into Talairach space (Talairach & Tournoux, 1988).

Data series were submitted to a single-subject analysis for event-related designs using general linear models (GLM). The four unilateral conditions were modeled by boxcar waveforms and convolved with the hemodynamic response function (HRF). BSS trials in which the left-side stimulus was detected versus extinguished, as determined by the patient's response during scanning, were modeled separately. This resulted in eight predictors, four unilateral conditions depending on the side of presentation (LVF or RVF) and on the expression (neutral or fearful), and four BSS conditions as a function of whether the left-side stimulus was neutral or fearful, detected or extinguished. Whole-brain analysis was performed and a fixed statistical threshold of $q < .05$ corrected for false discovery rate (FDR) in multiple comparisons was used to display results and activation maps (Genovese, Lazar, & Nichols, 2002). A cluster-size threshold >200 contiguous voxels was also applied.

Additionally, to further functionally qualify the activations in extrastriate visual areas along the ventral stream, which show category-specific selectivity to human bodies, we compared by superimposition the locations of patient M.P.'s activations in the temporal and occipital lobes with functionally-defined body-selective regions, as reported by Julian and co-authors, who used a localizer design on a large group of healthy subjects (Julian, Fedorenko, Webster, & Kanwisher, 2012) (downloaded from http://web.mit.edu/bcs/nklab/GSS.shtml). The regions, or body patches, that were activated systematically across subjects in the study by Julian and collaborators (2012), are the fusiform face/body area (FBA) in the fusiform gyrus, and the extrastriate body area (EBA) in the posterior inferior temporal sulcus/middle temporal gyrus.

3. Results

3.1. Behavioral results

Table 1 reports M.P.'s performance as a function of the six different conditions. Nonparametric tests were used to compare the patient's performance across conditions.

A preliminary analysis assessed the rate of extinction (i.e., the detection of left-side stimuli in BSS trials) independent of the different expressions. Response accuracy in detecting unilateral LVF, RVF, and BSS stimuli was significantly affected by the conditions of presentation [$c^2(2) = 1108.196, p < .00001$]. Accuracy was better in the RVF than LVF unilateral conditions [$V^2(1) = 5.13, p = .024$; which is a variant of the c^2 that corrects for small number of observations in 2 x 2 contingency tables]. In BSS trials, the patient showed severe extinction of left contralesional stimuli compared to unilateral LVF trials [$V^2(1) = 10.93, p = .0009$].

The accuracy in detecting unilateral LVF and RVF stimuli was not influenced by the bodily expression (neutral or fearful) [LVF: $V^2(1) = .11, p = .74$; RVF: $V^2(1) = .35, p = .56$]. Critically, however, the rate of extinction in the BSS trials was significantly affected by the expression of the left-side stimulus, as fearful bodies were extinguished much less often than neutral bodies [$V^2(1) = 8.62, p = .003$]. We therefore replicated in patient M.P. our previous observations that fearful bodily expressions are better attended and more often consciously perceived than neutral body actions when competing for limited attention.

3.2. Signal detection results

Parameters of the four ROC curves originating from patient M.P.'s ratings were computed with RscorePlus (Harvey, 2010), and the resultant graphs are displayed in Fig. 3.

ROCs were fitted to the data using a maximum-likelihood algorithm and the c^2 was used as goodness-of-fit measure. Results showed non-significant c^2 for all four distributions, indicating a good fit between model and data [$c^2(5) < 5.21$, $ps > .39$]. M.P.'s perceptual sensitivity to unilateral LVF stimuli was not influenced by expression as shown by d_a values as well as by A_z values, the latter corresponding to the area under the ROC curve, which expresses sensitivity in terms of probability (Neutral bodies: $d_a = 2.144$, $A_z = .935$; Fearful bodies: $d_a = 2.228$, $A_z = .942$). Accordingly, the difference in sensitivity between theses two unilateral conditions was not statistically significant ($Z = -.154$, $p = .877$).

However, perceptual sensitivity to unilateral LVF neutral expressions was significantly decreased by the presence of competing right-side neutral bodies in BSS displays ($d_a = 1.141$, $A_z = .79$; $Z = -.182$, $p = .029$). Critically, this was not the case for fearful expressions, whose sensitivity in unilateral LVF trials was not significantly reduced by competing right-side neutral bodies ($d_a = 2.072$, $A_z = .93$; $Z = .323$, $p = .747$). According to these findings, a further direct comparison of the sensitivities for left-side neutral and fearful expressions in BSS displays revealed a significant difference ($Z = -2.447$, $p = .014$).

3.3. Pupillometric results

Mean pupillary response waveforms from baseline are shown in Fig. 4 for the two critical BSS conditions as a function of extinction. The maximum dilation was induced by extinguished left-side fearful expressions, followed by consciously perceived left-side fearful bodies, and then by consciously perceived and extinguished left-side neutral bodies, which, in turn, largely overlap.

Mean peak amplitudes of phasic pupil dilation for BBS trials were submitted to a KruskaleWallis ANOVA with a four-levels factor (left-side neutral conscious, left-side neutral extinguished, left-side fearful conscious, and left-side fearful extinguished). The KruskaleWallis ANOVA is a nonparametric variant of the one-way ANOVA and is more sensitive to possible deviations from the normal distribution, which are likely in single-case studies. There was a significant main effect, showing that pupil dilation varied significantly in the four conditions [$H(3) = 35.658$, $p < .00001$]. Post-hoc tests of mean ranks showed that the difference in pupil dilation between extinguished and consciously perceived fearful expressions was marginally significant ($Z = 2.509$, $p = .073$; corrected for multiple comparisons). Extinguished as well as consciously perceived fearful bodies evoked significantly more dilation than either conscious or extinguished neural bodies ($Z > 3.133$, $ps < .01$). Finally, pupil dilation was not influenced by whether a left-side neutral body was consciously perceived or extinguished ($Z = .582$, $p = 1$).

Table 1 e Stimuli missed by patient M.P. as a function of the six display conditions.

Unilateral LVF		Unilateral RVF		Left misses in BSS displays	
Neural	Fearful	Neutral	Fearful	Left-side Neutral þ Right-side Neutral	Left-side Fearful þ Right-side Neutral
6/30 (20%)	5/30 (16.7%)	1/30 (3.3%)	2/30 (6.7%)	34/60 (56.7%)	18/60 (30%)

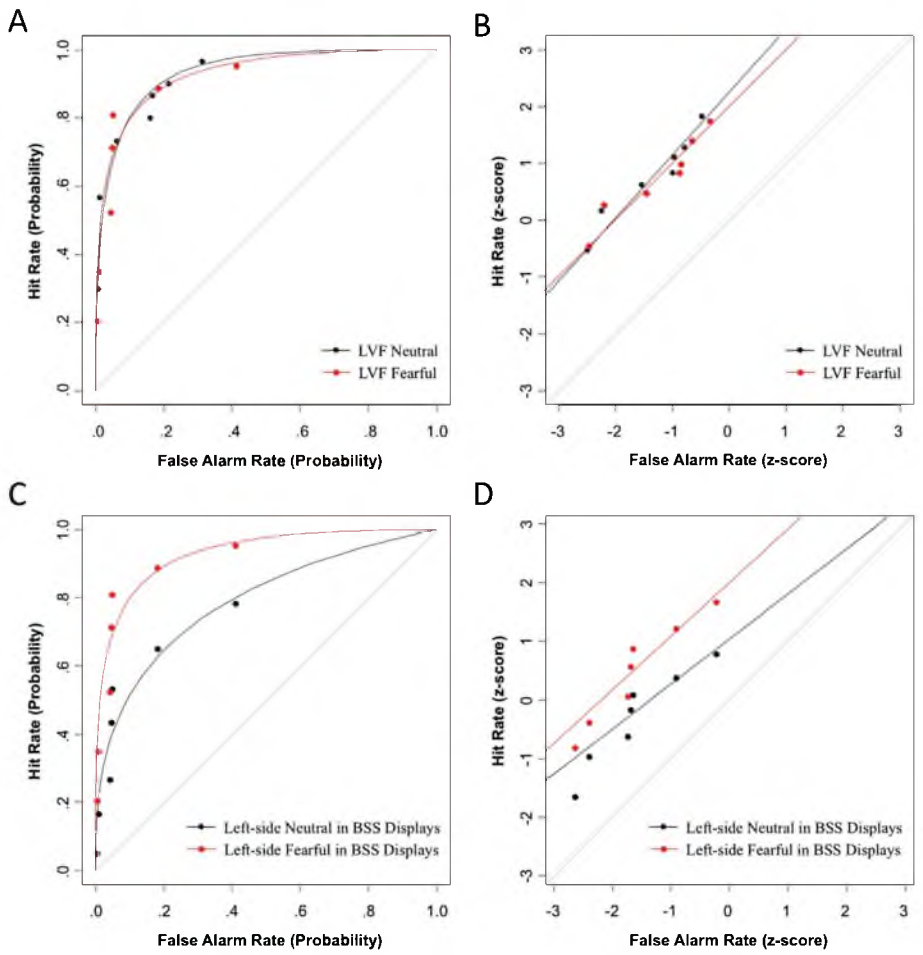

Fig. 3 e A) ROC curves derived from M.P.'s ratings showing probability of hit rates versus false alarm rates for LVF neutral and fearful bodies in unilateral displays; B) Z-scores transformed ROC curves for the same conditions; C) ROC curves for left-side neutral and fearful bodies in BSS displays; D) Z-scores transformed ROC curves for the same conditions.

3.4. *fMRI results*

3.4.1. *Conscious perception of fearful expressions in unilateral displays*

We first investigated the neural responses evoked by conscious perception of fearful expressions in unilateral trials across visual fields [i.e., (LVF fearful þ RVF fearful) e (LVF neutral þ RVF neutral)]. Increased activity was found in emotion-sensitive areas, such as the amygdala and the orbitofrontal cortex, in striate and extrastriate visual areas, including body-selective regions along the ventral stream like FBA, EBA and the superior temporal sulcus (STS), and in the dorsolateral and ventrolateral prefrontal cortex (dlPFC, vlPFC) (Table 2).

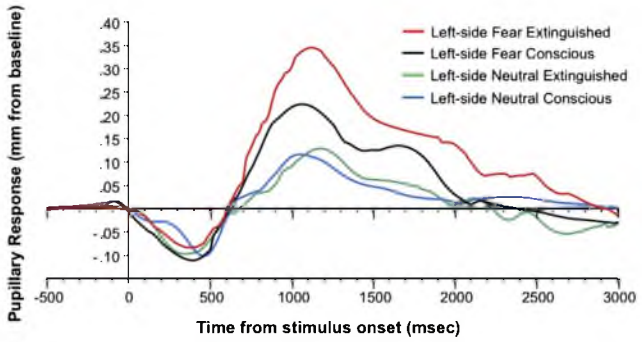

Fig. 4 e Mean pupil responses in BSS displays as a function of emotion and extinction of left-side stimuli.

3.4.2. *Nonconscious perception of neutral and fearful expressions in BSS displays*

We next examined the neural correlates of nonconscious perception of neutral and fearful bodily expressions separately, comparing unilateral RVF trials, where a single right-side stimulus was presented and detected, with BSS trials in which the left-side stimulus was extinguished. Hence, these analyses compared conditions of different physical stimulation (unilateral RVF *vs* BSS trials) that nevertheless induced an identical conscious experience, where in both cases the patient detected only one stimulus in the right-side.

Extinguished left-side neutral bodies did not evoke any significant response compared to unilateral RVF neutral stimuli [BSS left-side neutral extinguished e unilateral RVF neutral].

Table 2 e Significant activations for conscious perception of fearful bodies in unilateral displays [(LVF fearful þ RVF fearful) e (LVF neutral þ RVF neutral)].

Lobe	Surface	Brain area (Brodmann area)	Hemisphere	N. Voxels	Talairach coordinates		
					X	*Y*	*Z*
Frontal							
	Lateral						
		MFG/vlPFC(47)	L	236	-33	37	-6
		MFG/dlPFC (8)	L	2870	-42	20	41
		MFG/dlPFC (9)	R	2018	43	9	37
	Orbital						
		MFG/OFC (32)	L	301	-10	33	-8
		MFG/OFC (11)	R	277	8	33	-13
Limbic							
		AMG	L	502	-28	-5	-17
		AMG	R	213	25	-9	-10
Temporal							
	Lateral						
		MTG (21)	L	387	-58	-38	-2
		MTG/EBA(39)	L	1620	-42	-68	20
		STS (22)	L	240	-55	-50	7
	Orbital						
		FG/FBA (20)	L	2749	-43	-30	-23
Occipital							
	Mesial						
		V2eV3/LG (17/18)	L	860	-18	-76	-17
		V2eV3/LG (17/18)	R	1190	18	-86	-18

All activations are significant at $q < .05$ corrected for FDR.
Abbreviations: AMG ¼ amygdala; dlPFC ¼ dorso-lateral prefrontal cortex; EBA ¼ extrastriate body area; FBA ¼ fusiform body area; FG ¼ fusiform gyrus; LG ¼ lingual gyrus; MFG ¼ middle frontal gyrus; MTG ¼ middle temporal gyrus; OFC ¼ orbitofrontal cortex; STS ¼ superior temporal sulcus; vlPFC ¼ ventro-lateral prefrontal cortex.

Conversely, extinguished fearful bodies still activated the left amygdala and posterior cingulate cortex (PCC), as well as striate and extrastriate areas [BSS left-side fearful extinguished e unilateral RVF neutral] (see Fig. 5 and Table 3). Remarkably, subgenual (sgPFC) and the medial prefrontal cortex (mPFC) were significantly activated during nonconscious perception of fearful bodies. These areas have been involved in top-down emotion regulation, in the suppression of previously learned emotional associations, and in reducing the effect of emotional distracters (Amting, Greening, & Mitchell, 2010; Bishop, Duncan, & Lawrence, 2004; Lerner et al., 2012; Ochsner & Gross, 2005; Ochsner et al., 2004; Pessoa, 2008; Quirk & Gehlert, 2003).

3.4.3. *Conscious perception of neutral and fearful expressions in BSS displays*

A central question in the present study concerns the neural signature selectively associated with conscious perception of fearful and neutral bodily expressions. We therefore compared neural activity in BSS trials in which the patient consciously reported both stimuli, with activity in BSS trials in which the left-side stimulus underwent extinction. These contrasts, performed separately for neutral and fearful expressions, mirror those reported in the previous section, in that they analyze conditions of identical physical stimulation (the same BSS display was always presented), but different conscious perception (with *vs* without extinction).

Comparison of conscious with nonconscious perception of neutral bodies (BSS neutral conscious e BSS left-side neutral extinguished) yielded significant activity in structures composing the fronto-parietal network involved in the top-down regulation of attention, such as the lPFC and the IPL, alongside with body-selective areas in the temporal cortex, such as EBA, and in primary visual areas (see Fig. 6 and Table 4).

Conscious perception of fearful bodies revealed significant increase in areas related to emotion processing, such as the amygdala and cingulate cortex, bilaterally, and in the striate and extrastriate visual areas in the ventral stream (BSS left-side fearful conscious e BSS left-side fearful extinguished) (see Fig. 7 and Table 5). These areas were also activated during nonconscious perception of fearful expressions. In addition, areas involved in selective attention, and active during conscious perception of neutral bodies, such as the IPL, also responded to consciously perceived fearful bodies. Crucially, conscious, as compared to nonconscious perception of fearful expressions, was uniquely associated with activity in the anterior insula (antINS), primary motor (MI) and PMC, primary somatosensory cortex (SI), and in the cerebellum. Lastly, the same comparison also revealed significant deactivations in the bilateral sgPFC, indicating that this area was more active during nonconscious than conscious perception of fearful bodies in BSS displays.

To further characterize the relationship between visual awareness and brain activity, we correlated confidence ratings of perceptual (un)awareness with neural responses observed during conscious and nonconscious perception of left-side fearful expressions in BSS trials. For this purpose, we initially defined regions of interest (ROIs) in those areas

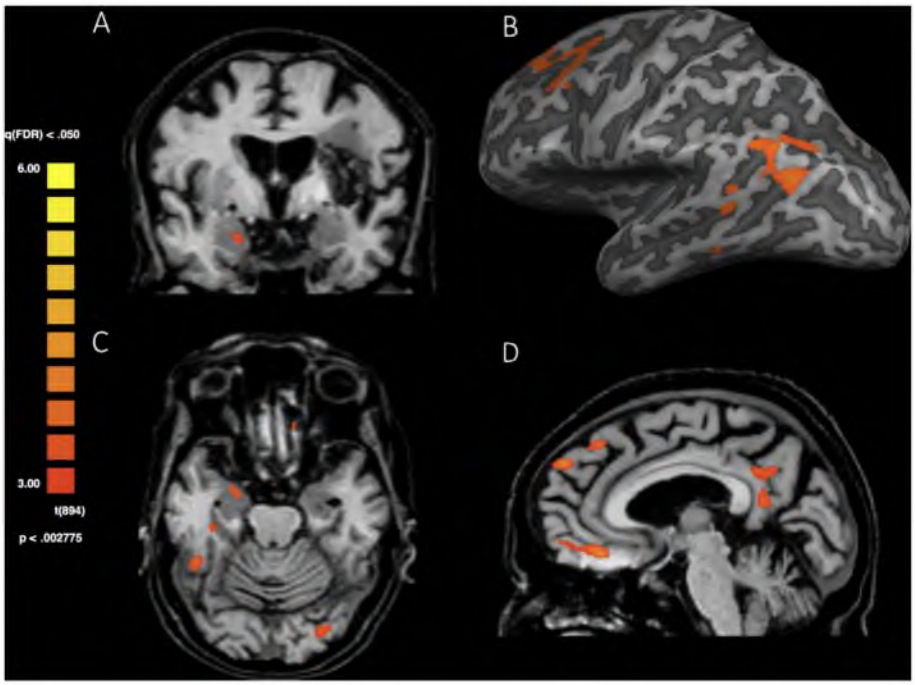

Fig. 5 e Significant activations for the nonconscious perception of left-side extinguished fearful bodies in BSS displays, superimposed on patient M.P.'s brain (BSS left-side fearful extinguished e unilateral RVF neutral). A) Activity in the left amygdala on a coronal slice (Talairach coordinate: Y ¼ ¡5); B) Activity in the EBA and STS superimposed on a 3-D inflated reconstruction of M.P.' brain; C) Activity in the left amygdala and fusiform gyrus on a transversal slice (Z ¼ ¡18); D) Activity in the sgPFC, mPFC, and PCC on a sagittal slice (X ¼ ¡4).

Table 3 e Significant activations for the nonconscious perception of extinguished fearful bodies in BSS displays (BSS left-side fearful extinguished e unilateral RVF neutral).

Lobe	Surface	Brain area (Brodmann area)	Hemisphere	N. Voxels	Talairach coordinates		
					X	*Y*	*Z*
Frontal							
	Lateral						
		MFG/dlPFC (8)	L	1126	-31	24	41
	Mesial						
		SFG/mPFC (8)	L	5342	-9	52	38
		SFG/mPFC (8)	R	963	9	37	46
Limbic							
		AMG	L	142	-20	-5	-19
	Mesial						
		PCC (30)	L	1015	-3	-50	20
		PCC (23)	R	1723	9	-53	19
		ACC/sgPFC (32)	L	3024	-2	37	-8
		ACC/sgPFC (32)	R	3863	4	36	-9
Temporal							
	Lateral						
		MTG (10)	L	566	-50	-39	-10
		MTG/EBA (39)	L	3681	-41	-66	18
		STS (39)	L	714	-47	-49	6
	Orbital						
		FG/FBA (37)	L	357	-41	-43	-18

All activations are significant at $q < .05$ corrected for FDR.

Abbreviations: ACC ¼ anterior cingulate cortex; AMG ¼ amygdala; dlPFC ¼ dorso-lateral prefrontal cortex; EBA ¼ extrastriate body area; FBA ¼ fusiform body area; FG ¼ fusiform gyrus; MFG ¼ middle frontal gyrus; mPFC ¼ middle prefrontal cortex; MTG ¼ middle temporal gyrus; PCC ¼ posterior cingulate cortex; SFG ¼ superior frontal gyrus; sgPFC ¼ subgenual prefrontal cortex; STS ¼ superior temporal sulcus.

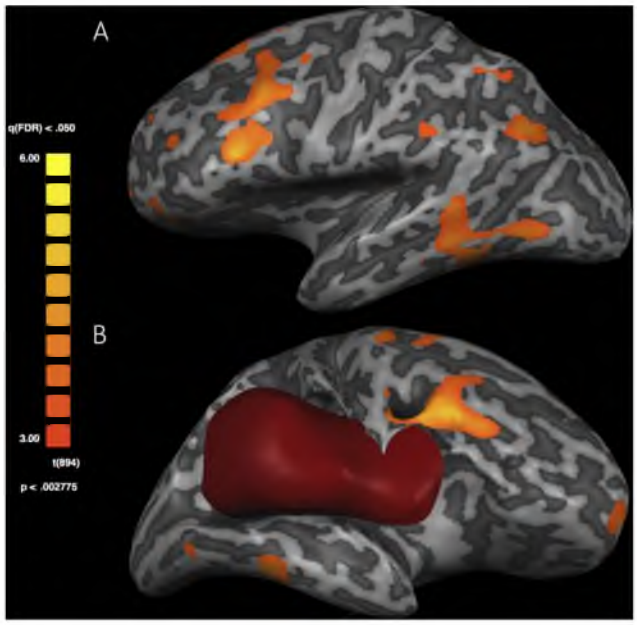

Fig. 6 e Significant activations for the conscious perception of neutral bodies in BSS displays superimposed on a 3-D inflated reconstruction of patient M.P.'s brain (the lesion is displayed in dark red) (BSS left-side fearful extinguished e unilateral RVF neutral).

uniquely activated or deactivated in the comparison of conscious with nonconscious perception of fear. This resulted in nine ROIs, seven significantly more active during conscious perception (i.e., left and right antINS, left MI, left PMC, left SI, left and right cerebellum) and two significantly more active during extinction of left-side fearful expressions (i.e., left and right sgPFC) (see also Table 5). Then, for each of the 60 BSS trials with left-side fearful bodies, we extracted the mean beta values averaged across all voxels composing each single ROI and associated with the consciously perceived (42 trials) and extinguished left-side stimuli (18 trials), as modeled with separate predictors. Beta weights quantify indeed the contribution of each predictor in explaining the level of neural activity measured in a given region. Finally, we tested the possible interaction between conscious perception, as measured continuously with the 8-point ratings, and beta weights of neural activity in each of the nine ROIs separately.

Activity in the left antINS and SI showed a mild, though significant, positive correlation with visual awareness of left-side fearful expressions (Pearson r ¼ .31, p ¼ .018; r ¼ .34, p ¼ .007, respectively), whereas activity in the right sgPFG was negatively correlated with conscious perception of the same stimuli (r ¼ -.3, p ¼ .019) (see Fig. 8).

4. Discussion

The present study investigated the relation between peripheral arousal and visual awareness for fearful and neutral bodily expressions, as well as the influence of these processes on brain activity during attentional competition. There were four main findings, as discussed below in the following sections.

4.1. Behavioral profile of visual extinction as revealed by signal detection

First, we extended our previous behavioral results showing in a new patient that bodily expressions may bias the

Table 4 e Significant activations for the conscious perception of neutral bodies in BSS displays (BSS neutral conscious e BSS left-side neutral extinguished).

Lobe	Surface	Brain area (Brodmann area)	Hemisphere	N. Voxels	Talairach coordinates		
					X	*Y*	*Z*
Frontal							
	Lateral						
		MFG/lPFC(9)	L	27334	-42	27	32
		MFG/dlPFC(6)	R	5357	42	10	45
		SFG/dlPFC (8)	L	17130/2	-25	28	48
	Mesial						
		SFG/mPFC (8)	R	10204	4	32	45
Parietal							
	Lateral						
		IPL (40)	L	716	-52	-34	24
Temporal							
	Lateral						
		MTG/EBA(39)	L	1323	-39	-62	30
	Orbital						
		FG/FBA (37)	L	6209	-47	-46	-14
		FG/FBA (37)	R	2554	52	-46	-13

All activations are significant at $q < .05$ corrected for FDR.
Abbreviations: dlPFC ¼ dorso-lateral prefrontal cortex; EBA ¼ extrastriate body area; FBA ¼ fusiform body area; FG ¼ fusiform gyrus; IPL ¼ inferior parietal lobule; lPFC ¼ lateral prefrontal cortex; MFG ¼ middle frontal gyrus; mPFC ¼ middle prefrontal cortex; MTG ¼ middle temporal gyrus; SFG ¼ superior frontal gyrus.

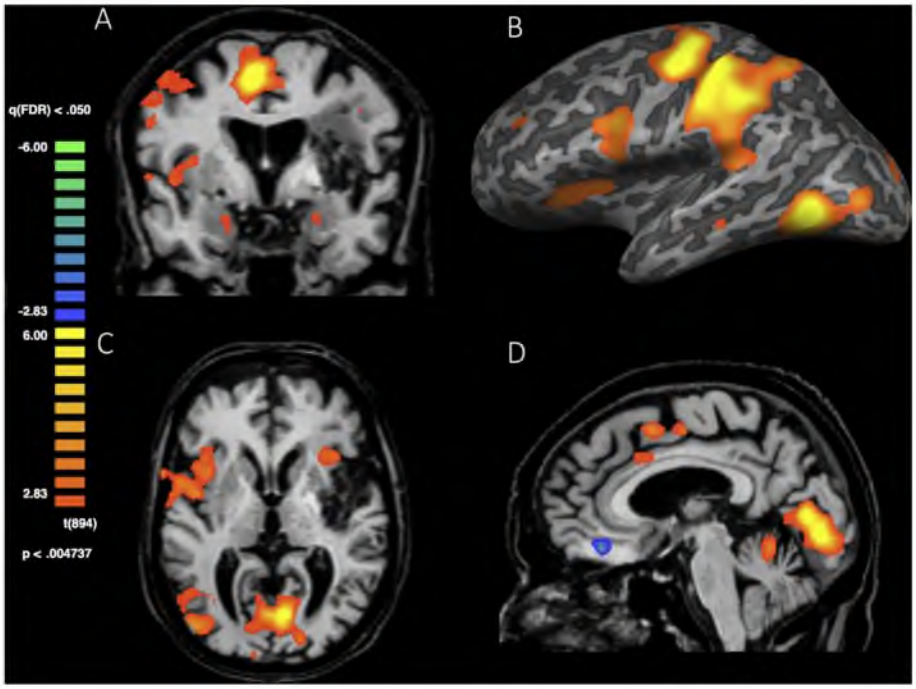

Fig. 7 e Significant activations for the conscious perception of fearful bodies in BSS displays, superimposed on patient M.P.'s brain (BSS left-side fearful conscious e BSS left-side fearful extinguished). A) Activity in the amygdala, bilaterally, anterior insula, motor and cingulate cortex on a coronal slice (Talairach coordinate: Y ¼ ¡5); B) Activity superimposed on a 3-D reconstruction of M.P.'s left hemisphere outlining responses in the insula, sensory-motor cortices and ventral extrastriate visual areas; C) Activity in the anterior insula and striate cortex, bilaterally, on a transversal slice (Z ¼ 3); D) Activity cingulate cortex, striate cortex and cerebellum, and deactivation (in blue) in the sgPFC, on a sagittal slice (X ¼ 5).

competition for attention and gain privileged access to visual awareness, despite pathological inattention following parietal damage (Tamietto et al., 2007). To our knowledge this is the first time that a procedure in which the subject provides a confidence rating on the accuracy of his own conscious perception is applied to the study of visual extinction. It has been suggested that, under ambiguous perceptual conditions, observers tend to underestimate awareness and show a response bias toward reporting that the stimulus has not been consciously perceived (Kouider & Dehaene, 2007; Pessoa, Japee, Sturman, & Ungerleider, 2006; Pessoa, Japee, & Ungerleider, 2005). Moreover, confidence ratings enabled us to approach visual awareness as a graded and dimensional, rather than discrete, phenomenon (Mitchell & Greening, 2012; Szczepanowski & Pessoa, 2007). In combination with signal detection methods, confidence rating provides a measure of perceptual sensitivity that is unaffected by response bias. We found that perceptual sensitivity for left-side fearful bodies was unaltered by the presence of a competing right-side stimulus, whereas sensitivity for left-side neutral expressions was significantly decreased under the same conditions. This selectivity for fear rules-out an interpretation in terms of response bias, and indicates that the pre-attentive sensitivity to emotional salience is relatively preserved in the contralesional LVF and able to contrast the pathologically limited capacity to process visual information under competitive situations.

4.2. *Autonomic changes related to conscious and nonconscious perception*

Secondly, we analyzed phasic pupil dilatation in relation to emotion processing and visual awareness. Pupil dilation is indeed a measure of increase in autonomic arousal induced by sympathetic system activity (Barbur, 2004), and is influenced differentially by the emotional content of facial as well as bodily expressions (Tamietto et al., 2009). Our results show additive effects of emotion and awareness. In fact, whereas exposure to fearful expressions induced more dilation than neutral expressions independent of visual awareness, nonconscious perception further induced additional dilation, although only for fearful expressions. This indicates that the relation between visual awareness and peripheral changes is sensitive to stimulus content and possibly entails partly different mechanisms depending on whether awareness occurs for emotional or neutral signals (Amting et al., 2010). Decoupling of (increased) somatic changes and (lack of) conscious visual experience has been previously reported in patients with cortical blindness and suggests that enhanced physiological arousal is not sufficient by itself to lower the threshold for visual awareness (Anders et al., 2004, 2009; Tamietto et al., 2009). This argues against the hypothesis of a direct relationship between visual awareness for emotional signals and peripheral changes. The present findings thus lead to the question of how bodily changes are mapped and

Table 5 e Significant activations for the conscious perception of fearful bodies in BSS displays (BSS left-side fearful conscious e BSS left-side fearful extinguished).

	Lobe	Surface	Brain area (Brodmann area)	Hemisphere	N. Voxels	Talairach coordinates		
						X	Y	Z
Activations								
	Frontal							
		Lateral						
			IFG/PMC (9)	L	15996	-52	1	22
			PrG/MI (4)	L	5687	-38	-12	47
	Insular							
			antINS (13)	L	3530	-35	13	4
			antINS (13)	R	1898	35	20	5
	Limbic							
			AMG	L	199	-21	-2	-17
			AMG	R	212	24	-7	-11
		Mesial						
			CING (32)	L	10220	-8	-4	-44
			CING (32)	R	793	3	14	36
	Parietal							
		Lateral						
			IPL (40)	L	7759	-44	-36	36
			PoG/SI (2)	L	8353	-49	-27	50
	Temporal							
		Orbital						
			FG/FBA(37)	L	5538	-39	-59	-12
	Occipital							
		Mesial						
			LG/CAS (18)	L	9656	-6	-80	-5
		Lateral						
			MOG (37)	L	5064	-48	-66	-5
	Cerebellum							
			Culmen	L	8326	-29	-61	-24
			Culmen	R	7934	27	-59	-21
Deactivations								
	Limbic							
		Mesial						
			ACC/sgPFC(32)	L	300	-4	42	-4
			ACC/sgPFC(32)	R	1307	5	36	-9

All activations and deactivations are significant at $q < .05$ corrected for FDR.
Abbreviations: ACC ¼ anterior cingulate cortex; AMG ¼ amygdala; antINS ¼ anterior insula; CAS ¼ calcarine sulcus; CING ¼ cingulate cortex; FBA ¼ fusiform body area; FG ¼ fusiform gyrus; IFG ¼ inferior frontal gyrus; IPL ¼ inferior parietal lobule; LG ¼ lingual gyrus; MI ¼ primary motor cortex; MOG ¼ middle occipital gyrus; PoG ¼ postcentral gyrus; PrG ¼ precentral gyrus; PMC ¼ premotor cortex; sgPFC ¼ subgenual prefrontal cortex; SI ¼ primary somatosensory cortex.

integrated at the central neural level with mechanisms for emotion processing and interoception in order to foster visual awareness. We discuss this issue below while considering the neural signature of conscious perception of fearful and neutral bodily expressions.

4.3. *The neural fate of nonconscious fearful perception*

Thirdly, our neuroimaging results demonstrate that several areas, such as the amygdala, the PCC and striate and extrastriate ventral visual areas, still responded to fearful bodily expressions despite unawareness. This is in line with previous findings on nonconscious processing of emotional signals in healthy subjects as well as in neurological patients with extinction or blindsight (Amting et al., 2010; Morris, Friston, et al., 1998; Morris, Ohman, et al., 1998; Tamietto & de Gelder, 2010; Van den Stock et al., 2011; Vuilleumier, 2005; Vuilleumier et al., 2002, 2004; Whalen et al., 1998). It has been suggested that this neural network, which is centered on direct amygdala modulatory influences over visual areas, is responsible for the privileged access of emotional signals to awareness and operates as a bottom-up amplifier of sensory processing (Garrido, Barnes, Sahani, & Dolan, 2012; Morris, Friston, et al., 1998; Vuilleumier, 2005; Vuilleumier et al., 2004). Noteworthy, however, we observed activity in the same structures irrespectively of awareness, as these areas were also responsive during conscious perception of fearful bodies. This indicates that the present mechanism cannot be considered the selective neural signature of emotional awareness. Our evidence also converges with results showing that purely sensory-driven activation of visual pathways is not sufficient to induce conscious perception when it is disconnected from complementary top-down influences from fronto-parietal areas (Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009; Desimone & Duncan, 1995; O'Craven, Downing, & Kanwisher, 1999; Pessoa et al., 2002; Vuilleumier et al., 2008).

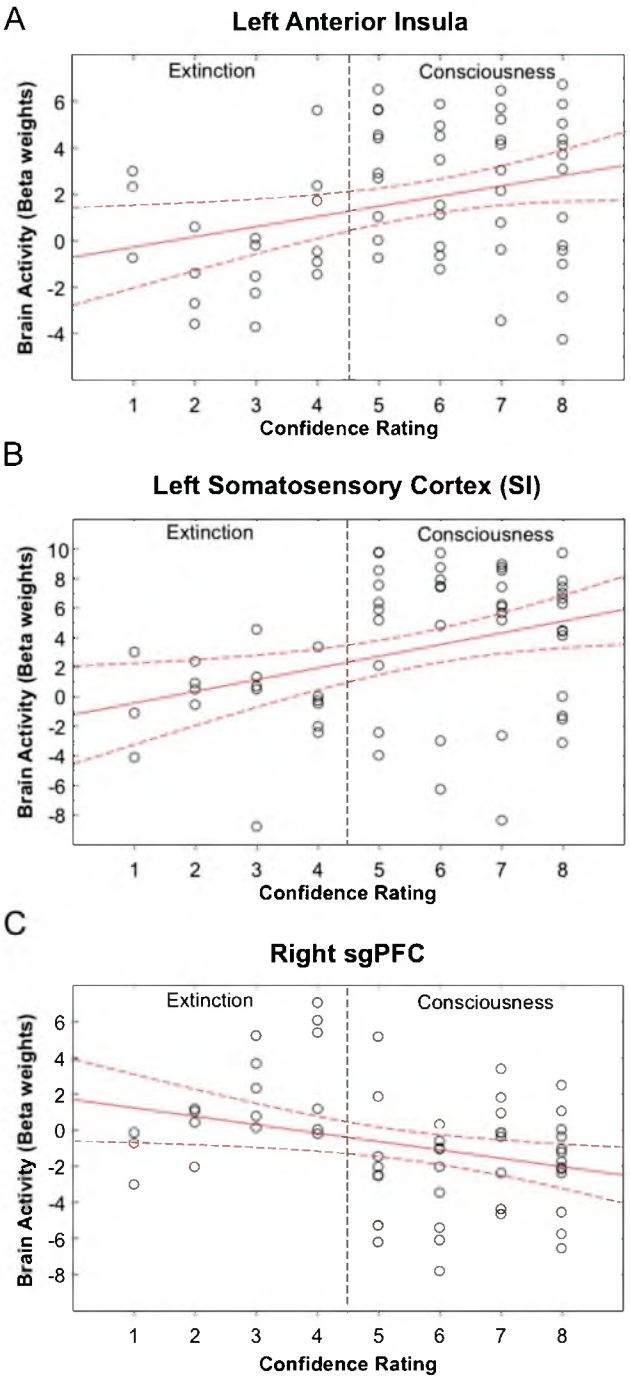

Fig. 8 e Correlations between confidence ratings of visual awareness and brain activity in A) left anterior insula; B) left primary somatosensory cortex; C) subgenual prefrontal cortex. The solid red line represents predicted (i.e., fitted) correlation between behavioral and brain measures, while the dashed red lines represent 95% confidence limits.

Interestingly, neural response in the sgPFC and in the mPFC increased when fearful bodily expressions were physically present but not consciously perceived, a finding that was consistent across two different contrasts (see Tables 3 and 5). These areas are involved in emotional regulation (Ochsner & Gross, 2005) and have been previously reported during visual suppression of fearful facial expressions in binocular rivalry (Amting et al., 2010; Lerner et al., 2012). Moreover, an inverse relationship has been observed between sympathetic arousal, on the one hand, and activity in the sgPFC and mPFC, on the other (Nagai, Critchley, Featherstone, Trimble, & Dolan, 2004). Our findings thus suggest that sgPFC and mPFC may also exert a similar top-down regulatory influence over limbic areas for bodily expressions. In support of this surmise, we found more extended activity in limbic areas for conscious than nonconscious perception of fear, with bilateral amygdala, cingulate and insular activity in the former condition.

4.4. *Neural signature of conscious perception of neutral and fearful signals*

Fourthly, we considered the neural correlates selective for the conscious perception of neutral and fearful bodily expressions. Visual awareness of neutral bodies was associated with lPFC and parietal cortex activity. These areas constitute a network for the top-down control of attention that enhances the neural representation of sensory stimuli in visual areas, thus favoring conscious perception of target stimuli among multiple competing signals (Rastelli et al., 2013). Activity in this network appears independent of the particular visual task and is insensitive to the specific content of the stimulus. For example, distributed activity in frontal and parietal areas is observed during directed attention in both the presence and absence of visual stimulation, but not when visual stimuli are presented at unattended locations (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). Moreover, lesions to the lPFC reduce the likelihood that masked stimuli reach awareness (Del Cul et al., 2009). These findings show that the fronto-parietal network is the source of top-down feedback biasing stimulus representation in visual areas rather than its consequence. Our results indicate that, despite attention depletion in visual extinction, the partial functioning of this fronto-parietal network is still critically associated to visual awareness of neutral stimuli. Therefore, depending on the emotional or neutral content of the stimuli, ventral visual areas appear to be subjected to two sources of excitatory feedforward influences; a bottom-up influence originating from the amygdala in the case of emotional stimuli, and a top-down influence from the fronto-parietal network in the case of more mundane stimuli.

Unlike neutral bodily expressions, conscious perception of fearful bodies was uniquely associated with activity in the anterior insula, somatosensory, motor and premotor cortex, and in the cerebellum; a finding further corroborated by the significant correlation between neural activity in some of these regions and measures of visual awareness. These areas are implicated in interoception, perception of sensory-motor changes in the organism, and afford an integral neural mechanism for the moment-to-moment mapping of bodily states (Craig, 2009; Critchley, 2005; Critchley et al., 2002, 2005; Khalsa et al., 2009). Although the role of the cerebellum in motor coordination is well established, recent studies also indicate its critical contribution to the integration of somatic-visceral signals (Zhu, Yung, Kwok-Chong Chow, Chan, &

Wang, 2006). Moreover, cerebellar lesions induce a deficit in conscious emotion recognition and reduce emotional experience (D'Agata et al., 2011; Turner et al., 2007). Hence, when physiologic arousal was reflected in the activity of brain regions underlying afferent representations of peripheral bodily states, the patient also experienced visual awareness of the fearful bodies. Conversely, the decoupling of peripheral arousal and the representation at central neural level of these ongoing physiological changes was associated with perceptual unawareness. This indicates that similar states of arousal can be associated with different conditions of visual experience for emotional signals, depending on the level of cortical representation of these physiological changes.

Physiological arousal was enhanced during nonconscious compared to conscious perception of fearful expressions, a result that may appear paradoxical. However, previous studies in healthy subjects as well as brain damaged patients also reported that autonomic arousal or phenomenal affective experience may be more intense when triggered by stimuli that remain inaccessible to awareness (Anders et al., 2004, 2009; Ladavas, Cimatti, Del Pesce, & Tuozzi, 1993; Tamietto et al., 2009; Winkielman & Berridge, 2004). Tentatively, we suggest that this enhanced physiological response for extinguished fearful expressions can reflect the lack of inhibitory cortical feedback, mainly from the insula, cingulate and parietal cortex, over subcortical limbic areas (Bush & Sejnowski, 1996; Tamietto & de Gelder, 2010). In fact, passive suppression or unawareness of emotional signals reduces or abolishes cortical activity in the insula or parietal cortex (Kalisch et al., 2005; Northoff et al., 2004; Wager et al., 2004), whereas activity in the amygdala, which is one important neural generator of affective somatic responses, sometimes increases during the same conditions of unawareness (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Bishop et al., 2004). Moreover, direct evidence in animal models suggests that insular activity can inhibit amygdala responses. For example, exogenous manipulation of peripheral physiological parameters, such as cardiovascular pressure, produces a decline of signal intensity in the insula and a concomitant signal increase in the amygdala (Henderson et al., 1985). Therefore, the insula, also considering the extensive reciprocal connections with the amygdala (Shi & Cassell, 1998), seems ideally placed to modulate and, in the case of conscious perception, down-regulate arousal responses triggered by the amygdala. Our results also show additive effects of emotion and visual awareness that appear selectively expressed in a network of brain areas involved in interoception and sensory-motor representation. In fact, whereas enhanced amygdala activity was specific for emotion, but evident for both conscious as well as nonconscious perception of fearful bodies, activity in the insula, sensory-motor areas and cerebellum was modulated only by visual awareness of emotional stimuli.

Taken together, the present findings suggest that the integration between peripheral arousal and the central mapping of ongoing visceral and sensory-motor changes is critical for conscious visual experience of emotional signals. This integration seems to occur in the anterior insula, motor and somatosensory cortex, and in the cerebellum. Clearly, whether this patter of activity induces visual awareness of emotions, rather then being its consequence, remains open to future investigation.

Conflict of interest

The authors declare no competing financial interests.

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Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2014.10.009.

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