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## Unseen fearful faces facilitate visual discrimination in the intact field

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Prof. Elisabetta Làdavas Department of Psychology, University of Bologna Viale Berti Pichat, 5 tel: +39 0512091347 40127 Bologna, Italy **Abstract** 

Implicit visual processing of emotional stimuli has been widely investigated since the classical studies on affective

blindsight, in which patients with primary visual cortex lesions showed discriminatory abilities for unseen emotional

stimuli in the absence of awareness. In addition, more recent evidence from hemianopic patients showed response

facilitation and enhanced early visual encoding of seen faces, only when fearful faces were presented concurrently in

the blind field. However, it is still unclear whether unseen fearful faces specifically facilitate visual processing of

facial stimuli, or whether the facilitatory effect constitutes an adaptive mechanism prioritizing the visual analysis of

any stimulus. To test this question, we tested a group of hemianopic patients who perform at chance in forced-choice

discrimination tasks of stimuli in the blind field. Patients performed a go/no-go task in which they were asked to

discriminate simple visual stimuli (Gabor patches) presented in their intact field, while fearful, happy and neutral

faces were concurrently presented in the blind field. The results showed a reduction in response times to the Gabor

patches presented in the intact field, when fearful faces were concurrently presented in the blind field, but only in

patients with left hemispheric lesions. No facilitatory effect was observed in patients with right hemispheric lesions.

These results suggest that unseen fearful faces are implicitly processed and can facilitate the visual analysis of simple

visual stimuli presented in the intact field. This effect might be subserved by activity in the spared colliculo-

amygdala-extrastriate pathway that promotes efficient visual analysis of the environment and rapid execution of

defensive responses. Such a facilitation is observed only in patients with left lesions, favouring the hypothesis that

the right hemisphere mediates implicit visual processing of fear signals.

**Keywords** 

Hemianopia; Affective blindsight; Fear; Amygdala; Visual residual functions.

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## 1 Introduction

Implicit visual processing of emotional information without awareness has been extensively investigated, due to its importance for survival (for a review, Celeghin et al., 2015; Diano et al., 2017; Tamietto and de Gelder, 2010). The pioneering studies conducted by Larry Weiskrantz on blindsight (Weiskrantz et al., 1974) showed that patients with lesions of the primary visual cortex (V1) could discriminate above the chance level specific features of stimuli presented in their scotoma. Subsequent studies, with the contribution of the same research group, provided evidence of the peculiar ability of these patients to unconsciously perceive emotional signals, a phenomenon called affective blindsight (de Gelder et al., 2001, 1999). Patients with affective blindsight show performance above chance when they are asked to discriminate the emotional content of faces presented in their blind field (i.e., two-alternative forced choice tasks; de Gelder et al., 1999; Pegna et al., 2005). In addition, their responses to emotional target stimuli, presented in the intact field, are facilitated when an emotionally congruent stimulus is presented concurrently in the blind field (de Gelder et al., 2001). They also show reduced event related potentials (ERPs) when emotionally incongruent unseen faces and voices are presented together (de Gelder et al., 2002).

More recently, residual visual processing of the emotional content of unseen stimuli has also been shown in patients with visual field defects without blindsight (Bertini et al., 2013; Cecere et al., 2014). Indeed, hemianopic patients who do not demonstrate any form of blindsight or affective blindsight in classical terms (i.e., they perform at the chance level when asked to discriminate any content, emotional or otherwise, of stimuli presented in their blind field in two alternative forced choice tasks), have shown implicit processing of unseen fearful stimuli both at the behavioural level and at the electrophysiological level. Specifically, hemianopic patients evaluated with indirect tests in which they were asked to respond to seen faces presented in the intact field, during the concurrent presentation of faces in their blind field, showed a response facilitation (i.e. reduced reaction times) only when fearful faces were presented at the same time in the blind field, but not when happy faces were presented in the blind field (Bertini et al., 2013). Similarly, at the electrophysiological level, presenting fearful faces in the blind field increases the amplitude of the N170 component evoked by faces presented in the intact field, indicating enhanced early structural encoding of the seen faces (Cecere et al., 2014). These findings from hemianopic patients show that when the cortical visual

pathway is lesioned, threat-related emotional information in the blind field can still be extracted and processed in order to improve visual processing in the intact field.

This fear-related specificity in implicit visual processing seems to be mediated by the spared, alternative subcortical visual circuit, which encompasses structures important for visual and emotional processing such as the superior colliculus (SC), the pulvinar and the amygdala (LeDoux, 1998). The subcortical colliculo-pulvinar-amygdala circuit represents a critical route for coarse and rapid visual processing of salient and emotional visual information (Garrido et al., 2012; Garvert et al., 2014). Indeed, superior colliculus' neurons in primates have been shown to encode coarse facial information around 25-50 ms after stimulus onset (Nguyen et al., 2016, 2014). In keeping with this finding, the pulvinar shows differential neural responses to facial expressions within 100 ms after stimulus onset (Maior et al., 2010). Similarly, in humans, early responses to fearful faces in the pulvinar and the amygdala have been found as early as 40 ms after stimulus onset (Luo et al., 2007). Evidence of direct anatomical connections between these subcortical sites has been provided by diffusion tensor imaging studies in both monkeys and humans (Rafal et al., 2015; Tamietto et al., 2012). Crucially, the fibers connecting the structures of this subcortical pathway are spared and reportedly strengthened after V1 lesions in blindsight patients (Tamietto et al., 2012), supporting the hypothesis that they might represent the pathway for implicit emotional visual processing.

So far, the behavioural and electrophysiological findings in hemianopic patients (Bertini et al., 2013; Cecere et al., 2014) have shown that presenting unseen fearful faces facilitates early visual encoding and behavioural discrimination of faces presented in the intact field. However, the engagement of the colliculo-pulvinar-amygdala circuit in implicit visual processing of fearful faces without awareness suggests that the facilitatory effects could generalize to other stimuli outside the facial domain. Indeed, the subcortical circuit allows rapid detection of stimuli for survival (Adolphs, 2013; LeDoux, 2014), therefore suggesting an adaptive role in prioritizing visual analysis of the environment. In line with this idea, the present study was designed to investigate whether presenting fearful faces in the blind field of hemianopic patients without blindsight could facilitate the visual analysis of simple visual stimuli presented in the intact field. Specifically, patients were asked to discriminate Gabor patches presented in the intact visual field, during concurrent presentation of fearful, happy and neutral faces in the blind field. Indeed, the orientation discrimination of Gabor patches is

known to rely on the activation of striate and early ventral extrastriate cortices (Fang et al., 2005) and, is therefore, suitable for testing basic visual processing. If unseen fear signals are processed by the spared subcortical pathway and facilitate visual processing in the intact field, then responses to Gabor patches in the intact field should be facilitated, when fearful faces, but not happy or neutral faces, are concurrently presented in the blind field.

#### 2 Methods

#### 2.1 Participants

Sixteen right-handed patients with chronic visual field defects participated in Experiments 1 and 2. Eight patients had a left visual field defect (3 females; mean age: 45.7 years; mean years of education: 15 years; mean time since lesion onset: 16.9 months), and the other eight patients had a right visual field defect (2 females; mean age: 49.9 years; mean years of education: 11.5 years; mean time since lesion onset: 12.6 months), as documented by an automated perimetry test. The two groups of patients did not differ in terms of age (t(14)=-0.64; p=.53), education (t(14)=1.89; p=.08) or time since lesion onset (t(14)=0.5; p=.62). All patients had postgeniculate lesions resulting in deafferentation or destruction of the striate cortex, confirmed by computed tomography (CT) or magnetic resonance imaging (MRI). Clinical details and lesion reconstruction images, based on CT or MRI scans are reported in Table 1 and Fig. 1, respectively. All patients had normal or corrected-to-normal vision and no coexisting neurological or psychiatric disorders or cognitive deficits. In accordance with the Declaration of Helsinki, patients provided written informed consent to participate in the study, which was approved by the Departmental Ethics Committee.

Mapping of brain lesions was performed using MRIcron (Rorden et al., 2007; Rorden and Brett, 2000). Lesions documented by the most recent clinical CT or MRI were traced onto the T1-weighted MRI template from the Montreal Neurological Institute provided with MRIcron software (Rorden et al., 2007; Rorden and Brett, 2000). Lesion volumes were computed for each patient and the extents of the lesions were compared between the two groups with Mann-Whitney test, revealing no significant differences between patients with left (19253).

mm $^3$ ) and right (30762 mm $^3$ ) hemispheric damage (U = 29; Z = 0.32; p = .75). All patients had lesions of cortical areas that excluded the amygdala, posterior thalamus, and superior colliculus (Figure 2C, D, E).

## Please insert Figures 1 and 2 about here.

## 2.2 Apparatus

During the experimental sessions, patients sat in a dimly lit and sound attenuated room in front of a 17" LCD monitor (refresh rate: 60 Hz) at a distance of 57 cm. Eye movements were monitored via a Pan/Tilt optic eye-tracker (Eye-Track ASL-6000; sampling rate 60 Hz). Stimulus presentation was controlled by a PC running Presentation software (Version 0.60, www.neurobs.com). Patients were asked to hold constant fixation on a central white cross subtending a visual angle of 2°. For patients with quadrantopia, P4 (right inferior quadrantopia) and P7 and P8 (right superior quadrantopia), the fixation cross was horizontally centered, but presented at the top or bottom of the screen (2° from the upper/lower edge), respectively, in order to ensure presentation of stimuli in the blind field. In both experimental sessions, the central fixation cross and the stimuli were presented on a grey background.

#### 2.3 Experiment 1 - Two-alternative forced choice tasks

In order to ensure that patients had no form of blindsight, they underwent four separate sessions of a twoalternative forced choice (2AFC) task using different types of stimuli. Stimuli were only presented in the blind field, with their center aligned to the center of the screen on the vertical axis (0°) and at  $\pm 10^\circ$  eccentricity on the horizontal axis (either to left or to the right based on each patient's scotoma lateralization). For patients with quadrantopia, the stimuli were presented at the same horizontal ( $\pm 10^\circ$ ) and vertical (0°) eccentricity from the center of the screen, but the fixation cross was presented at the top (for lower quadrantopia) or at the bottom (for upper quadrantopia) of the screen, such that the vertical distance of the center of the stimuli from the fixation was 11°. In the visual detection task, the stimulus consisted of a white dot (2° diameter). In the emotional task, 12 greyscale photographs (Ekman and Friesen, 1976) of six different identities (3 females) showing fearful or happy expressions (7° x 5°) were used as stimuli. In the gender task, stimuli consisted of six greyscale photographs (Ekman and Friesen, 1976) of different faces (Three females) with a neutral expression (7°x 5°). The photographs were modified using Adobe Photoshop to extract an area centered on the face and to remove the hairline. In the geometrical shapes task, white squares and circles (5° x 5°) were used as stimuli. Each trial (2250 ms overall duration) started with a central fixation cross (500 ms). followed by the target stimulus, if present (1500 ms) and again by a fixation cross (250 ms). After the presentation of each stimulus, a sound prompted patients to verbally respond and responses were manually recorded by the experimenter. A new trial began when patients were fixating the central fixation cross. Trial onset was manually controlled by the experimenter. Patients were instructed to keep fixation on the central cross during the task and trials where eye movements occurred were discarded from the analysis (2%). Stimuli were randomly presented in the blind visual field; no stimuli were shown in the intact field. In the visual detection task, patients were asked to indicate whether or not a white dot was presented in the blind field (50% valid trials, 50% catch trials). In the remaining three tasks they were required to guess, between two choices, which type of image was presented in the blind field: fearful versus happy faces in the emotional task, male versus female faces in the gender task and circle versus square in the geometrical shapes task. Sessions were performed in a counterbalanced order. In each of the four experimental tasks, patients performed a single block of 180 trials (90 trials of each of the two possible choices). For each task, the mean percentage of correct responses was computed and the accuracy was compared to the chance level (50% correct responses) using a Binomial test.

## 2.4 Experiment 2 - Go/no-go task with redundant stimuli

Patients performed a go/no-go orientation discrimination task with stimuli presented in both the intact and the blind field. Target stimuli were presented in the intact field and coupled with concurrent stimuli in the blind field. Pairs of stimuli appeared pseudo-randomly at  $10^{\circ}$  on the horizontal axis to the left and to the right of the center of the screen with their center aligned to the center of the screen on the vertical axis  $(0^{\circ})$ . For patients with quadrantopia, the stimuli were presented at the same horizontal  $(\pm 10^{\circ})$  and vertical  $(0^{\circ})$  eccentricity from the center of the screen, but the fixation cross was presented at the top (for lower

quadrantopia) or at the bottom (for upper quadrantopia) of the screen, such that the vertical distance of the center of the stimuli from the fixation was 11°.

Target stimuli, presented in the intact field, consisted of Gabor patches (diameter:  $2^{\circ}$ ; spatial frequency: 8Hz) that were created using Matlab (The MathWorks Inc., Natick, MA) and exported in a format compatible with Presentation software. Concurrent stimuli presented in the blind field consisted of 18 greyscale photographs (Ekman and Friesen, 1976) of six different identities (3 females) showing fearful, happy or neutral expressions ( $7^{\circ}$  x  $5^{\circ}$ ). Photographs were modified using Adobe Photoshop, to extract an area centred on the face and to remove the hairline.

The structure of each trial consisted of a central fixation cross (500 ms), followed by the stimuli (200 ms) and a subsequent blank screen (1000 ms). A new trial automatically began after an inter-trial interval of random duration (500-800 msec). Trials with eye movements were discarded from the analysis (4%). Overall, patients performed six blocks of the go/no-go task. In half of the blocks, they were asked to quickly respond to Gabor patches with a vertical orientation (by pressing the spacebar on a keyboard) and to refrain from responding to Gabor patches with a horizontal orientation; in the other half of the blocks, target and non-target stimuli were reversed. Concurrently with target presentation in the intact field, a face with a fearful expression, a happy expression or a neutral expression was presented in the blind visual field. A total of 216 trials were presented (108 trials when the target was the horizontal Gabor patch: 18 repetitions x 3 unseen emotional faces x 2 target/distractor; 108 trials when the target was the vertical Gabor patch: 18 repetitions x 3 unseen emotional faces x 2 target/distractor). To control for outliers, trials with response times (RTs) exceeding 2 standard deviations above or below the mean were excluded from the analysis (5%). Responses to horizontal and vertical Gabor patch targets were collapsed and RTs and hit rates were analysed using two separate analyses of variance (ANOVA) with Group (right-hemisphere lesion patients, left-hemisphere lesion patients) and Condition (unseen fearful, unseen happy, unseen neutral), as factors. Post-hoc comparisons were run with Newman-Keuls test.

#### 3 Results

## 3.1 Experiment 1 - Two-alternative forced choice tasks

In the visual detection task, performance did not significantly differ from chance (see Table 2; all ps>.23). Performance also did not differ significantly from chance in the discrimination tasks: emotional task (all ps>.1), gender task (all ps>.1), geometrical shapes task (all ps>.18). These results indicate that patients were not aware of the presence or the nature of stimuli presented in the blind field and did not show any form of blindsight. Moreover, anecdotally, both left and right lesioned patients spontaneously reported the absence of any visual sensation throughout the entire test, regardless the type of stimulus presented in the blind field.

#### 3.2 Experiment 2 - Go/no-go task with redundant stimuli

Results of the ANOVA on the RTs to horizontal and vertical Gabor patches presented in the intact field revealed no significant main effect of Group  $[F(1,14)=0.013,p=.9;\eta_p^2<.0009]$  or Condition  $[F(2,28)=1.76,p=.19;\eta_p^2=.11]$ . In contrast, a significant Group x Condition interaction was found  $[F(2,28)=8.71,p=.001;\eta_p^2=.38]$ . Post-hoc comparisons revealed that, in patients with left hemispheric lesions, RTs to Gabor patches presented in the intact field were reduced when they were concurrently presented with fearful faces in the blind field (555 ms), compared to the conditions in which they were presented with happy faces (586 ms; p=.005) or neutral faces (579 ms; p=.032; see Figure 3). No significant difference was found between these two latter conditions (p=.38). In contrast, in patients with right hemispheric lesions, RTs to seen Gabor patches coupled with concurrent unseen fearful faces (575 ms) were not significantly different from RTs in the conditions with concurrent happy (565 ms; p=.19) and neutral faces (562 ms; p=.22). Again, no significant difference was found between the happy and neutral conditions (p=. 74; see Figure 3).

Results of the ANOVA on the hit rates revealed no significant main effect or interaction (all ps > .17). The mean hit rates was 93% ( $\pm 6\%$ ).

Please insert Figure 3 about here.

#### 4 Discussion

In patients with visual field defects without blindsight, unseen fearful faces facilitated visual processing of and behavioural responses to simple visual stimuli (i.e. Gabor patches) presented in the intact field. In a task requiring patients to discriminate the orientation of Gabor patches in their intact field, a reduction in response times was found only when fearful faces were concurrently presented in the blind field. No modulation of the response was observed in the presence of unseen neutral or happy faces.

These results are in line with previous findings in hemianopics without blindsight, showing that unseen fearful faces represent the only visual information that is implicitly processed and able to facilitate early visual encoding (Cecere et al., 2014) and response times (Bertini et al., 2013) to faces presented in the intact field. This suggests that, when the cortical visual pathway is damaged, threat-related information can be processed in the absence of awareness. This effect might be subserved by the subcortical colliculo-pulvinar-amygdala circuit, which is spared after the lesion (Tamietto et al., 2012). Indeed, fearful faces represent an optimal cue for engaging the subcortical visual circuit, as they have been shown to enhance amygdala responses even in the absence of awareness (Morris et al., 2001). In addition, recent electrophysiological evidence in primates has shown that superior colliculus' neurons respond to face and face-like stimuli (Nguyen et al., 2016, 2014) and that pulvinar neurons show differential activation to emotional faces (Maior et al., 2010).

The present findings add to previous data by showing that unseen fearful faces can facilitate not only the processing of other faces in the intact field, but also the visual processing of simple visual stimuli, such as Gabor patches. This suggests that the effects of engaging of the subcortical colliculo-pulvinar-amygdala pathway by presenting unseen fearful faces extend outside the facial domain and can influence visual processes mediated by the striate and early extrastriate cortices (Fang et al., 2005). Emotional images can enhance activity in early occipital cortices (Lang et al., 1998; Morris et al., 1998; Vuilleumier, 2005) and modulate early visual components in event-related potentials (Batty and Taylor, 2003; Borhani et al., 2015; Frühholz et al., 2011; Schupp et al., 2004; Stekelenburg and de Gelder, 2004), possibly through reciprocal connections between the amygdala and visual processing regions (Diano et al., 2017; LeDoux, 1998). Moreover, stimuli such as highly distressing noises, which reliably activate the subcortical defensive circuit and induce acute cardiac changes consistent with defense responses (Vila et al., 2007), are also associated with heightened visual perceptual processing (Keil et al., 2010). Furthermore, novel (Schomaker and Meeter, 2012) and emotionally salient visual stimuli, such as fearful faces (Bocanegra and Zeelenberg, 2009; Phelps et al., 2006), have

been shown to facilitate early visual processing and enhance contrast sensitivity. In line with this reasoning, previous ERP findings from hemianopic patients (Cecere et al., 2014) support the idea that unseen fearful faces can enhance early visual processing; indeed, hemianopic patients showed an increase in the amplitude of early ERP components (i.e., N170) related to the early structural visual encoding of faces.

It is worth noting that the fear-specific implicit visual processing observed in hemianopic patients here and in previous findings (Bertini et al., 2013; Cecere et al., 2014) is different from the performance of patients with affective blindsight, who demonstrate above-chance emotional discrimination and congruency-dependent facilitation effects with emotional stimuli (de Gelder et al., 2001, 1999; Pegna et al., 2005). Different neural substrates might account for these distinct patterns of performance. Specifically, affective blindsight might reflect the contribution of spared and functionally reorganized cortical visual areas, while the fear-specific implicit visual processing of hemianopic patients might rely only on the activity of the colliculo-pulvinaramygdala subcortical pathway. This has also been suggested by similar findings in healthy participants tested with backward-masked emotional faces, who showed fear-specific response facilitation (i.e. similar to that found in hemianopic patients) when the occipital cortex was inhibited by transcranial direct current stimulation (tDCS), and congruency-dependent effects (i.e. similar to those found in blindsight patients) when tDCS was applied to a control site without suppressing activity in visual cortical areas (Cecere et al., 2013). Notably, in line with previous electrophysiological findings (Cecere et al., 2014), in the present study only patients with left hemispheric lesions showed response facilitation with unseen fearful stimuli, suggesting that the intact right hemisphere mediates the facilitatory effect. The relevance of the right hemisphere subcortical route to emotional processing has been extensively documented, especially for unconscious affective stimuli (for a review: Gainotti, 2012). In line with these findings, masked emotional faces have been reported to elicit right-lateralized amygdala activation (Costafreda et al., 2008). Additionally, unconscious fear-conditioned stimuli and subliminal fearful faces have been found to enhance activity in the right amygdala (Morris et al., 1998) and increase connectivity between the right hemisphere subcortical route, including the right amygdala, superior colliculus and pulvinar (Morris et al., 1999; Williams et al., 2006).

Although the two groups of patients did not differ in terms of age, lesion onset and size, possible differences in their lesional profile or the extent of visual field sparing could represent a potential confound. Therefore,

further studies are needed to confirm the different role of the left and right hemisphere in mediating the facilitation related to unseen fear.

In summary, the present findings provide evidence from hemianopic patients that unseen fear signals can be implicitly processed in the absence of awareness and facilitate visual processing in the intact visual field. This facilitatory effect, possibly mediated by the subcortical route for emotional processing, might represent an adaptive mechanism in which implicitly processed fear information acts as a warning signal and enhances early perceptual processing, in order to ensure rapid visual analysis of the environment and a timely reaction to an imminent threat.

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## **Figure Legends**

**Figure 1:** Lesion reconstruction images from MRI or CT scans, projected onto the normalized MNI template for patients with left hemisphere lesions (left column) and right hemisphere lesions (right column).

**Figure 2:** Location and overlap of brain lesions. (A, B) The image shows the lesions of the left-lesioned patients (A) and right-lesioned patients (B) projected onto four axial slices of the standard MNI brain. In each slice, the left hemisphere is on the left side. The levels of the axial slices are marked by white lines on the sagittal view of the brain. The color bar indicates the number of overlapping lesions. (C–E) Overlap of the lesions of both left- and right-lesioned patients projected onto the axial slices where the amygdala (C), the posterior thalamus (D), and the superior colliculus (E) are visible. The arrows indicate the amygdala (C), the posterior thalamus (D), and the superior colliculus (E).

**Figure 3:** Mean RTs for each condition (unseen fearful, unseen happy, unseen neutral) in patients with left hemisphere (LH) lesions and right hemisphere (RH) lesions. Error bars represent the standard error of the mean (s. e. m). Asterisks indicate a p < .05. A significant reduction in reaction times was found in the unseen fearful face condition relative to the unseen happy and neutral face conditions.

Case	Sex	Age	Years of Education	Time since lesion onset (months)	Visual Field Defect	Aetiology	Lesion site
P1	М	52	8	25	Right hemianopia	Traumatic	Left temporal
P2	М	57	13	5	Right hemianopia	Vascular	Left occipital
Р3	М	58	8	17	Right hemianopia	Vascular	Left occipital
P4	М	65	8	5	Right inferior quadrantopia	Vascular	Left occipital
P5	F	54	18	8	Right hemianopia	Vascular	Left temporal-occipital
P6	М	34	11	18	Right hemianopia	Vascular	Left parietal-occipital
P7	F	29	13	8	Right superior quadrantopia	Vascular (AVM)	Left temporal-parietal-occipital
P8	М	50	13	15	Right superior quadrantopia	Vascular	Left temporal-parietal-occipital
Р9	М	47	13	8	Left hemianopia	Vascular	Right temporal-parietal-occipital
P10	М	33	13	4	Left hemianopia	Vascular	Right temporal-parietal
P11	М	41	11	9	Left hemianopia	Vascular	Right parietal-occipital
P12	F	56	16	72	Left hemianopia	Vascular	Right parietal-occipital
P13	М	74	23	6	Left hemianopia	Vascular	Right occipital
P14	М	40	13	12	Left hemianopia	Vascular (AVM)	Right occipital
P15	F	37	13	6	Left hemianopia	Tumoral	Right temporal-occipital
P16	F	38	18	18	Left hemianopia	Vascular	Right temporal-parietal

**Table 1.** Summary of clinical, demographic, and lesional data. M = male; F = female; AVM = arteriovenous malformation.

Case	Visual Detection Task	Emotional Task	Gender Task	Shape Task
P1	47%	47%	48%	47%
P2	46%	54%	52%	46%
Р3	53%	50%	49%	48%
P4	54%	56%	48%	51%
P5	54%	49%	53%	55%
P6	49%	46%	47%	53%
P7	53%	50%	54%	47%
P8	47%	51%	46%	46%
P9	50%	53%	44%	50%
P10	47%	54%	50%	48%
P11	53%	46%	50%	53%
P12	49%	47%	47%	50%
P13	53%	50%	48%	54%
P14	54%	48%	46%	51%
P15	46%	50%	52%	53%
P16	53%	56%	46%	46%

**Table 2.** Percentages of correct answers in the two-alternative forced choice tasks.

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#### References

- Adolphs, R., 2013. The biology of fear. Curr. Biol. 23, R79-R93. doi:10.1016/j.cub.2012.11.055
- Batty, M., Taylor, M.J., 2003. Early processing of the six basic facial emotional expressions. Cogn. Brain Res. 17, 613–620. doi:10.1016/S0926-6410(03)00174-5
- Bertini, C., Cecere, R., Làdavas, E., 2013. I am blind, but I "see" fear. Cortex 49, 985–993.
- Bocanegra, B.R., Zeelenberg, R., 2009. Emotion improves and impairs early vision. Psychol. Sci. 20, 707–713. doi:10.1111/j.1467-9280.2009.02354.x
- Borhani, K., Làdavas, E., Maier, M.E., Avenanti, A., Bertini, C., 2015. Emotional and movement-related body postures modulate visual processing. Soc. Cogn. Affect. Neurosci. 10, 1092–1101. doi:10.1093/scan/nsu167
- Cecere, R., Bertini, C., Ladavas, E., 2013. Differential contribution of cortical and subcortical visual pathways to the implicit processing of emotional faces: a tDCS study. J Neurosci 33, 6469–6475.
- Cecere, R., Bertini, C., Maier, M.E., Làdavas, E., 2014. Unseen fearful faces influence face encoding: evidence from ERPs in hemianopic patients. J. Cogn. Neurosci. 26, 2564–77. doi:10.1162/jocn\_a\_00671
- Celeghin, A., de Gelder, B., Tamietto, M., 2015. From affective blindsight to emotional consciousness. Conscious. Cogn. 36, 414–425. doi:10.1016/j.concog.2015.05.007
- Costafreda, S.G., Brammer, M.J., David, A.S., Fu, C.H.Y., 2008. Predictors of amygdala activation during the processing of emotional stimuli: A meta-analysis of 385 PET and fMRI studies. Brain Res. Rev. 58, 57–70. doi:10.1016/j.brainresrev.2007.10.012
- de Gelder, B., Pourtois, G., van Raamsdonk, M., Vroomen, J., Weiskrantz, L., 2001. Unseen stimuli modulate conscious visual experience: evidence from inter-hemispheric summation. Neuroreport 12, 385–91. doi:10.1097/00001756-200102120-00040
- de Gelder, B., Pourtois, G., Weiskrantz, L., 2002. Fear recognition in the voice is modulated by unconsciously recognized facial expressions but not by unconsciously recognized affective pictures. Proc. Natl. Acad. Sci. U. S. A. 99, 4121–4126. doi:10.1073/pnas.062018499
- de Gelder, B., Vroomen, J., Pourtois, G., Weiskrantz, L., 1999. Non-conscious recognition of affect in the absence of striate cortex. Neuroreport 10, 3759–3763. doi:10.1097/00001756-199912160-00007
- Diano, M., Celeghin, A., Bagnis, A., Tamietto, M., 2017. Amygdala response to emotional stimuli without awareness: Facts and interpretations. Front. Psychol. doi:10.3389/fpsyg.2016.02029
- Ekman, P., Friesen, W., 1976. Pictures of Facial Affect. Consulting Psychologists Press, Palo Alto.
- Fang, F., Murray, S.O., Kersten, D., He, S., 2005. Orientation-tuned FMRI adaptation in human visual cortex. J. Neurophysiol. 94, 4188–4195. doi:10.1152/jn.00378.2005
- Frühholz, S., Jellinghaus, A., Herrmann, M., 2011. Time course of implicit processing and explicit processing of emotional faces and emotional words. Biol. Psychol. 87, 265–274. doi:10.1016/j.biopsycho.2011.03.008
- Gainotti, G., 2012. Unconscious processing of emotions and the right hemisphere. Neuropsychologia. doi:10.1016/j.neuropsychologia.2011.12.005
- Garrido, M.I., Barnes, G.R., Sahani, M., Dolan, R.J., 2012. Functional evidence for a dual route to amygdala. Curr. Biol. 22, 129–134. doi:10.1016/j.cub.2011.11.056
- Garvert, M.M., Friston, K.J., Dolan, R.J., Garrido, M.I., 2014. Subcortical amygdala pathways enable rapid face processing. Neuroimage 102, 309–316. doi:10.1016/j.neuroimage.2014.07.047
- Keil, A., Bradley, M.M., Ihssen, N., Heim, S., Vila, J., Guerra, P., Lang, P.J., 2010. Defensive engagement and perceptual enhancement. Neuropsychologia 48, 3580–3584. doi:10.1016/j.neuropsychologia.2010.08.007

- Lang, P.J., Bradley, M.M., Fitzsimmons, J.R., Cuthbert, B.N., Scott, J.D., Moulder, B., Nangia, V., 1998. Emotional arousal and activation of the visual cortex: An fMRI analysis. Psychophysiology 35, 199–210. doi:10.1111/1469-8986.3520199
- LeDoux, J.E., 2014. Coming to terms with fear. PNAS 111, 2871-2878. doi:10.1073/pnas.1400335111
- LeDoux, J.E., 1998. The emotional brain: The mysterious underpinnings of emotional life, The emotional brain: The mysterious underpinnings of emotional life. Simon and Schuster, New York. doi:10.2307/3953278
- Luo, Q., Holroyd, T., Jones, M., Hendler, T., Blair, J., 2007. Neural dynamics for facial threat processing as revealed by gamma band synchronization using MEG. Neuroimage 34, 839–847. doi:10.1016/j.neuroimage.2006.09.023
- Maior, R.S., Hori, E., Tomaz, C., Ono, T., Nishijo, H., 2010. The monkey pulvinar neurons differentially respond to emotional expressions of human faces. Behav. Brain Res. 215, 129–135. doi:10.1016/j.bbr.2010.07.009
- Morris, J.S., DeGelder, B., Weiskrantz, L., Dolan, R.J., 2001. Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field. Brain 124, 1241–1252. doi:10.1093/brain/124.6.1241
- Morris, J.S., Ohman, A., Dolan, R.J., 1999. A subcortical pathway to the right amygdala mediating "unseen" fear. Proc. Natl. Acad. Sci. U. S. A. 96, 1680–5. doi:10.1073/pnas.96.4.1680
- Morris, J.S., Öhman, A., Dolan, R.J., 1998. Conscious and unconscious emotional learning in the human amygdala. Nature 393, 467–70. doi:10.1038/30976
- Nguyen, M.N., Matsumoto, J., Hori, E., Maior, R.S., Tomaz, C., Tran, A.H., Ono, T., Nishijo, H., 2014. Neuronal responses to face-like and facial stimuli in the monkey superior colliculus. Front. Behav. Neurosci. 8. doi:10.3389/fnbeh.2014.00085
- Nguyen, M.N., Nishimaru, H., Matsumoto, J., Van Le, Q., Hori, E., Maior, R.S., Tomaz, C., Ono, T., Nishijo, H., 2016. Population coding of facial information in the monkey superior colliculus and pulvinar. Front. Neurosci. 10. doi:10.3389/fnins.2016.00583
- Pegna, A.J., Khateb, A., Lazeyras, F., Seghier, M.L., 2005. Discriminating emotional faces without primary visual cortices involves the right amygdala. Nat. Neurosci. 8, 24–25. doi:10.1038/nn1364
- Phelps, E.A., Ling, S., Carrasco, M., 2006. Emotion facilitates perception and potentiates the perceptual benefits of attention. Psychol. Sci. 17, 292–299. doi:10.1111/j.1467-9280.2006.01701.x
- Rafal, R.D., Koller, K., Bultitude, J.H., Mullins, P., Ward, R., Mitchell, A.S., Bell, A.H., 2015. Connectivity between the superior colliculus and the amygdala in humans and macaque monkeys: virtual dissection with probabilistic DTI tractography. J. Neurophysiol. 114, 1947–62. doi:10.1152/jn.01016.2014
- Rorden, C., Brett, M., 2000. Stereotaxic Display of Brain Lesions. Behav. Neurol. 12, 191–200. doi:10.1155/2000/421719
- Rorden, C., Karnath, H.-O., Bonilha, L., 2007. Improving Lesion-Symptom Mapping. J. Cogn. Neurosci. 19, 1081–1088. doi:10.1162/jocn.2007.19.7.1081
- Schomaker, J., Meeter, M., 2012. Novelty Enhances Visual Perception. PLoS One 7. doi:10.1371/journal.pone.0050599
- Schupp, H.T., Öhman, A., Junghöfer, M., Weike, A.I., Stockburger, J., Hamm, A.O., 2004. The Facilitated Processing of Threatening Faces: An ERP Analysis. Emotion 4, 189–200. doi:10.1037/1528-3542.4.2.189
- Stekelenburg, J.J., De Gelder, B., 2004. The neural correlates of perceiving human bodies: an ERP study on the body-inversion effect. Cogn. Neurosci. Neuropsychol. 15, 9–12. doi:10.1097/01.wnr.00001
- Tamietto, M., de Gelder, B., 2010. Neural bases of the non-conscious perception of emotional signals. Nat. Rev. Neurosci. 11, 697–709. doi:10.1038/nrn2889

- Tamietto, M., Pullens, P., De Gelder, B., Weiskrantz, L., Goebel, R., 2012. Subcortical connections to human amygdala and changes following destruction of the visual cortex. Curr. Biol. 22, 1449–1455. doi:10.1016/j.cub.2012.06.006
- Vila, J., Guerra, P., Muñoz, M.Á., Vico, C., Viedma-del Jesús, M.I., Delgado, L.C., Perakakis, P., Kley, E., Mata, J.L., Rodríguez, S., 2007. Cardiac defense: From attention to action. Int. J. Psychophysiol. doi:10.1016/j.ijpsycho.2007.07.004
- Vuilleumier, P., 2005. How brains beware: Neural mechanisms of emotional attention. Trends Cogn. Sci. doi:10.1016/j.tics.2005.10.011
- Weiskrantz, L., Warrington, E.K., Sanders, M.D., Marshall, J., 1974. Visual capacity in the hemianopic field following a restricted occipital ablation. Brain 97, 709–728.
- Williams, L.M., Das, P., Liddell, B.J., Kemp, A.H., Rennie, C.J., Gordon, E., 2006. Mode of functional connectivity in amygdala pathways dissociates level of awareness for signals of fear. J. Neurosci. 26, 9264–9271. doi:10.1523/JNEUROSCI.1016-06.2006

Figure 1

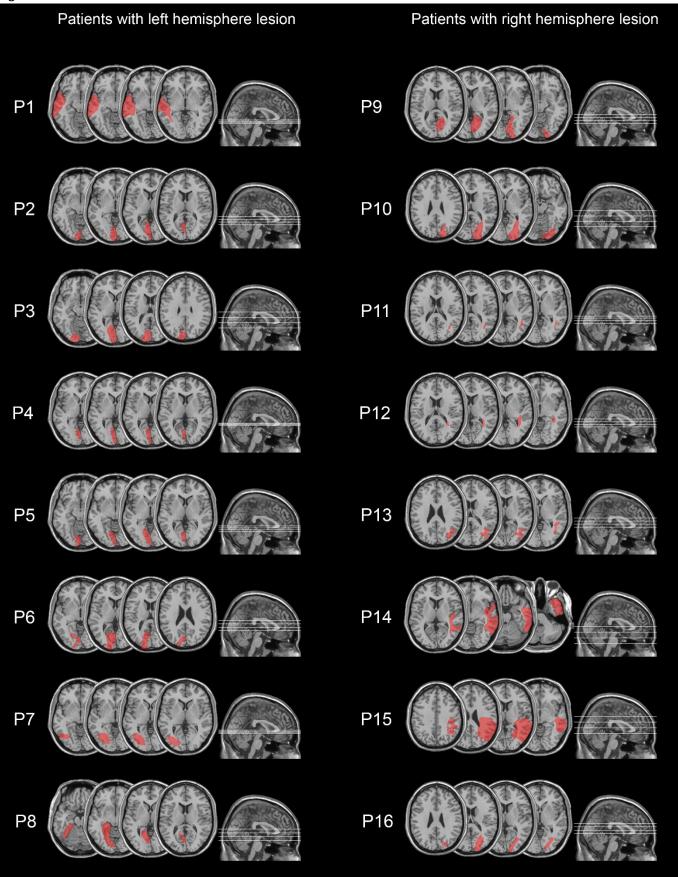


Figure 2

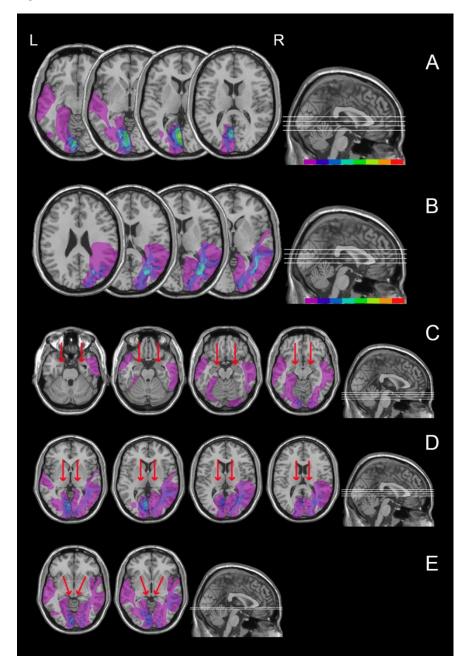


Figure 3

