

Seeing Fearful Body Language Overcomes Attentional Deficits in Patients with Neglect

Marco Tamietto¹, Giuliano Geminiani¹, Rosanna Genero²,
and Beatrice de Gelder^{3,4}

Abstract

■ Survival depends to some extent on the ability to detect salient signals and prepare an appropriate response even when attention is engaged elsewhere. Fearful body language is a salient signal of imminent danger, easily observable from a distance and indicating to the observer which adaptive action to prepare for. Here we investigated for the first time whether fearful body language modulates the spatial distribution of attention and enhances visual awareness in neurological patients with severe attentional disorders. Patients with visual extinction and hemispatial neglect following right parietal injury have a rightward attentional bias accompanied by loss of awareness for contralesional left stimuli, especially when competing stimuli appear to the right. Three such patients were tested with pictures of fearful, happy, and neutral bodily expressions briefly presented either unilaterally in the left or

right visual field, or to both fields simultaneously. On bilateral trials, unattended and task-irrelevant fearful bodily expressions modulated attentional selection and visual awareness. Fearful bodily expressions presented in the contralesional unattended visual field simultaneously with neutral bodies in the ipsilesional field were detected more often than left-side neutral or happy bodies. This demonstrates that despite pathological inattention and parietal damage, emotion and action-related information in fearful body language may be extracted automatically, biasing attentional selection and visual awareness. Our findings open new perspectives on the role of bodily expressions in attentional selection and suggest that a neural network in intact fronto-limbic and visual areas may still mediate reorienting of attention and preparation for action upon perceiving fear in others. ■

INTRODUCTION

Attention contributes to the selection of relevant sensory information for conscious perception and action in order to contrast the limited processing capacity of the visual system (Desimone & Duncan, 1995). Indeed, normal vision depends critically on selective attention as many stimuli often escape awareness if unattended (Mack & Rock, 1998). Nonetheless, some processing seems to occur in a “preattentive,” seemingly automatic, fashion, raising the question of which stimulus properties can be encoded even when focused attention is lacking (Treisman & Gelade, 1980). Neurological deficits affecting visuospatial attentional selection may thus help to elucidate which sets of features are relevant for a stimulus to reach awareness. Visual extinction is commonly associated with hemispatial neglect and frequently occurs following focal unilateral brain damage to the right parietal lobe (Rafal, 1994). This disorder entails a pathological limitation in attention that favors

the (right) ipsilesional stimulus, with a failure to direct attention toward the (left) contralesional stimulus in competitive situations (Driver & Mattingley, 1998). Patients with visual extinction perceive a stimulus in either hemispace if it is presented alone; however, when two stimuli are simultaneously presented, the contralesional stimulus goes undetected and is “extinguished” from awareness.

The constraint on visual selection in patients with extinction can be overcome by preattentive operations that parse the visual scene into candidate objects (Mattingley, Davis, & Driver, 1997) or group stimuli according to Gestalt principles (Gilchrist, Humphreys, & Riddoch, 1996; Ward, Goodrich, & Driver, 1994). Whether or not a contralesional object is extinguished in bilateral stimulation also depends on similarities between stimuli on the dimension to be reported (Rafal, Danziger, Grossi, Machado, & Ward, 2002), specific task demands (Bisiach, Vallar, & Geminiani, 1989), meaningfulness (Ward & Goodrich, 1996), and their potential biological or social relevance (Riddoch, Humphreys, Edwards, Baker, & Willson, 2003; Vuilleumier & Schwartz, 2001). This last factor is of particular interest as the prompt and automatic detection of salient events contributes to the regulation of adaptive interactions with the environment.

¹University of Torino, Italy, ²Papa Giovanni XXIII Hospital, Pianezza, Italy, ³Harvard Medical School, ⁴Tilburg University, The Netherlands

Two independent lines of research focused on emotional significance and relevance for action as two distinct aspects of environmental stimuli that may be processed preattentively and overcome extinction. First, extinction is less likely when emotional facial expressions (angry and happy), rather than neutral faces, are presented simultaneously with concurrent meaningless shapes on the right side of the space (Vuilleumier & Schwartz, 2001). However, this effect of emotion on attention and awareness seems liable to habituation and, most importantly, it has never been tested in a situation where emotional faces compete for attention with other meaningful stimuli of similar biological value (Vuilleumier et al., 2002). Furthermore, most investigations on preattentive and implicit emotional processing have concentrated only on facial expressions, whereas few studies, such as the classic “burning house” experiment by Marshall and Halligan (1988), also used threatening nonfacial stimuli (e.g., Compton, 2003; Adolphs, 2002, for reviews). Because emotions are easily communicated also by vocal signals or body language, it is unclear whether the critical information for implicit emotional processing is dependent upon extraction of expressive signals from key regions of the face or also extends to other signals communicating emotions (Adolphs et al., 2005; Whalen et al., 2004; Morris, deBonis, & Dolan, 2002). Secondly, recent findings indicate that aside from the emotional dimension, visual attention is influenced by the presence of an active relation between objects, as extinction decreases when two contralesional objects are spatially positioned such that they may be used together (e.g., a corkscrew about to be inserted into the cork of the bottle) (Riddoch et al., 2003). Similarly, visual affordances in familiar objects, such as the visibility of the handle on a cup, result in automatic activation of motor programs that, in turn, bias visual selection and reduce extinction (di Pellegrino, Rafal, & Tipper, 2005). This correspondence between perceiving and acting is not confined to object affordances but is also well known in the domain of biological movement and described under the terms “motor contagion” or “motor resonance” (Gallese, Keysers, & Rizzolatti, 2004; Levenson, 2003). However, the role of action evoked by implicit body movements in summoning spatial attention has never been studied in extinction.

Information concerning emotion and action are often equally prominent aspects of body language. Indeed, similarly to facial expressions, body language communicates emotions through characteristic postural configurations, but in addition to the former, it also evokes at the same time the adaptive actions that emotions typically trigger (de Gelder, 2006). For instance, whereas a fearful face signals a threat but does not provide information about the best way to cope with it, a fearful bodily expression also specifies the flight reaction undertaken by the individual. Passive observation of fearful bodily expressions

produces increased activity in brain areas associated with emotional processing and vision (e.g., amygdala, orbito-frontal cortex [OFC], and fusiform gyrus) and this emotion-related activity occurs together with activation of areas linked with representation of action and movement (e.g., premotor and supplementary motor areas) (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Hadjikhani & de Gelder, 2003). It has been proposed that this integrated activity constitutes a mechanism for fear contagion and preparation for action in response to seeing fear in others (de Gelder et al., 2004). Emotional body language thus provides a unique opportunity to study the joint contribution of emotional significance and implicit action representation in attentional selection and visual awareness. Here we investigated for the first time whether unattended and task-irrelevant emotional bodily expressions modulate spatial attention and enhance visual awareness in patients with visual extinction and pathologically limited attention.

METHODS

Patients

The study focused on three neurological patients (CL, PC, and BS) with visual extinction and mild signs of hemispatial neglect following unilateral brain damage from ischemia to the right parietal lobe. The patients were administered a battery of tests for the diagnosis of the general cognitive functions (Folstein, Folstein, & McHugh, 1975), visual extinction and visual field defects (Bisiach et al., 1989; Bisiach, Cappa, & Vallar, 1983), and unilateral spatial neglect (Wilson, Cockburn, & Halligan, 1987). Visual extinction and visual field defects were assessed separately for the upper and lower quadrants through the standard clinical confrontation test, in which rapid movements of the examiner’s left and/or right index finger were presented in random sequence either unilaterally in the patient’s left or right visual field, or to both visual fields simultaneously. Scores ranged from 0 (normal vision, if the patient missed less than 3 contralesional stimuli out of 10 correctly detected ipsilesional stimuli in bilateral presentation) to 3 (severe defect, if the patient missed more than 6 contralesional stimuli out of 10 correctly detected ipsilesional stimuli in unilateral presentation). Typically, a score of 1 indicates visual extinction and is assigned if the patient misses 3 or more contralesional stimuli out of 10 correctly detected ipsilesional stimuli in bilateral presentation (Bisiach et al., 1983, 1989). Unilateral neglect was assessed by the Behavioral Inattention Test (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 et al., 1987). Demographic, clinical, and neuropsychological data of the patients are summarized in Table 1.

Table 1. Demographic, Clinical, and Neuropsychological Data of the Patients

Patient	Sex	Age	Education (years)	Hand preference	Etiology	Onset (days)	MMSE	VFD	BIT
CL	F	73	5	Right	I	146	25/30	1–1	120/146
PC	M	72	5	Right	I	213	27/30	1–1	122/146
BS	M	47	8	Right	I	395	30/30	1–0	128/146

I = ischemia; MMSE = Mini Mental State Examination; VFD = visual field defects within the contralesional hemispace measured on the standard confrontation test (the two values refer to the upper and lower quadrants, respectively), scores ranged from normal vision (0) to severe defect (3); BIT = Behavioral Inattention Test, conventional part (cutoff = 129).

The side and localization of the lesions were assessed by CT scan and mapped with MRIcro software (Rorden & Brett, 2000) onto standard T1-weighted MRI templates from the Montreal Neurological Institute that matched Talairach space (Figure 1).

The study was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and all participants provided written informed consent approved by the Ethical Committee of the Department of Psychology, University of Torino, Italy.

Stimuli and Apparatus

Twenty-four gray-scale whole-body photographs (12 women, between 22 and 35 years old), eight with a fearful bodily expression, eight with a happy bodily expression, and eight showing meaningful but emotionally neutral body actions, were presented against a dark background. To focus specifically on whole-body expressions, in all images the faces were blanked out (see de Gelder et al., 2004; Hadjikhani & de Gelder, 2003, for details on stimulus preparation and validation). Image size was 9.4 cm wide and 21.2 cm high sustaining a visual angle of $\sim 8.59^\circ \times \sim 20.14^\circ$ from a viewing distance of ~ 60 cm from the screen of a 21-in. CRT monitor. Stimuli were centered vertically with the innermost edge at 9.1 cm ($\sim 8.41^\circ$) left or right of the central fixation cross ($\sim 1.26^\circ$). Mean luminance of the happy bodies was 11.05 cd/m^2 , of the fearful bodies was 10.85 cd/m^2 , and

of the neutral bodies was 10.84 cd/m^2 . Mean luminance of the dark background was 24 cd/m^2 . There was no significant difference in overall luminance between happy, fearful, and neutral bodies sets ($U \leq 30, p \geq .67$ for all comparisons in Mann–Whitney U tests). Thus, any influence related to low-level perceptual properties, such as brightness or size, can safely be discarded. Likewise, images of neutral instrumental actions (pouring water into a glass, putting on trousers, combining one's hair, and opening a door) provided an appropriate and extremely conservative control condition for higher-level properties because, like bodily emotional expressions, they belong to the same stimulus category, induce perception of biological movement, have semantic properties, are familiar, and share the same elementary components and global configuration.

The monitor was connected to an IBM-compatible Pentium PC that controlled stimulus presentation by means of Presentation 9.3 software (Neurobehavioral Systems). Eye movements were monitored via an infrared camera (RED-III pan tilt) connected to an eye-tracking system that analyzed on-line monocular pupil and corneal reflection (sampling rate 50 Hz; iViewX, SensoMotoric Instruments).

Experimental Procedure

The patients were tested in a dimly lit room during an experimental session lasting approximately 1 hour. They

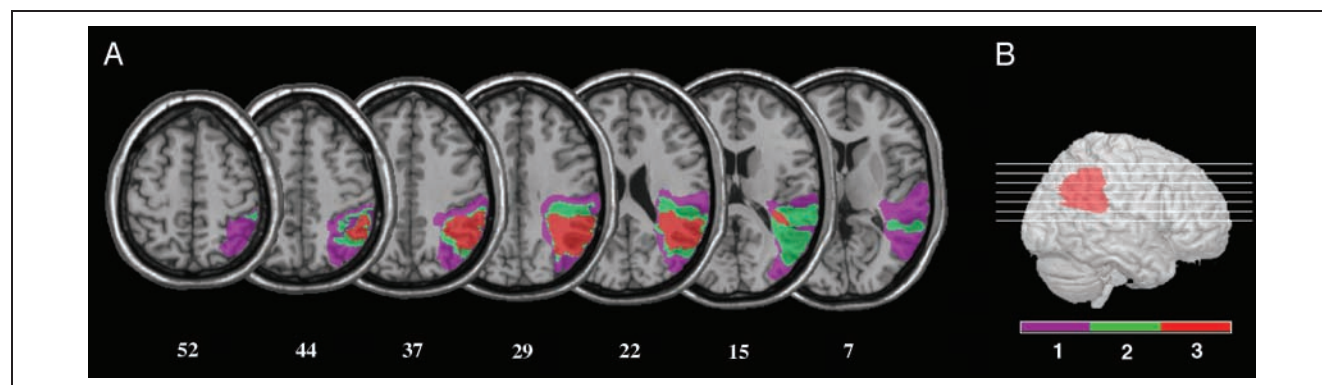


Figure 1. Regions of lesions overlap for the three patients. (A) Overlay plots in transverse sections (Talairach z-coordinates are given). The number of overlapping lesions is illustrated by color, from violet ($n = 1$) to red ($n = 3$). (B) Surface view of the centers of lesion overlap (red).

were seated at the distance of ~60 cm from the monitor, the vertical midline of which lay on the sagittal midplane of their trunk and head. Each trial started with a central fixation cross that remained on the screen until proper fixation (here defined as the persistence of the eye gaze within the cross area on the screen—2.25 cm²—for at least 500 msec). At fixation the cross was immediately followed by the stimulus, thereby avoiding the need to replace trials previously discarded because of unsteady gaze. The patients were tested in a standard extinction paradigm in which neutral, happy, and fearful bodily expressions were briefly presented either unilaterally in the left (LVF) or right (RVF) visual field, or to both visual fields in bilateral simultaneous stimulation (BSS). There were six equiprobable types of unilateral trials (a neutral, happy, or fearful bodily expression in the LVF; and a neutral, happy, or fearful bodily expression in the RVF); five types of BSS trials, with two neutral body images (always showing two different neutral actions), or with either a happy or fearful bodily expression on one side (left or right) and a neutral expression on the other side; and the no-stimulus condition where the central fixation cross was not followed by any stimulus (Figure 2). Each of these 12 conditions was repeated for 32 trials, resulting in the overall presentation of 384 randomized trials divided in two subsequent blocks of 192 trials each.

The patients simply reported 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 that were completely irrelevant to the task. Therefore, the critical experimental conditions to investigate whether emotional body language might facilitate the reorienting of attention and conscious stimulus detection were BSS displays with left happy or fearful versus left neutral bodily expressions. In this framework, we measured the rate of extinction, that is, the detection of left stimuli in BSS.

Stimulus duration was set during a practice phase for each patient in order to obtain reliable extinction on BSS

trials (~50%), together with good detection on unilateral LVF trials (~90%). Different stimuli to those shown in the experimental session were used in the practice phase. Duration was then kept constant throughout the experiment and for all stimulus conditions (CL: 170 msec; PC: 130 msec; BS: 120 msec). After each stimulus presentation, the examiner entered the patient’s verbal response into a computer. There was an interval of 2 sec before the next trial started.

Signal Detection Analysis

In addition to conventional statistical analysis on the rate of extinction at the group and single-subject level, we also carried out the signal detection analysis to determine the perceptual sensitivity, d' , and the response criterion, c , used by the patients when reporting contralesional left stimuli (Green & Swets, 1966). This distinction cannot be posed by simply comparing accuracy of detection and may provide new insights into the mechanisms underlying extinction (Gorea & Sagi, 2000). The d' index computes the distance between the signal and noise distribution means in standard deviation units. A d' value of 0 indicates inability to distinguish a contralesional left stimulus (signal) from background (noise), whereas higher values mean better sensitivity. The response bias is defined as the distance in standard deviation units between the response criterion and the neutral point, where neither “stimulus present” nor “stimulus absent” response is favored. The neutral point is located where the noise and signal distributions cross over and where the decision variable (measured in arbitrary units) is 0. Positive c values signify a conservative response criterion (i.e., the subjects are less likely to report the stimulus regardless of its actual presence), whereas negative values indicate a liberal criterion (i.e., a bias toward reporting the presence of a stimulus). The two parameters

Figure 2. Examples of the five bilateral simultaneous stimulation (BSS) displays (not to scale). The five BSS conditions consisted of two neutral expressions (control condition, left panel), one left-side happy plus one right-side neutral, one left-side fearful plus one right-side neutral, one left-side neutral plus one right-side happy, and one left-side fearful plus one right-side neutral bodily expression (right panel).

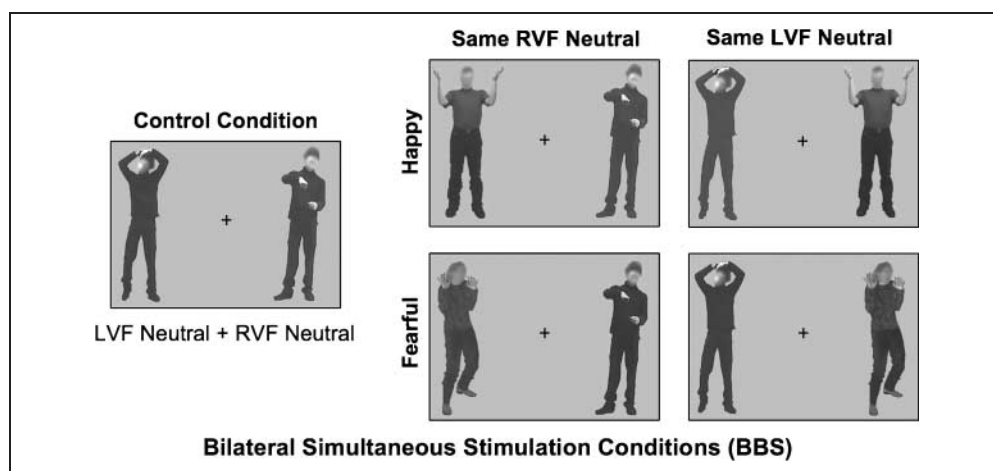


Table 2. Percentages of Stimuli Missed for Each Patient and Condition of Presentation

Patient	Unilateral LVF				Unilateral RVF				Left Misses in BSS Trials					
	Neural		Fearful		Neutral		Happy		Neutral		Happy		Fearful	
	6.25%	9.38%	9.38%	9.38%	0%	0%	0%	0%	59.38%	59.38%	25%	62.5%	53.13%	59.38%
CL	6.25%	9.38%	9.38%	9.38%	0%	0%	0%	0%	59.38%	59.38%	25%	62.5%	53.13%	59.38%
PC	25%	9.38%	15.63%	15.63%	0%	0%	3.13%	3.13%	59.38%	59.38%	28.13%	65.63%	62.5%	62.5%
BS	12.5%	6.25%	6.25%	6.25%	0%	0%	0%	0%	46.88%	46.88%	18.75%	50%	43.75%	43.75%
Mean (SD)	14.58% (9.55)	8.34% (1.8)	10.42% (4.78)	10.42% (4.78)	0% (0)	1.04% (1.8)	1.04% (1.8)	1.04% (1.8)	55.21% (7.22)	53.13% (9.38)	23.96% (4.78)	59.38% (8.27)	53.13% (9.38)	59.38% (8.27)

LVF = left visual field; RVF = right visual field; BSS = bilateral simultaneous stimulation.

were calculated as follows (Stanislaw & Todorov, 1999; Macmillan, 1993):

$$d' = \Phi^{-1}(H') - \Phi^{-1}(F')$$

$$c = -0.5 * [\Phi^{-1}(H') + \Phi^{-1}(F')]$$

where H' is the corrected hit rate, F' is the corrected false alarm rate, and Φ^{-1} is the function that converts probabilities into z scores. As proposed by Snodgrass and Corwin (1988), we used corrected values of H and F to protect against ceiling effects with H of 1 or F of 0, as the corresponding z values would be of $+\infty$ or $-\infty$, respectively. Accordingly:

$$H' = (b + 0.5)/(b + m + 1)$$

$$F' = (f + 0.5)/(f + cr + 1)$$

where b is the number of hits, m is the number of misses on signal trials, f is the number of false alarms, and cr is the number of correct rejections on noise trials.

RESULTS

Table 2 reports separately for each patient and condition the percentages of stimuli missed.

Group Analysis

A preliminary repeated-measures analysis of variance (ANOVA) on the percentage of stimuli missed in the unilateral LVF, RVF, and BSS for all different types of stimuli combined together showed a significant effect of the conditions of presentation [$F(2,4) = 200.45$, $p < .0001$]. On BSS displays, the patients markedly extinguished left-side stimuli (mean = 55.21%) as compared to unilateral LVF trials (mean = 11.11%) ($p = .0003$, post hoc Bonferroni-corrected test for all comparisons henceforth), whereas the difference between unilateral left and right stimuli (mean = 0.69%) was marginally significant ($p = .068$) (Figure 3).

The accuracy in detecting unilateral LVF and RVF stimuli was not influenced by the bodily expression (neutral, happy, or fearful) [LVF: $F(2,4) = 1.27$, $p = .37$; RVF: $F(2,4) = 0.4$, $p = .69$]. Critically, however, the rate of extinction in the five BSS trials was significantly affected by stimulus conditions [$F(4,8) = 123.48$, $p < .0001$] (Figure 4). Among all BSS trials with the same RVF neutral expression, extinction was consistently less for LVF fearful than LVF neutral or happy bodily expression ($p < .0001$ for both comparisons). Conversely, among all BSS trials with the same LVF neutral expression, extinction increased with RVF fearful as compared

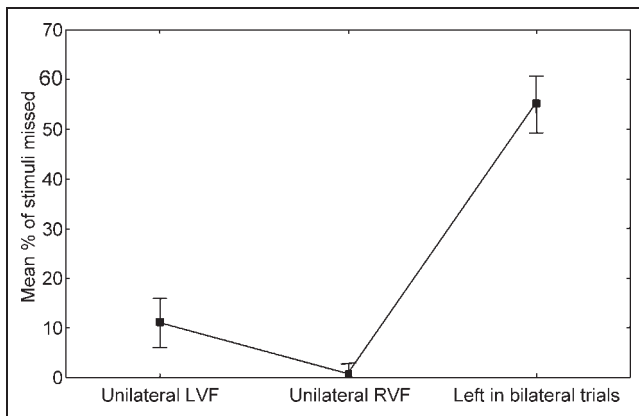


Figure 3. Mean percentage of stimuli missed in unilateral and bilateral trials for all types of stimuli combined together.

to RVF neutral or happy expressions ($p \leq .0002$ for both comparisons).

Single-subject Analysis

Given the relative small size of our sample and the possible variability of the patients, their performance was also compared across conditions using nonparametric statistical tests (chi-square and Fisher's exact tests) for each subject individually.

Response accuracy in detecting unilateral LVF, RVF, and BSS stimuli combined together for different types of stimuli showed a significant effect of the conditions of presentation in all three patients [$\chi^2(2) \geq 93.89$, $p \leq .0001$ for each patient]. Accuracy was better in the RVF than in the LVF for all patients in unilateral conditions ($p \leq .035$ by Fisher's tests for each patient). On BSS trials, all patients showed severe extinction of (left) contralesional stimuli ($p \leq .0001$ for each patient).

Again, the bodily expression (neutral, happy, or fearful) did not influence accuracy in any of the patients and for either unilateral LVF or RVF displays [LVF: $\chi^2(2) \leq 2.85$, $p \geq 0.24$; RVF: $\chi^2(2) \leq 2.02$, $p \geq 0.36$ for each patient].

Nonparametric analysis at the single-subject level confirmed the results on mean values at the group level, showing that the rate of extinction in the five BSS trials was significantly affected by expressions and conditions of presentation [$\chi^2(4) \geq 21.98$, $p \leq .0001$, for each patients]. In BSS displays with the same RVF neutral expression, an LVF fearful bodily expression was extinguished much less often than an LVF neutral ($p \leq .032$ for each patient) or happy expression ($p \leq .039$ in patients CL and PC, $p = .058$ in patient BS). Conversely, in BSS displays with the same LVF neutral expression, an RVF fearful expression increased contralesional extinction by reference to RVF neutral ($p \leq .05$ for each patient) and happy bodily expressions ($p \leq .041$ in patients CL and BS, $p = .14$ in patient PC).

Signal Detection Analysis

Subject-averaged signal and noise distributions for LVF stimuli by stimulus type and conditions of presentation are shown in Figure 5.

Perceptual sensitivity to unilateral LVF neutral expressions (mean $d' = 3.07$) was decreased by the presence of a competing RVF neutral [mean $d' = 2.04$; $t(2) = 11.57$, $p = .007$], happy [mean $d' = 1.77$; $t(2) = 10.63$, $p = .009$] or fearful expression in BSS displays [mean $d' = 1.04$; $t(2) = 7.62$, $p = .017$]. Likewise, sensitivity to unilateral LVF happy bodily expressions (mean $d' = 3.32$) was reduced by the presence of an opposite RVF neutral expression [mean $d' = 2.09$; $t(2) = 5.96$, $p = .027$]. Importantly, however, visual sensitivity for unilateral LVF fearful expressions (mean $d' = 3.22$) was not significantly reduced by RVF neutral expressions [mean $d' = 2.85$; $t(2) = 2.76$, $p = .11$]. The response criterion used to decide about the presence of a unilateral LVF neutral expression (mean $c = 0.47$) was biased in a conservative direction by competing RVF fearful [mean $c = 1.49$; $t(2) = 7.62$, $p = .017$], but not by RVF neutral [mean $c = 1.15$; $t(2) = 3.38$, $p = .08$] or happy expressions in BSS conditions [mean $c = 1.77$; $t(2) = 3.43$, $p = .08$]. Conversely, the response criterion for unilateral LVF fearful stimuli (mean $c = 0.4$) was not significantly biased by the presence of a simultaneous RVF neutral expression [mean $c = 0.74$; $t(2) = 3.45$, $p = .08$].

DISCUSSION

The present findings provide the first evidence that fearful bodily expressions are better attended to and more often consciously perceived than neutral or happy bodily expressions. Because any low-level perceptual confounds can be ruled out, our results are consistent

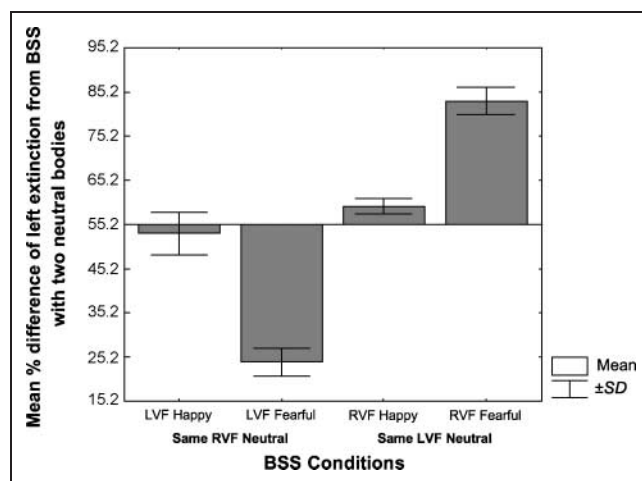


Figure 4. Mean difference in the percentage of contralesional left extinction from the BSS control condition with left-side neutral plus right-side neutral bodily images.

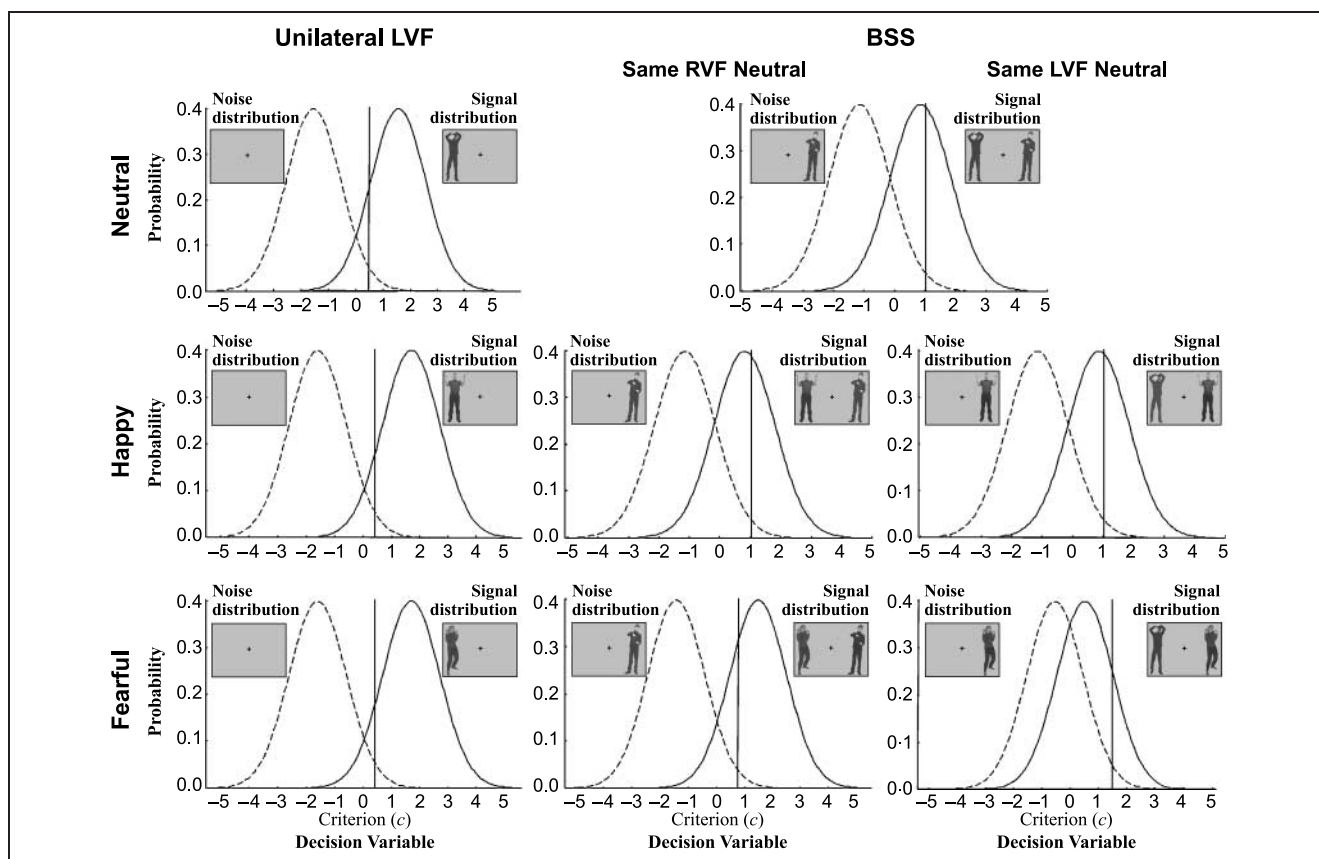


Figure 5. Subject-averaged signal (continuous line) and noise distributions (dashed line) for LVF stimuli by stimulus type and conditions of presentation. High perceptual sensitivity, d' , is graphically represented by reduced overlapping between the signal and noise distributions, and vice-versa. Response criterion, c , is represented by the vertical line. Positive c values signify a conservative response criterion, and vice-versa.

with the notion that, in patients with extinction, residual processing may precede the allocation of spatial attention before selection for awareness occurs (Rafal, 1994). Indeed, the loss of awareness following right parietal injury can be overcome by several stimulus factors biasing attention, including emotional value and significance for action (Dolan, 2002; Driver & Mattingley, 1998).

Notwithstanding, three new major findings characterize our study as compared to prior investigations. First, we provide initial evidence that fearful body language receives priority for attentional selection and increases awareness of contralesional stimuli in an automatic fashion, similar to what has so far been argued only for facial expressions (Adolphs & Tranel, 2003; Dolan, 2002). In support of an interpretation in terms of attentional salience of the stimuli, we also observed that right-side presentation of fearful bodily expressions reduced awareness of left-side neutral or happy bodies. This indicates that fearful body language may capture attention irrespectively of the side of presentation and independently of whether attentional biases may favor or disadvantage visual processing. Importantly, the influence of fearful bodily expressions reported here cannot be ascribed to top-down factors, as it arose in

comparison to other stimuli belonging to the same category and even though their nature or expression was irrelevant to the task. Conversely, in previous works, facial expressions competed for attention with different classes of stimuli such as houses or meaningless shapes, and the subjects were asked to report the category the stimuli belonged to (Vuilleumier et al., 2002; Vuilleumier & Schwartz, 2001). This procedure may have partially biased the competition for attention in favor of faces and may have boosted the subsequent processing of the facial expressions.

Secondly, in contrast to previous research reporting attentional modulation by both negative and positive emotional facial expressions (Tamietto et al., 2005; Vuilleumier & Schwartz, 2001), only fearful body language biased attention in the present study. Passive viewing of still images of fearful, but not of happy, bodily expressions results in automatic encoding of emotion and action-related information even in the absence of any explicit action intention or motor performance, as reflected by enhanced activity in brain regions dedicated to action representation, motor planning, and execution (de Gelder et al., 2004). A parallel line of evidence also showed that visuospatial selection can be biased by actions automatically activated by visual affordances in

familiar objects (di Pellegrino et al., 2005; Riddoch et al., 2003; Humphreys & Riddoch, 2001). Accordingly, it has been proposed that visual awareness is related to motor planning and that spatial attention mechanisms developed mainly to select and initiate actions in the environment (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). Our results complement this view and suggest that action representation implicitly evoked by fearful body language can automatically modulate attentional shift, thereby indicating a specific and nonintentional preparation to act in response to seeing fear in others.

Thirdly, the signal detection analysis allows us to disambiguate perceptual sensitivity from response criteria (Green & Swets, 1966). The results show that whereas perceptual sensitivity to unilateral LVF neutral or happy expressions was significantly decreased by the presence of a competing RVF stimulus, sensitivity to LVF fearful expressions was not altered by a concurrent RVF stimulus. Likewise, whereas the response criterion used to decide on the presence of an LVF neutral body was biased toward conservative decisions by competing RVF fearful but not by RVF happy or neutral expressions, the criterion for LVF fearful expressions was not modulated by RVF competitors in BSS conditions. This provides new insights on the nature of the influence exerted by fearful bodily expressions on attention and, more generally, on the mechanisms responsible for visual extinction (Ricci, Genero, Colombatti, Zampieri, & Chatterjee, 2005; Ricci & Chatterjee, 2004; Gorea & Sagi, 2000). The present findings seem to characterize extinction as the by-product of two contingent processes: first, a preserved implicit analysis of the salience of contralesional stimuli that modulates LVF perceptual sensitivity in order to contrast the limited capacity to process sensory information in competitive situations; second, an overt processing of the relevance of ipsilesional stimuli that influences decision making. This latter factor shifts responses in a conservative direction when the properties of ipsilesional events readily recruit attention.

Residual processing of fearful body language under pathologically limited attention makes considerable sense from both an anatomical and functional perspective, and comments directly on the mechanisms involved in visual awareness. Indeed, the brain structures, thus far, known to be implicated in the perception of human bodies, in recognition of emotion, and in action representation, are generally intact in patients with visual extinction and neglect, none of which involve the damaged right parietal lobe (de Gelder, 2006; di Pellegrino et al., 2005; Adolphs, 2002; Armony & Dolan, 2002; Downing, Jiang, Shuman, & Kanwisher, 2001; Rizzolatti et al., 1987).

Emotionally neutral human bodies may capture attention and increase awareness in healthy subjects (Downing, Bray, Rogers, & Childs, 2004), and there is initial evidence of brain regions in the ventral occipito-temporal cortex (fusiform gyrus, inferior and middle occipital

cortex) specialized for encoding body images (Downing et al., 2001). There is also evidence from recent observations that task-irrelevant bodily expressions influence emotional evaluation in facial expressions, and that conflicts in the emotion expressed by the face and body enhance event-related brain potentials in visual areas as early as 110 msec from stimulus onset (Meeren, van Heijnsbergen, & de Gelder, 2005). This P1 component is thought to indicate initial stages of visual processing in the occipital cortex, which are relatively automatic and insensitive to voluntary attention. Moreover, activity in these visual cortices and in subcortical structures for automatic stimulus detection and orientation (colliculi and pulvinar) is enhanced by fearful bodily expressions (de Gelder et al., 2004; Hadjikhani & de Gelder, 2003), possibly reflecting feedback modulatory influences from emotion-related limbic areas (e.g., amygdala and posterior cingulate cortex) and the OFC that favor processing of salient visual stimuli (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004; Armony & Dolan, 2002; Anderson & Phelps, 2001; Morris et al., 1998).

All those regions were bilaterally intact in our patients and may have received sufficient input from the ventral pathway to sustain visual perception and emotional evaluation in both hemispaces, despite parietal damage and pathological inattention. The OFC and the amygdala, in particular, are ideally placed to provide an interface between emotion, action, and attention, as important bidirectional connections exist between the OFC and the amygdala, on the one hand, and the premotor, parietal, and dorsolateral prefrontal cortices, on the other (Pessoa, Kastner, & Ungerleider, 2002; Mesulam, 1999; Carmichael & Price, 1995a, 1995b; Morecraft, Geula, & Mesulam, 1993). Both these areas are activated by fearful body language in healthy subjects (de Gelder et al., 2004) and by unseen fearful facial expressions in patients with visual extinction (Vuilleumier et al., 2002), indicating that processing of unattended emotional stimuli may proceed well beyond early visual pathways. Besides their role in emotional evaluation, the OFC and the amygdala have been associated with fast orienting of attention (Armony & Dolan, 2002), and largely overlap with a neural network in fronto-limbic and subcortical areas (e.g., basal ganglia) involved in attentional selection, action representation, and motor execution that also includes the right parietal cortex (Corbetta & Shulman, 2002; Pessoa et al., 2002). Thus, the present findings suggest that intact fronto-limbic and visual areas may still mediate representation of emotional and action-related information conveyed by fearful body language despite damage to the right parietal lobe.

Lastly, our results have potentially important clinical implications for rehabilitation of neurological patients with attentional deficits following parietal injury. Indeed, although patients with visual extinction and hemispatial neglect seem oblivious of contralesional events, manipulation of the salience of contralesional stimuli

may nonetheless contribute to alleviate their attentional disorder.

Acknowledgments

We thank Raffaella Ricci and Anna Berti for valuable comments.

This study was supported by a Post-Doc Lagrange Fellow Project–CRT Foundation grant “The challenge of complexity” from the ISI Foundation to Marco Tamietto, and partly supported by a Human Frontier Science Program grant RGP0054 to Beatrice de Gelder.

This research project was presented as part of the PRIN 2006 grant application by Giuliano Geminiani to the Italian MIUR, but received no financial support.

Reprint requests should be sent to Beatrice de Gelder, Martinos Center for Biomedical Imaging, Massachusetts General Hospital, Harvard Medical School, First Street Building 36, Charlestown, MA 02129, USA, or via e-mail: degelder@nmr.mgh.harvard.edu, or to Marco Tamietto, Dipartimento di Psicologia, Università di Torino, Via Po 14, 10123 Torino, Italy or via e-mail: tamietto@psych.unito.it.

REFERENCES

- Adolphs, R. (2002). Neural systems for recognizing emotion. *Current Opinion in Neurobiology*, *12*, 169–177.
- Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, *433*, 68–72.
- Adolphs, R., & Tranel, D. (2003). Amygdala damage impairs emotion recognition from scenes only when they contain facial expressions. *Neuropsychologia*, *41*, 1281–1289.
- Anderson, A. K., & Phelps, E. A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature*, *411*, 305–309.
- Armony, J. L., & Dolan, R. J. (2002). Modulation of spatial attention by fear-conditioned stimuli: An event-related fMRI study. *Neuropsychologia*, *40*, 817–826.
- Bisiach, E., Cappa, S., & Vallar, G. (1983). *Guida all'esame neuropsicologico*. Milan: Raffaello Cortina Editore.
- Bisiach, E., Vallar, G., & Geminiani, G. (1989). Influence of response modality on perceptual awareness of contralesional visual stimuli. *Brain*, *112*, 1627–1636.
- Carmichael, S. T., & Price, J. L. (1995a). Limbic connections of the orbital and medial prefrontal cortex in macaque monkeys. *Journal of Comparative Neurology*, *363*, 615–641.
- Carmichael, S. T., & Price, J. L. (1995b). Sensory and premotor connections of the orbital and medial prefrontal cortex of macaque monkeys. *Journal of Comparative Neurology*, *363*, 642–664.
- Compton, R. J. (2003). The interface between emotion and attention: A review of evidence from psychology and neuroscience. *Behavioral and Cognitive Neuroscience Reviews*, *2*, 115–129.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews: Neuroscience*, *3*, 201–215.
- de Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nature Reviews: Neuroscience*, *7*, 242–249.
- de Gelder, B., Snyder, J., Greve, D., Gerard, G., & Hadjikhani, N. (2004). Fear fosters flight: A mechanism for fear contagion when perceiving emotion expressed by a whole body. *Proceedings of the National Academy of Sciences, U.S.A.*, *101*, 16701–16706.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- di Pellegrino, G., Rafal, R., & Tipper, S. P. (2005). Implicitly evoked actions modulate visual selection: Evidence from parietal extinction. *Current Biology*, *15*, 1469–1472.
- Dolan, R. J. (2002). Emotion, cognition, and behavior. *Science*, *298*, 1191–1194.
- Downing, P. E., Bray, D., Rogers, J., & Childs, C. (2004). Bodies capture attention when nothing is expected. *Cognition*, *93*, B27–B38.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*, 2470–2473.
- Driver, J., & Mattingley, J. B. (1998). Parietal neglect and visual awareness. *Nature Neuroscience*, *1*, 17–22.
- Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). “Mini-mental state”. A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*, *12*, 189–198.
- Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, *8*, 396–403.
- Gilchrist, I. D., Humphreys, G. W., & Riddoch, M. J. (1996). Grouping and extinction: Evidence for low-level modulation of visual selection. *Cognitive Neuropsychology*, *13*, 1223–1249.
- Gorea, A., & Sagi, D. (2000). Failure to handle more than one internal representation in visual detection tasks. *Proceedings of the National Academy of Sciences, U.S.A.*, *97*, 12380–12384.
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.
- Hadjikhani, N., & de Gelder, B. (2003). Seeing fearful body expressions activates the fusiform cortex and amygdala. *Current Biology*, *13*, 2201–2205.
- Humphreys, G. W., & Riddoch, M. J. (2001). Detection by action: Neuropsychological evidence for action-defined templates in search. *Nature Neuroscience*, *4*, 84–88.
- Levenson, R. W. (2003). Blood, sweat, and fears: The autonomic architecture of emotion. *Annals of the New York Academy of Sciences*, *1000*, 348–366.
- Mack, A., & Rock, I. (1998). *Inattention blindness*. Cambridge: MIT Press.
- Macmillan, N. A. (1993). Signal detection theory as data analysis method and psychological decision model. In G. Keren & C. Lewis (Eds.), *A handbook for data analysis in the behavioral sciences: Methodological issues* (pp. 21–57). Hillsdale, NJ: Erlbaum.
- Marshall, J. C., & Halligan, P. W. (1988). Blindsight and insight in visuo-spatial neglect. *Nature*, *336*, 766–767.
- Mattingley, J. B., Davis, G., & Driver, J. (1997). Preattentive filling-in of visual surfaces in parietal extinction. *Science*, *275*, 671–674.
- Meeren, H. K., van Heijnsbergen, C. C., & de Gelder, B. (2005). Rapid perceptual integration of facial expression and emotional body language. *Proceedings of the National Academy of Sciences, U.S.A.*, *102*, 16518–16523.
- Mesulam, M. M. (1999). Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *354*, 1325–1346.

- Morecraft, R. J., Geula, C., & Mesulam, M. M. (1993). Architecture of connectivity within a cingulo-fronto-parietal neurocognitive network for directed attention. *Archives of Neurology*, *50*, 279–284.
- Morris, J. S., deBonis, M., & Dolan, R. J. (2002). Human amygdala responses to fearful eyes. *Neuroimage*, *17*, 214–222.
- Morris, J. S., Friston, K. J., Buchel, C., Frith, C. D., Young, A. W., Calder, A. J., et al. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, *121*, 47–57.
- Pessoa, L., Kastner, S., & Ungerleider, L. G. (2002). Attentional control of the processing of neural and emotional stimuli. *Brain Research, Cognitive Brain Research*, *15*, 31–45.
- Rafal, R. D. (1994). Neglect. *Current Opinion in Neurobiology*, *4*, 231–236.
- Rafal, R., Danziger, S., Grossi, G., Machado, L., & Ward, R. (2002). Visual detection is gated by attending for action: Evidence from hemispatial neglect. *Proceedings of the National Academy of Sciences, U.S.A.*, *99*, 16371–16375.
- Ricci, R., & Chatterjee, A. (2004). Sensory and response contributions to visual awareness in extinction. *Experimental Brain Research*, *157*, 85–93.
- Ricci, R., Genero, R., Colombatti, S., Zampieri, D., & Chatterjee, A. (2005). Visuomotor links in awareness: Evidence from extinction. *NeuroReport*, *16*, 843–847.
- Riddoch, M. J., Humphreys, G. W., Edwards, S., Baker, T., & Willson, K. (2003). Seeing the action: Neuropsychological evidence for action-based effects on object selection. *Nature Neuroscience*, *6*, 82–89.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*, 31–40.
- Rorden, C., & Brett, M. (2000). Stereotaxic display of brain lesions. *Behavioural Neurology*, *12*, 191–200.
- Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory: Applications to dementia and amnesia. *Journal of Experimental Psychology—General*, *117*, 34–50.
- Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*, *31*, 137–149.
- Tamietto, M., Latini Corazzini, L., Pia, L., Zettin, M., Gionco, M., & Geminiani, G. (2005). Effects of emotional face cueing on line bisection in neglect: A single case study. *Neurocase*, *11*, 399–404.
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*, 97–136.
- Vuilleumier, P., Armony, J. L., Clarke, K., Husain, M., Driver, J., & Dolan, R. J. (2002). Neural response to emotional faces with and without awareness: Event-related fMRI in a parietal patient with visual extinction and spatial neglect. *Neuropsychologia*, *40*, 2156–2166.
- Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience*, *7*, 1271–1278.
- Vuilleumier, P., & Schwartz, S. (2001). Emotional facial expressions capture attention. *Neurology*, *56*, 153–158.
- Ward, R., & Goodrich, S. (1996). Differences between objects and nonobjects in visual extinction: A competition for attention. *Psychological Science*, *7*, 177–180.
- Ward, R., Goodrich, S., & Driver, J. (1994). Grouping reduces visual extinction: Neuropsychological evidence for weight-linkage in visual selection. *Visual Cognition*, *1*, 101–129.
- Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., et al. (2004). Human amygdala responsiveness to masked fearful eye whites. *Science*, *306*, 2061.
- Wilson, B., Cockburn, J., & Halligan, P. (1987). Development of a behavioral test of visuospatial neglect. *Archives of Physical Medicine and Rehabilitation*, *68*, 98–102.