ELSEVIER

Neuropsychologia 46 (2008) 820–828

NEUROPSYCHOLOGIA

www.elsevier.com/locate/neuropsychologia

Affective blindsight in the intact brain: Neural interhemispheric summation for unseen fearful expressions

Marco Tamietto[a,b,*], Beatrice de Gelder[b,c,**]

[a] Department of Psychology, University of Torino, Via Po 14, 10123 Torino, Italy
[b] Cognitive and Affective Neurosciences Laboratory, Tilburg University, PO Box 90153, 5000 LE, Tilburg, The Netherlands
[c] Martinos Center for Biomedical Imaging, Massachusetts General Hospital, Harvard Medical School,
First Street Building 120, Charlestown, MA 02129, USA

Received 22 March 2007; received in revised form 30 September 2007; accepted 3 November 2007
Available online 26 December 2007

Abstract

The emotional valence of facial expressions can be reliably discriminated even in the absence of conscious visual experience by patients with lesions to the primary visual cortex (affective blindsight). Prior studies in one such patient (GY) also showed that this non-conscious perception can influence conscious recognition of normally seen emotional faces. Here we report a similar online interaction across hemispheres between conscious and non-conscious perception of emotions in normal observers. Fearful and happy facial expressions were presented either unilaterally (to the left or right visual field) or simultaneously to both visual fields. In bilateral displays, conscious perception of one face in a pair was prevented by backward masking after 20 ms, while the opposite expression remained normally visible. The results showed a bidirectional influence of non-conscious fear processing over conscious recognition of happy as well as fearful expressions. Consciously perceived fearful faces were more readily recognized when they were paired with invisible emotionally congruent fearful expressions in the opposite field, as compared to the single presentation of the same unmasked faces. On the other hand, recognition of unmasked happy faces was delayed by the simultaneous presence of a masked fearful face. No such effect was reported for masked happy expressions. These findings show that non-conscious processing of fear may modulate ongoing conscious evaluation of facial expressions via neural interhemispheric summation even in the intact brain.

Keywords: Emotion; Affective blindsight; Backward masking; Non-conscious perception; Redundant target effect; Interhemispheric summation

1. Introduction

Automatic and non-conscious perceptual mechanisms are sufficient for processing facial expressions, most notably fearful ones (de Gelder, de Haan, & Heywood, 2001; Eastwood & Smilek, 2005). Major insights come from two parallel lines of evidence: lesion studies in patients who lack conscious vision following brain damage to the primary visual cortex (V1), and studies on experimentally induced non-conscious vision in neurologically intact subjects (Anders et al., 2004; de Gelder, Morris, & Dolan, 2005; de Gelder, Pourtois, van Raamsdonk, Vroomen, & Weiskrantz, 2001; de Gelder, Pourtois, & Weiskrantz, 2002; de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999; Hamm et al., 2003; Liddell et al., 2005; Milders, Sahraie, Logan, & Donnellon, 2006; Morris, DeGelder, Weiskrantz, & Dolan, 2001; Morris, Ohman, & Dolan, 1998, 1999; Pegna, Khateb, Lazeyras, & Seghier, 2005; Whalen et al., 2004, 1998; Williams et al., 2006, 2004).

Patients with V1 lesions can reliably discriminate the affective valence of facial expressions projected in their blind fields by guessing, despite having no conscious perception of the stimuli (affective blindsight) (Anders et al., 2004; de Gelder, de Hann, et al., 2001; de Gelder, Pourtois, et al., 2001; de Gelder et al., 2002, 1999; de Gelder, Vroomen, Pourtois, & Weiskrantz, 2000; Pegna et al., 2005). Indirect behavioral methods, such as the redundant target paradigm, have often proven particular sensitivity in showing implicit processing of unseen stimuli without requiring patients to make counterintuitive guesses

---

* Corresponding author at: Department of Psychology, University of Torino, Via Po 14, 10123 Torino, Italy. Tel.: +39 011 670 3050; fax: +39 011 814 6231.
** Corresponding author at: Martinos Center for Biomedical Imaging, Massachusetts General Hospital, Harvard Medical School, First Street Building 120, Charlestown, MA 02129, USA. Tel.: +1 617 726 7956; fax: +1 617 726 7422.
E-mail addresses: tamietto@psych.unito.it (M. Tamietto), degelder@nmr.mgh.harvard.edu (B. de Gelder).

0028-3932/$ – see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2007.11.002

about events occurring in their blind fields (Marzi, Minelli, & Savazzi, 2004). Indeed, reaction times (RTs) are typically faster for double versus single stimuli, even when one stimulus in a pair cannot be consciously detected because of hemianopia, visual extinction, hemispherectomy, or split-brain (redundant target effect, RTE) (Corballis, 1995, 1998; Corballis, Hamm, Barnett, & Corballis, 2002; Forster & Corballis, 2000; Marzi et al., 1996; Marzi, Tassinari, Aglioti, & Lutzemberger, 1986; Roser & Corballis, 2003; Savazzi & Marzi, 2004; Tomaiuolo, Ptito, Marzi, Paus, & Ptito, 1997). This online interaction between consciously and non-consciously perceived stimuli is thought to reflect interhemispheric cooperation and neural summation across the hemispheres.

In the past, using this method on the blindsight patient GY with right hemianopia, we reported faster RTs for two emotionally congruent facial expressions of sadness or fear (one of which presented in his right blind field) than for the unilateral presentation of the same faces in the intact left field (de Gelder, de Hann, et al., 2001; de Gelder, Pourtois, et al., 2001); akin to what has been observed also in healthy subjects aware of both stimuli (Tamietto, Adenzato, Geminiani, & de Gelder, 2007; Tamietto, Latini Corazzini, de Gelder, & Geminiani, 2006). More recently, we also showed that this neural RTE for congruent fearful expressions is associated with enhanced activity in a subcortical pathway involving the superior colliculus and the amygdala that bypasses geniculo-striate projections (de Gelder et al., 2005). However, the generalization of the affective RTE for non-consciously perceived facial expressions has been questioned, based on possible post-lesion and experience-dependent plasticity in GY's superior colliculi due to the early onset of occipital lesion at age 7 (Cowey, 2004; Pessoa, 2005). Evidence of the influence of unseen facial expressions over conscious recognition of seen faces in a sample of subjects where the argument of post-lesion modifications cannot be claimed for is thus particularly timely and helpful to clarify this issue.

Backward masking is one of the key experimental paradigms to prevent conscious visual perception in healthy subjects and it has been frequently used to study non-conscious emotional processing (Esteves & Ohman, 1993; Killgore & Yurgelun-Todd, 2004; Liddell et al., 2005; Macknik & Livingstone, 1998; Marcel, 1983; Morris et al., 1998, 1999; Pessoa, Japee, & Ungerleider, 2005; Phillips et al., 2004; Rolls & Tovee, 1994; Whalen et al., 2004, 1998; Williams et al., 2006, 2004). In this technique, an initial emotional target face is briefly presented and immediately replaced by a neutral masking face. If the stimulus onset asynchrony (SOA; i.e., the interval between the onset of the target and the mask) is sufficiently brief (typically <40 ms), subjects are unaware of the emotional content of the first face and only report the second neutral expression (Esteves & Ohman, 1993; Whalen et al., 1998). Prior studies showed that masked expressions elicit skin conductance response changes, specific ERP components, and facial muscle activity in the observer that mimic the emotion conveyed by the unseen face stimulus (Dimberg, Thunberg, & Elmehed, 2000; Esteves & Ohman, 1993; Williams et al., 2004). Even more interestingly, invisible fearful expressions activate in healthy subjects the same subcortical colliculo-pulvinar-amygdala pathway advocated as the most likely alternative to fear processing in cases of affective blindsight following striate cortex lesions (Liddell et al., 2005; Morris et al., 1999; Williams et al., 2006). Analogous considerations about the functional efficacy of this subcortical pathway in the normal brain are also supported by parallel evidence that affective blindsight may be induced in healthy observers by applying transcranial magnetic stimulation to the visual cortex (Jolij & Lamme, 2005). To our knowledge, however, no prior study has investigated the behavioral outcomes associated with the presentation of backwardly masked facial expressions and their interhemispheric interaction with consciously seen faces in neurologically intact subjects.

In the present study we combined a backward masking procedure, to induce non-conscious perception of facial expressions, with a redundant target paradigm previously used as a measure of affective blindsight. Therefore, this design allowed both, investigation of the behavioral effects of interhemispheric interaction between seen and unseen facial expressions in healthy subjects, and a direct comparison with previous findings obtained in blindsight patients using the same redundant target procedure.

2. Method

2.1. Participants

Twenty-five healthy volunteers (14 women) were tested ($M = 25.47$ years, $SD = 3.79$, age-range = 20–31). All participants reported normal or corrected-to-normal visual acuity and no history of neurological or psychiatric illness. The majority of participants were right-handed as assessed by the Edinburgh Handedness Inventory ($M = 74.12$, $SD = 29.22$) (Oldfield, 1971). 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.

2.2. Stimuli and apparatus

Twelve grayscale photographs of six different identities (three females) each expressing fear and happiness served as target emotional stimuli (∼7.38° wide × ∼ 12.25° high, 60 cm from the screen; mean luminance = 6.7 cd/m^2) (Ekman & Friesen, 1976). A scrambled face with the same rectangular shape, size, luminance, and spatial frequency of the target face stimuli was used as mask. This mask was constructed by randomly swapping small parts (18 × 18 pixels) of pictures showing neutral expressions of the same six actors used as target emotional faces.

Stimuli were centered vertically at 8 cm (∼7.38°) of eccentricity from the central fixation cross (∼1.26° × ∼1.26°) and presented unilaterally to the left (LVF) or right visual field (RVF), or simultaneously to both hemifields (BVF) against a dark background (2 cd/m^2) on a 21-in. Sony® CRT monitor (120 Hz refresh rate).

The monitor was connected to an IBM-compatible Pentium PC controlling stimulus presentation and response recording by means of Presentation 9.3 software (Neurobehavioral Systems®). Participants responded by pressing keys on a response box (RB-610, Cedrus Corporation®). 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®).

2.3. SOA parameters and detection threshold setting

Backward masking literature focused on SOA parameters that may effectively prevent subjects from *discriminating* the affective valence of the first expression (but nonetheless allow face detection to occur) or from *detecting* whether a face stimulus or a blank screen has been presented (Esteves &

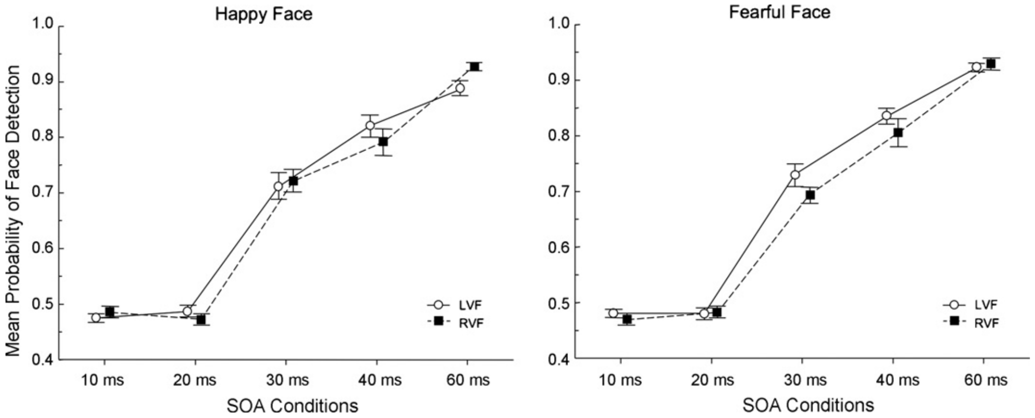

Fig. 1. Mean probability (±standard errors, *SE*s) of face detection in the threshold-setting experiment for the five SOAs as a function of facial expression and side of presentation.

Ohman, 1993; Pessoa et al., 2005; Whalen et al., 1998; Williams et al., 2004). Equally different are the criteria used to assess below-awareness thresholds; ranging from objective to subjective measures and from recall to recognition procedures (Greenwald, Draine, & Abrams, 1996; Merikle, 1992; Merikle, Smilek, & Eastwood, 2001). In all cases, however, backward masking has been studied for foveally presented facial expressions followed by neutral face masks.

Since our main design required presentation of facial expressions at peripheral visual locations followed by a non-facial mask, a pilot experiment was first run to set the detection threshold and to provide a stringent control of non-conscious perception under these specific conditions, as defined by objective forced-choice criteria based on signal detection analysis (Green & Swetz, 1966; Stanislaw & Todorov, 1999). For this purpose, twenty subjects (who did not participate in the main experiment) underwent a psychophysical detection threshold-setting task where the SOA between target faces and mask was parametrically varied to objectively determine the point at which subjects cannot detect whether a face versus blank screen stimulus was presented ($M = 24.13$ years, $SD = 4.23$, age-range = 21–34). Exactly the same face and mask stimuli presented in the main experiment were used. Also, the stimuli were projected at the same horizontal eccentricity from central fixation cross adopted in the following redundant target experiment. The blank stimulus was of the same rectangular shape, size, and filled with the same isoluminant gray background tone of facial stimuli.

Five SOAs were used: 10, 20, 30, 40, and 60 ms. The total duration of the target plus mask presentation was fixed for all conditions at 200 ms with target offset temporally and spatially coincident with mask onset. One-hundred and ninety-two trial repetitions were presented for each of the five SOAs, further subdivided in the following conditions: half (96) of the targets were facial expressions (48 in the LVF—out of which 24 were happy and 24 fearful expressions; 48 in the RVF—24 happy and 24 fearful) and the remaining half were blank stimuli (48 in the LVF and 48 in the RVF). The 960 trials (192 trials × 5 SOAs) were randomized and divided in five blocks.

The task of the subjects was to keep steady fixation on the central cross and to tell whether a face stimulus or a blank screen preceded the mask by pressing two different keys (counterbalanced within subjects and between blocks). The objective criterion for lack of conscious detection was drawn from signal detection theory, which provides a measure of perceptual sensitivity (d') that is independent of a subject's response bias (c) (see Tamietto, Geminiani, Genero, and de Gelder (2007) for a detailed description of the computations actually used to calculate the parameters). A given SOA was deemed as preventing conscious perception of the target stimulus if the corresponding d' value was not significantly different from 0 (i.e., indicating inability to distinguish a face from a blank stimulus with above chance accuracy). This was assessed by comparing d' values to a theoretical distribution with a mean of 0 in a single-sample *t*-test.

In keeping with the past literature investigating detection thresholds (Pessoa et al., 2005; Williams et al., 2004), face detection was above chance level for SOAs of 30, 40, and 60 ms, irrespectively of emotion and side of presentation [mean $d' \geq 0.95$; single-sample $t(19) \geq 6.87$, $p \leq 0.0001$, for all comparisons] (Fig. 1).

However, for both emotions and visual fields, performance was not significantly different from chance at 10 ms as well as at 20 ms SOA [mean $d' \leq 0.11$; $t(19) \leq 1.77$, $p \geq 0.09$ for all comparisons], and there was no significant increase in accuracy with 20 ms as compared to 10 ms SOA [paired-sample $t(19) \leq 0.54$, $p \geq 0.6$ for all comparisons]. Importantly, face detection accuracy was not influenced by either side of presentation or emotional expression at any SOA, as further indicated by Chi-square analyses carried out for each of the five SOAs separately [$\chi^2(1) \leq 0.35$, $p \geq 0.55$ for all cross-tabulations].

Since a SOA of 20 ms was sufficient to establish non-conscious perception of peripheral facial targets for both emotions and visual fields, this threshold was directly applied in the main experiment for all conditions.

2.4. Procedure

Each trial started with a central cross that remained on the screen until steady fixation (e.g., eye gaze for 500 ms within the cross area; 2.25 cm^2). The cross was then immediately followed by stimulus presentation at the visual periphery (LVF, RVF, or BVF). Unmasked face stimuli and target/mask pairs were all projected for 200 ms (with 20 ms presentation for the target and 180 ms for the mask in the target/mask compounds; i.e., with 20 ms SOA), so that onset and offset of all types of stimuli were coincident. A blank screen lasting 1800 ms followed stimulus presentation. Each trial was interleaved by an inter-trial interval (ITI) of 1000 ms announced by an acoustic tone at its onset.

The design consisted of three possible display types for each of the two expressions (happy and fearful): (1) a single display with a unilateral unmasked face (half trials in the LVF and half in the RVF); (2) a double BVF display with an unmasked facial expression in one visual field (LVF or RVF) and a masked facial expression showing the same emotion in the opposite field (congruent conditions); (3) a double BVF display with an unmasked face in one field (again LVF or RVF) and a masked face with the different expression in the other field (incongruent condition). In all BVF displays, the two faces were of different actors – one male and one female – (i.e., there was never physical/perceptual identity between pairs of stimuli).

Subjects were naïve with respect to the backward masking procedure and were unaware of the actual aims of the experiment. A go/no-go task was used requiring participants to press the response key as fast and accurately as possible when the consciously seen face conveyed the pre-specified target expression, and to withhold from reacting when seeing the other (non-target) expression. The target expression (happy or fearful) and the response hand (left or right) were fixed for each block of trials and counterbalanced between blocks. Immediately following the acoustic tone indicating ITI onset (i.e., after the manual response), participants were also requested to verbally report the number and location of the (normal) faces they had just seen in order to provide an additional trial-by-trial control of non-conscious perception in the actual sample. This secondary task has been demonstrated not to affect the likelihood of finding an RTE (Marzi et al., 1996).

Four blocks were run following an ABBA or BAAB design, each applied to half of the subjects (A = happy target, B = fear target). Each block comprised 256 randomized target trials (64 repetitions of 'go' trials with the target emotion in the LVF, RVF, BVF congruent, and BVF incongruent) and 128 catch trials (32 repetitions of 'no-go' trials with the non-target emotion in the LVF, RVF, BVF congruent, BVF incongruent).

3. Results

3.1. RTE assessment as evidence of non-conscious emotional processing

3.1.1. Latency analysis

Mean RTs for correct responses in the range 200–1000 ms to trials where the subjects reported having seen only one face were entered into a 2 × 3 ANOVA with the within-subjects factors of facial expression (happy vs. fearful) and stimulus condition (unilateral, congruent, and incongruent) (Fig. 2). Trials with anticipations or delays, and with subjects reporting having seen two faces were a negligible minority (<2%) and were removed from analysis. We thus present here the behavioral effects of non-conscious emotional processing over conscious facial expression recognition.

The main effect of facial expression was not significant [$F(1, 24) = 2.01$, $p = 0.17$], whereas the main effect of stimulus conditions and the interaction did turn out to be significant [$F(2, 48) = 17.37$, $p < 0.0001$; $F(2, 48) = 18.24$, $p < 0.0001$, respectively]. Post hoc Scheffé tests on the interaction showed a significant reduction of RTs in the congruent as compared to the unilateral condition for fearful ($p < 0.0001$) but not for happy target expressions ($p = 0.33$), thereby arguing for an RTE only in the case of emotional congruency between seen and unseen fearful expressions. By contrast, RTs to consciously perceived happy expressions were slowed by non-conscious fearful expressions, as revealed by the comparison between the unilateral and incongruent condition ($p < 0.0001$). The same comparison for fearful target expressions (i.e., with unseen happy expressions) yielded no significant difference ($p = 0.53$). These results clearly indicate a bidirectional influence of non-consciously perceived fear over conscious recognition of both, happy and fearful facial expressions.

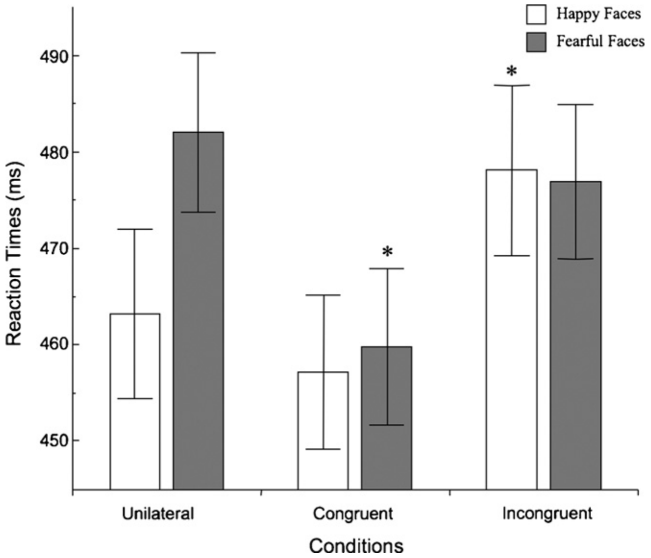

Fig. 2. Mean RTs (±*SE*s) by stimulus conditions and facial expressions. Asterisks indicate significant differences from the corresponding unilateral conditions at $p < 0.0001$.

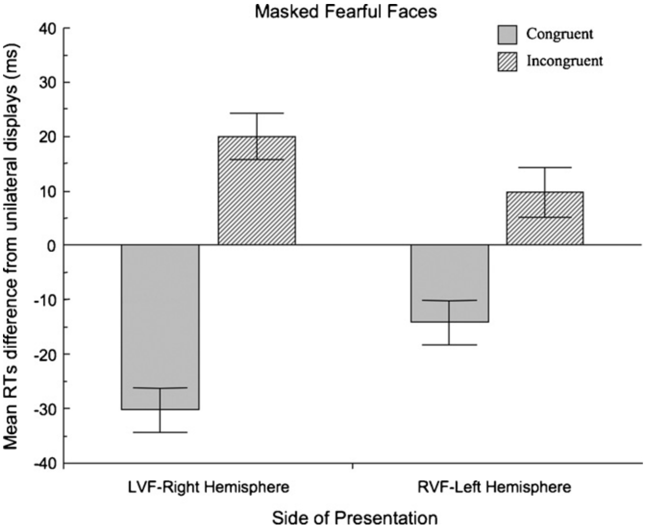

Fig. 3. Mean RTs (±*SE*s) differences between BVF displays with one masked fearful face and the corresponding unilateral displays as a function of side and condition of presentation.

Superimposed on this general effect of non-conscious fear, a higher sensitivity of the right hemisphere for processing unseen fearful expressions was also observed (Fig. 3). Indeed, a further 2 × 2 ANOVA was carried out on the absolute RTs difference between unilateral and BVF displays that distinguished when the masked fearful expression was projected to the LVF versus RVF (first factor), and when it was paired with an unmasked congruent fearful versus incongruent happy face (second factor). Only the main effect of side of presentation was significant, with the biggest RTs difference from unilateral conditions being for left-side (right hemisphere) presentation of masked fearful expressions [$F(1, 24) = 30.11$, $p < 0.0001$]. The lack of statistical significance for the main effect of congruency and for the interaction indicates a comparable absolute magnitude of the influence of left-side masked fearful expressions on consciously perceived fearful and happy faces alike [$F(1, 24) = 0.79, p = 0.38$; $F(1, 24) = 2.78$, $p = 0.11$, respectively]. This modulation leads to faster recognition of the former and slower detection of the latter.

3.1.2. Accuracy analysis

Errors (i.e., misses in "go" trials and false positives in "no-go" trials) were analyzed by an ANOVA with the same factors and levels considered in the latency analysis (Table 1).

None of the factors or interaction turned out to be statistically significant, thereby allowing us to rule-out any interpretation of latency findings in terms of speed/accuracy trade-off [facial expression: $F(1, 24) = 0.028$, $p = 0.87$; stimulus condition: $F(2, 48) = 0.137$, $p = 0.87$; interaction: $F(2, 48) = 2.17$, $p = 0.13$].

Table 1
Mean percentage (±standard error) of errors

Conditions	Facial expressions	
	Happy	Fearful
Unilateral	16.52% (±1.77)	18.56% (±2)
Congruent	17.09% (±1.85)	16.16% (±1.95)
Incongruent	17.53% (±1.94)	15.84% (±2.54)

3.2. *Test of neural interhemispheric summation between seen and unseen stimuli*

Observation of an RTE for congruent fearful expressions provides clear evidence that non-consciously perceived fear may nonetheless influence ongoing behavior that appears to be guided only by conscious recognition of emotional faces. However, this bilateral gain does not mean that a neural summation between seen and unseen faces actually took place across hemispheres. Indeed, the two stimuli may be processed in parallel by each hemisphere independently, with average RTs to double stimuli being faster than RTs to single stimuli for purely probabilistic reasons. Conversely, a neural interhemispheric summation between seen and unseen expressions would lead to a gain in latency that exceeds the limit posed by probability summation (see Tamietto, Adenzato, et al. (2007), Tamietto, Geminiani, et al. (2007) and Tamietto et al. (2006) for a detailed description of the rationale).

The inequality test of Miller (1982) provides a mathematical testing tool to discriminate between probability and neural summation and sets an upper limit on the facilitation produced by bilateral stimuli under the null hypothesis of probability summation. When the differences between the upper limit of probability summation and the observed RTs distribution for bilateral stimuli are plotted, positive values indicate a violation of the test consistent with neural summation.[1] Recently, Colonius and Diederich (2006) described a useful way to quantify the amount of inequality violation and reduce it to a single numerical index amenable of statistical testing. Briefly, the area under positive values indicating neural summation is estimated with the method of antithetic variates and is the result of a simple difference of two independent means: the mean RTs predicted by probability summation, and the observed mean RTs in the bilateral condition (see Colonius & Diederich, 2006 for a detailed description of the computations to obtain the index value). A conventional single-sample t-test carried out on this index can then establish whether the violation of the inequality is significantly different from 0, thereby testing the statistical reliability of neural summation.

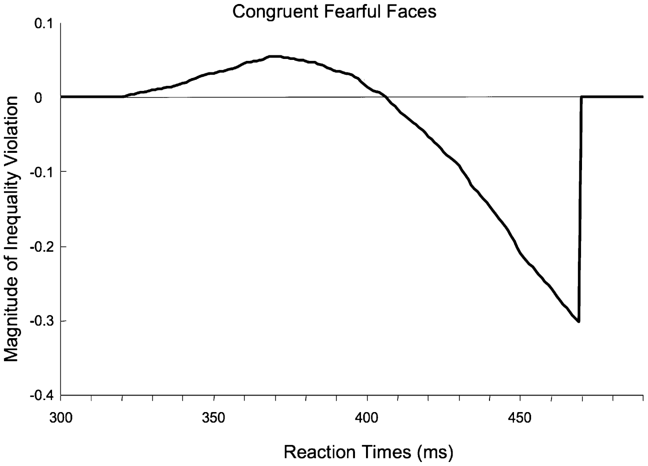

Fig. 4. Differences between the RTs distribution for congruent fearful expressions and the race inequality limit of probability summation. Violations are indicated by positive values.

We followed this procedure to assess whether the observed RTE for two congruent fearful expressions was indeed related to neural interhemispheric summation between seen and unseen faces. Fig. 4 shows the difference between the inequality limit of probability summation and the observed RTs distribution for congruent fearful expressions.

The amount of inequality violation calculated for the area of the curve under positive values was statistically different from 0, thereby showing that a significant neural summation of the two fearful expressions actually occurred in our sample [$t(25) = 2.31$, $p = 0.03$]. Notably, this interhemispheric cooperation was still significant when it was calculated separately for congruent displays with LVF masked and RVF unmasked fearful expressions, and for the inverted displays (i.e., with LVF unmasked and RVF masked faces) [$t(26) = 2.28, p = 0.03$; $t(19) = 2.37, p = 0.03$, respectively]. Moreover, there was no significant difference in the amount of inequality violation between these two conditions [$t(45) = 0.14$, $p = 0.89$]. Therefore, the strength of neural summation was unaffected by whether the right or left hemisphere received the masked face.

4. Discussion

Over the past decade, the existence of two separate processing routes and the *dissociation* between conscious and non-conscious emotional processing has been the subject of many behavioral and neuroimaging studies on brain-damaged patients as well as on neurologically intact subjects undergoing backward masking (Anders et al., 2004; de Gelder, de Hann, et

---

[1] The test of Miller is based on cumulative distribution functions (CDFs) for RTs and consists of the following inequality that assumes probability summation for any time t:<Normal>

$$P(RT \leq t|SL \text{ and } SR) \leq P(RT \leq t|SL) + P(RT \leq t|SR),$$

where $P(RT \leq t|SL \text{ and } SR)$ is the cumulative probability of a correct detection with double targets, $P(RT \leq t|SL)$ the cumulative probability of a response given one target in the LVF, and $P(RT \leq t|SR)$ is the cumulative probability of a response given one target in the RVF. Since probabilistic models of RTE predict no interaction between hemispheres, the probability of responding to double stimuli by time t cannot be higher than the sum of the probabilities associated to either single stimuli. Thus, when this upper limit is violated, a probabilistic interpretation is no longer tenable and the RTE can be only explained in terms of neural summation.
Specific values of the CDFs for the inequality test and for the estimate of Colonius and Diederich's index were calculated at 1% steps from the 1st to the 99th percentile for each display type and emotion separately, and in each participant individually. Composite CDFs were then obtained by averaging across subjects all the RTs at each percentile.

al., 2001; de Gelder, Pourtois, et al., 2001; de Gelder et al., 2002, 1999; Hamm et al., 2003; Liddell et al., 2005; Morris et al., 2001, 1998, 1999; Pegna et al., 2005; Phillips et al., 2004; Whalen et al., 1998; Williams et al., 2006, 2004). Yet, the possible on-line *interaction* between these two different modes of emotional processing (with and without awareness), and the influence exerted by unseen emotions over ongoing recognition of consciously perceived facial expressions is still poorly understood. Available evidence is essentially based on two successive studies exploring the behavioral effects and the neural substrate mediating this interaction in the blindsight patient GY (de Gelder et al., 2005; de Gelder, Pourtois, et al., 2001). Investigation of the same phenomenon in healthy subjects with experimentally induced non-conscious vision may thus help to bridge the gap, uncovering the behavioral outcomes of interhemispheric interaction between seen and unseen facial expressions in the intact brain. The present study reports several new findings concerning this issue.

Consciously perceived fearful faces were more readily recognized when they were paired with invisible emotionally congruent expressions in the opposite hemifield, as compared to the single presentation of the same unmasked faces. Moreover, this RTE for congruent fearful expressions was the result of neural summation, rather than the effect of independent parallel processing, thereby showing that masked fearful faces were not only processed without awareness, but also integrated across hemispheres with consciously perceived expressions. Notably, this neural RTE survived a very conservative backward masking procedure that provided a stringent control of non-conscious detection threshold, such that subjects were not aware of whether a target face or a blank stimulus in a pair had been presented.

The implicit modulation of non-conscious fear over conscious emotional evaluation in neurologically intact subjects shows interesting parallels with data from blindsight patients, and is consistent with current hypotheses about neural mechanisms mediating backward masking and interhemispheric interaction. Indeed, a comparable neural summation between seen and unseen fearful expressions has been reported in patient GY in association with enhanced activity in superior colliculi, amygdala, and extrastriate visual areas (de Gelder et al., 2005; de Gelder, de Hann, et al., 2001; de Gelder, Pourtois, et al., 2001). Remarkably, part of the same subcortical pathway (e.g., colliculi, pulvinar, and amygdala) bypassing the primary geniculo-striate visual system is also implicated in implicit perception of unseen fearful expressions in healthy observers when a backward masking technique is used (Liddell et al., 2005; Morris et al., 1999; Williams et al., 2006). Moreover, although direct evidence in neurologically intact human observers is still lacking, neural interhemispheric summation is at present most likely to be mediated by subcortical visual centers such as the superior colliculi, and is still present even when one stimulus in a pair cannot be consciously detected because of experimental manipulation or brain-damage (Corballis, 1998; Marzi et al., 2004, 1996, 1986; Savazzi & Marzi, 2002, 2004). Therefore, despite major differences in the physiology underlying the loss of visual awareness in blindsight and in backward masking (permanent damage to V1, in the former condition versus temporary inhibition of the transient excitatory after-discharge of V1 neurons, in the latter) (Macknik & Livingstone, 1998), important analogies exist between these two conditions with respect to the functional equivalence and the neural basis sustaining residual visual abilities (Marzi et al., 2004). Our current findings extend these analogies to the behavioral level in the emotional domain, showing that mechanisms implicated in non-conscious fear processing and interhemispheric summation normally interact in the intact brain, perhaps due to their partial overlapping at subcortical sites.

Unseen fearful expressions not only favored recognition of emotionally congruent faces, but also inhibited conscious evaluation of incongruent happy expressions. Indeed, recognition of unmasked happy faces was delayed by the simultaneous presence of a masked fearful face. Thus, implicit detection of emotional incongruence between seen (happy) and unseen (fearful) facial expressions seems to have started an interhemispheric inhibitory process that has overridden any response being prepared to the consciously perceived face. This hampering effect is in keeping with previous findings showing that unattended and task-irrelevant fearful expressions can interfere with an explicit ongoing task, thereby disrupting performance and resulting in response delay (Eastwood, Smilek, & Merikle, 2003; Vuilleumier, Armony, Driver, & Dolan, 2001). Notably, however, when subjects are aware of both stimuli and a similar redundant target design is used, emotional incongruence does not appear to slow down recognition of the target expression (Tamietto, Adenzato, et al., 2007; Tamietto, Geminiani, et al., 2007; Tamietto et al., 2006). The fact that interhemispheric interference is particularly effective when fearful signals are not explicitly noticed (because of inattention or non-conscious perception), further suggests that integration of emotional information across hemispheres might be predominantly sustained by subcortical (perhaps intercollicular) connections. This proposal needs additional investigation but, at present, seems supported by evidence from three independent lines of research. First, the shift from conscious to non-conscious fear perception in healthy subjects also modifies functional connectivity to the amygdala from cortical to subcortical networks (Williams et al., 2006). Secondly, interhemispheric interaction is generally enhanced in split-brain patients (in whom cortical interhemispheric cross-talk is prevented by callosal resection) as compared to healthy subjects, thereby envisaging a subcortical contribution that is normally inhibited at the cortical level in the intact brain (Corballis, 1998; Corballis et al., 2002; Forster & Corballis, 2000; Iacoboni, Ptito, Weekes, & Zaidel, 2000; Roser & Corballis, 2002, 2003; Savazzi & Marzi, 2004). Thirdly, in such patients, emotional stimuli produce greater autonomic responses when masked than when unmasked (Ladavas, Cimatti, Del Pesce, & Tuozzi, 1993).

Our balanced design allowed us to directly compare the behavioral influence of subliminally presented fearful faces with that produced by happy expressions, showing a selective contribution of the former in modulating conscious emotional evaluation. Conversely, the masking procedure seems to have suppressed not only conscious but also non-conscious processing of happy faces that were ineffective in biasing ongoing recognition of normally seen expressions. Analogous findings have been reported in psychophysiological and neuroimaging studies conducted on blindsight patients and healthy subjects, where positive results were obtained only for unseen fearful, but not happy, expressions (de Gelder et al., 2005; Esteves, Dimberg, & Ohman, 1994; Milders et al., 2006; Pegna et al., 2005; Whalen et al., 1998). It is worth noting that the differential sensitivity to fearful as opposed to happy facial expressions was specifically related to the non-conscious processing stage, as the same threshold for conscious detection was found for both emotions (i.e., >20 ms SOA). This is in line with the notion that threat-related emotions, in virtue of their unique relevance for survival, are distinct from other emotions in the degree of processing autonomy from conscious recognition they exhibit (LeDoux, 1996). A related, though controversial, question is whether automatic non-conscious processing is specific for fear only, or also extends to other expressions communicating potential danger, such as angry expressions (Johnson, 2005). Since angry expressions were not included in our design, we cannot directly address this issue here. Nonetheless, recent findings in both, healthy subjects and patients with amygdala lesions, tend to support the view that neuro-functional and behavioral effects induced by fearful and angry expressions are not too dissimilar, especially when these expressions are presented subliminally and contrasted to neutral or happy ones (Nomura et al., 2004; Sato & Aoki, 2006; Sato et al., 2002; Suslow et al., 2006; Whalen et al., 2001). Conversely, our findings seem to indicate that encoding of happy expressions rely critically on the functional integrity of the striate cortex and its feedforward connections to higher-order visual areas. The neural bases underlying happy face recognition are, however, less understood as compared to other emotions such as fear, anger or disgust (Fitzgerald, Angstadt, Jelsone, Nathan, & Phan, 2006). Further studies are thus needed to elucidate this point, and the direct comparison of happy with neutral expressions in both, explicit and implicit tasks, may provide new insights.

A final interesting result is the higher sensitivity of the right as compared to left hemisphere in non-conscious processing of fearful expressions. Indeed, the influence of unseen fearful expressions over conscious recognition of emotions was greater when masked expressions were projected to the LVF (right hemisphere) rather than RVF, and for either congruent or incongruent conditions (albeit the directionality of the effect was obviously reversed). The side of presentation of unseen fearful faces, however, did not modulate the amount of neural summation thereby revealing that interhemispheric cooperation was equally efficient irrespectively of which hemisphere processed the unseen fearful expression. This hemispheric laterality effect for non-conscious fear processing is consistent with a previous study reporting similar behavioral results for angry expressions in a subliminal affective priming paradigm (Sato & Aoki, 2006). Our findings are also broadly coherent with neuroimaging studies that showed a right hemisphere lateralization in response to unseen negative emotions. In fact, fearful expressions boosted activity in the right amygdala of a blindsight patient with total cortical blindness (Pegna et al., 2005), akin to what has been observed also in normal viewers when masked angry faces were presented (Morris et al., 1998). Thus, neuroimaging findings suggest that the higher sensitivity of the right hemisphere for unseen fearful expressions reported here on behavioral measures may likely have its physiological basis in the preferential engagement of the right amygdala in response to the same type of stimuli.

Acknowledgements

In May 1997 Larry Weiskrantz brought GY to the lab in Tilburg to give us the opportunity to test some of Paul Bertelson's ideas about the automaticity of ventriloquism and to participate in ongoing studies of Jean Vroomen and Bea de Gelder on the role of visual awareness in audiovisual speech perception. During one of the breaks of these long testing sessions (which ultimately yielded negative results) affective blindsight was born in a climate of healthy scepticism. Larry affectively turned a blind eye and we presented some facial expressions to GY's blind field, effectively challenging the notion that faces are the kind of complex stimuli that cannot be processed without V1 involvement. Affective blindsight continues to be the source of inspiring collaborations and friendship with Larry for the present authors and we owe him a debt of gratitude.

This study was supported by a Post-Doc Lagrange Fellow Project-CRT Foundation grant "The Challenge of Complex Systems" from the ISI Foundation to Marco Tamietto.

Beatrice de Gelder was partly supported by a grant from the Human Frontier Science Program HFSP-RGP0054/2004-C, a grant from FP6-2005-NEST-Path Imp 043403-COBOL, and by the NWO (Dutch Science organization).

References

Anders, S., Birbaumer, N., Sadowski, B., Erb, M., Mader, I., Grodd, W., et al. (2004). Parietal somatosensory association cortex mediates affective blindsight. *Nature Neuroscience*, *7*, 339–340.

Colonius, H., & Diederich, A. (2006). The race model inequality: Interpreting a geometric measure of the amount of violation. *Psychological Review*, *113*, 148–154.

Corballis, M. C. (1995). Visual integration in the split brain. *Neuropsychologia*, *33*, 937–959.

Corballis, M. C. (1998). Interhemispheric neural summation in the absence of the corpus callosum. *Brain*, *121*, 1795–1807.

Corballis, M. C., Hamm, J. P., Barnett, K. J., & Corballis, P. M. (2002). Paradoxical interhemispheric summation in the split brain. *Journal of Cognitive Neuroscience*, *14*, 1151–1157.

Cowey, A. (2004). The 30th Sir Frederick Bartlett lecture. Fact, artefact, and myth about blindsight. *Quarterly Journal of Experimental Psychology A*, *57*, 577–609.

de Gelder, B., de Haan, E., & Heywood, C. (2001). *Out of mind. Varieties of unconscious processes*. Oxford: Oxford University Press.

de Gelder, B., Morris, J. S., & Dolan, R. J. (2005). Unconscious fear influences emotional awareness of faces and voices. *Proceedings of the National Academy of Sciences United States of America*, *102*, 18682–18687.

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*, 385–391.

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. *Proceedings of* *the National Academy of Sciences United States of America*, *99*, 4121–4126.

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.

de Gelder, B., Vroomen, J., Pourtois, G., & Weiskrantz, L. (2000). Affective blindsight: Are we blindly led by emotions? Response to Heywood and Kentridge (2000). *Trends in Cognitive Sciences*, *4*, 126–127.

Dimberg, U., Thunberg, M., & Elmehed, K. (2000). Unconscious facial reactions to emotional facial expressions. *Psychological Science*, *11*, 86–89.

Eastwood, J. D., & Smilek, D. (2005). Functional consequences of perceiving facial expressions of emotion without awareness. *Consciousness and Cognition*, *14*, 565–584.

Eastwood, J. D., Smilek, D., & Merikle, P. M. (2003). Negative facial expression captures attention and disrupts performance. *Perception & Psychophysics*, *65*, 352–358.

Ekman, P., & Friesen, W. (1976). *Pictures of facial affect*. Palo Alto, CA: Consulting Psychologists Press.

Esteves, F., Dimberg, U., & Ohman, A. (1994). Automatically elicited fear: Conditioned skin conductance responses to masked facial expressions. *Cognition & Emotion*, *8*, 99–108.

Esteves, F., & Ohman, A. (1993). Masking the face: Recognition of emotional facial expressions as a function of the parameters of backward masking. *Scandinavian Journal of Psychology*, *34*, 1–18.

Fitzgerald, D. A., Angstadt, M., Jelsone, L. M., Nathan, P. J., & Phan, K. L. (2006). Beyond threat: Amygdala reactivity across multiple expressions of facial affect. *NeuroImage*, *30*, 1441–1448.

Forster, B., & Corballis, M. C. (2000). Interhemispheric transfer of colour and shape information in the presence and absence of the corpus callosum. *Neuropsychologia*, *38*, 32–45.

Green, D. M., & Swetz, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.

Greenwald, A. G., Draine, S. C., & Abrams, R. L. (1996). Three cognitive markers of unconscious semantic activation. *Science*, *273*, 1699–1702.

Hamm, A. O., Weike, A. I., Schupp, H. T., Treig, T., Dressel, A., & Kessler, C. (2003). Affective blindsight: Intact fear conditioning to a visual cue in a cortically blind patient. *Brain*, *126*, 267–275.

Iacoboni, M., Ptito, A., Weekes, N. Y., & Zaidel, E. (2000). Parallel visuomotor processing in the split brain: Cortico–subcortical interactions. *Brain*, *123*, 759–769.

Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience*, *6*, 766–774.

Jolij, J., & Lamme, V. A. (2005). Repression of unconscious information by conscious processing: Evidence from affective blindsight induced by transcranial magnetic stimulation. *Proceedings of the National Academy of Sciences United States of America*, *102*, 10747–10751.

Killgore, W. D., & Yurgelun-Todd, D. A. (2004). Activation of the amygdala and anterior cingulate during nonconscious processing of sad versus happy faces. *Neuroimage*, *21*, 1215–1223.

Ladavas, E., Cimatti, D., Del Pesce, M., & Tuozzi, G. (1993). Emotional evaluation with and without conscious stimulus identification: Evidence from a split-brain patient. *Cognition & Emotion*, *7*, 95–114.

LeDoux, J. E. (1996). *The emotional brain*. New York: Simon & Shuster.

Liddell, B. J., Brown, K. J., Kemp, A. H., Barton, M. J., Das, P., Peduto, A., et al. (2005). A direct brainstem-amygdala-cortical 'alarm' system for subliminal signals of fear. *Neuroimage*, *24*, 235–243.

Macknik, S. L., & Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual system. *Nature Neuroscience*, *1*, 144–149.

Marcel, A. J. (1983). Conscious and unconscious perception: Experiments on visual masking and word recognition. *Cognitive Psychology*, *15*, 197–237.

Marzi, C. A., Minelli, A., & Savazzi, S. (2004). Is blindsight in normals akin to blindsight following brain damage? *Progress in Brain Research*, *144*, 295–303.

Marzi, C. A., Smania, N., Martini, M. C., Gambina, G., Tomelleri, G., Palamara, A., et al. (1996). Implicit redundant-targets effect in visual extinction. *Neuropsychologia*, *34*, 9–22.

Marzi, C. A., Tassinari, G., Aglioti, S., & Lutzemberger, L. (1986). Spatial summation across the vertical meridian in hemianopics: A test of blindsight. *Neuropsychologia*, *24*, 749–758.

Merikle, P. M. (1992). Perception without awareness. Critical issues. *American Psychologist*, *47*, 792–795.

Merikle, P. M., Smilek, D., & Eastwood, J. D. (2001). Perception without awareness: Perspectives from cognitive psychology. *Cognition*, *79*, 115–134.

Milders, M., Sahraie, A., Logan, S., & Donnellon, N. (2006). Awareness of faces is modulated by their emotional meaning. *Emotion*, *6*, 10–17.

Miller, J. (1982). Divided attention: Evidence for coactivation with redundant signals. *Cognitive Psychology*, *14*, 247–279.

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.

Morris, J. S., Ohman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, *393*, 467–470.

Morris, J. S., Ohman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating "unseen" fear. *Proceedings of the National Academy of Sciences United States of America*, *96*, 1680–1685.

Nomura, M., Ohira, H., Haneda, K., Iidaka, T., Sadato, N., Okada, T., et al. (2004). Functional association of the amygdala and ventral prefrontal cortex during cognitive evaluation of facial expressions primed by masked angry faces: An event-related fMRI study. *NeuroImage*, *21*, 352–363.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.

Pegna, A. J., Khateb, A., Lazeyras, F., & Seghier, M. L. (2005). Discriminating emotional faces without primary visual cortices involves the right amygdala. *Nature Neuroscience*, *8*, 24–25.

Pessoa, L. (2005). To what extent are emotional visual stimuli processed without attention and awareness? *Current Opinion in Neurobiology*, *15*, 188–196.

Pessoa, L., Japee, S., & Ungerleider, L. G. (2005). Visual awareness and the detection of fearful faces. *Emotion*, *5*, 243–247.

Phillips, M. L., Williams, L. M., Heining, M., Herba, C. M., Russell, T., Andrew, C., et al. (2004). Differential neural responses to overt and covert presentations of facial expressions of fear and disgust. *Neuroimage*, *21*, 1484–1496.

Rolls, E. T., & Tovee, M. J. (1994). Processing speed in the cerebral cortex and the neurophysiology of visual masking. *Proceedings: Biological Sciences*, *257*, 9–15.

Roser, M., & Corballis, M. C. (2002). Interhemispheric neural summation in the split brain with symmetrical and asymmetrical displays. *Neuropsychologia*, *40*, 1300–1312.

Roser, M., & Corballis, M. C. (2003). Interhemispheric neural summation in the split brain: Effects of stimulus colour and task. *Neuropsychologia*, *41*, 830–846.

Sato, W., & Aoki, S. (2006). Right hemispheric dominance in processing of unconscious negative emotion. *Brain and Cognition*, *62*, 261–266.

Sato, W., Kubota, Y., Okada, T., Murai, T., Yoshikawa, S., & Sengoku, A. (2002). Seeing happy emotion in fearful and angry faces: Qualitative analysis of facial expression recognition in a bilateral amygdala-damaged patient. *Cortex*, *38*, 727–742.

Savazzi, S., & Marzi, C. A. (2002). Speeding up reaction time with invisible stimuli. *Current Biology*, *12*, 403–407.

Savazzi, S., & Marzi, C. A. (2004). The superior colliculus subserves interhemispheric neural summation in both normals and patients with a total section or agenesis of the corpus callosum. *Neuropsychologia*, *42*, 1608–1618.

Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*, *31*, 137–149.

Suslow, T., Ohrmann, P., Bauer, J., Rauch, A. V., Schwindt, W., Arolt, V., et al. (2006). Amygdala activation during maskd presentation of emotional faces predicts conscious detection of threat-related faces. *Brain and Cognition*, *61*, 243–248.

Tamietto, M., Adenzato, M., Geminiani, G., & de Gelder, B. (2007). Fast recognition of social emotions takes the whole brain: Interhemispheric cooperation in the absence of cerebral asymmetry. *Neuropsychologia*, *45*, 836–843.

Tamietto, M., Geminiani, G., Genero, R., & de Gelder, B. (2007). Seeing fearful body language overcomes attentional deficits in patients with neglect. *Journal of Cognitive Neuroscience*, *19*, 445–454.

Tamietto, M., Latini Corazzini, L., de Gelder, B., & Geminiani, G. (2006). Functional asymmetry and interhemispheric cooperation in the perception of emotions from facial expressions. *Experimental Brain Research*, *171*, 389–404.

Tomaiuolo, F., Ptito, M., Marzi, C. A., Paus, T., & Ptito, A. (1997). Blindsight in hemispherectomized patients as revealed by spatial summation across the vertical meridian. *Brain*, *120*, 795–803.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: An event-related fMRI study. *Neuron*, *30*, 829–841.

Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., et al. (2004). Human amygdala responsivity to masked fearful eye whites. *Science*, *306*, 2061.

Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *The Journal of Neuroscience*, *18*, 411–418.

Whalen, P. J., Shin, L. M., McInerney, S. C., Fischer, H., Wright, C. I., & Rauch, S. L. (2001). A functional MRI study of human amygdala responses to facial expressions of fear versus anger. *Emotion*, *1*, 70–83.

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. *The Journal of Neuroscience*, *26*, 9264–9271.

Williams, L. M., Liddell, B. J., Rathjen, J., Brown, K. J., Gray, J., Phillips, M., et al. (2004). Mapping the time course of nonconscious and conscious perception of fear: An integration of central and peripheral measures. *Human Brain Mapping*, *21*, 64–74.