

Cortical response to subjectively unconscious danger

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Received 26 January 2004; revised 6 September 2004; accepted 9 September 2004

Available online 18 November 2004

Cortical involvement in the evolution-favored automatic reaction to danger was studied. Electrical neural activity was recorded from 31 subjects, reporting fear of spiders, at 60 scalp locations. Visual stimuli containing spiders (negative elements) or, alternatively, nonnegative elements were presented to subjects, though they were unaware of their presence: a concurrent visual detection task using consciously perceived targets was administered. Spatial and temporal principal component analyses were employed to define and quantify, in a reliable manner, the main components of the neuroelectrical response to unconscious stimuli, and a source localization algorithm provided information on their neural origin. Results indicated that around 150 ms after stimulus onset, ventromedial prefrontal areas previously reported as responding rapidly to danger-related (conscious) stimuli were activated by unconsciously perceived spiders more markedly than by nonnegative unconscious stimuli. Subsequently, around 500 ms after stimulus onset, activation of the posterior cingulate and visual association cortices increased in this same direction. These data support previous results indicating that the ventromedial prefrontal cortex is involved in the top-down regulation of attention (through its capability to modulate the activity of posterior cortices in charge of visual processing) and that it automatically facilitates danger processing.

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Keywords: Cortical response; Electrical neural activity; Danger

Introduction

More than any other type of stimulation, dangers require processing and response resources to be intensely and urgently mobilized. Evolutionary success needs then nervous system to guarantee this mobilization even when recognition of danger clues is difficult and does not reach awareness (e.g., they are brief, occluded, or with poor contrast). In fact, experimental data from human subjects show that unconsciously perceived negative

images (e.g., snakes, spiders, or angry faces) elicit significant cognitive, vegetative, and motor responses. For example, these stimuli increase skin conductance response (Esteves and Öhman, 1993; Öhman and Soares, 1993), influence facial expression (Dimberg et al., 2000), facilitate the detection of forthcoming events (Bradley et al., 2000; Mogg and Bradley, 1999), and negatively affect the subjective evaluation of other elements of the environment (Berridge and Winkielman, 2003; Murphy and Zajonc, 1993).

The involvement of the amygdala in these reactions to danger seems obvious since this subcortical structure, capable of organizing rapid reactions to danger (even without the participation of the cerebral cortex; e.g., LeDoux, 1998), is able to respond to unconsciously perceived negative stimuli (Morris et al., 1998; Whalen et al., 1998). However, it is impossible to understand the wide and rich range of consequences elicited by unconscious danger, mainly those of a cognitive nature, if the intervention of the cerebral cortex is not assumed. Cortical mechanisms specializing in the processing of danger have, nevertheless, scarcely been studied. The main candidates are those cortical areas receiving inputs from the amygdala, such as the visual cortex (see a review on amygdalinal-visual connections in LeDoux, 1998) or the prefrontal cortex (see a review in Bar, 2003). Indeed, though using consciously perceived stimuli only, some studies show a greater and/or more rapid response in these areas to emotionally negative than to nonnegative stimulation (prefrontal cortex: Kawasaki et al., 2001; Northoff et al., 2000; Simpson et al., 2000; visual cortex: Carretié et al., 2001; Mourao-Miranda et al., 2003; Simpson et al., 2000).

The present research aimed to explore whether the prefrontal cortex and/or visual cortex, candidate cortical areas for intervening in reactions to danger, are activated even in response to stimuli presented under conditions of restricted awareness. The use of unconscious stimuli ensures that the observed neural reaction to them (if it is produced) is purely automatic, noncontrolled, as would be expected in neural mechanisms specializing in coping urgently with danger. Due to the very short latency of cortical responses to emotional stimuli (beginning around 100–150 ms; Kawasaki et al., 2001; Holmes et al., 2003; Carretié et al., 2004), neural activity needs to be studied by means of a temporally agile

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signal. In particular, we recorded event-related potentials (ERPs), which achieve a temporal resolution unattainable by brain-related hemodynamic signals.

Materials and methods

Subjects

Thirty-one students (23 women) from the Universidad Autónoma de Madrid, with an age range of 20–31 years (mean = 21.35, SD = 2.32), took part in this experiment. They participated voluntarily and reported normal or corrected-to-normal visual acuity. These subjects were selected from a wider sample of 87 volunteers, as those who reported fear of spiders (they scored over 6 on a 0—nil fear—to 10—maximum fear—scale of fears of different animals, objects, and situations).

Stimuli and procedure

Each presentation contained a set of visual elements, some of them remaining outside the subject's awareness (procedures employed to achieve this are described below) and others being consciously perceived, all in black on a white background (Fig. 1). Out-of-awareness elements were of two types: Spiders (i.e., frightening or aversive for the subjects, who had reported fear of spiders, as explained in the Subjects section) and 'Nonspiders' (nonfrightening). Nonspider stimuli consisted of two different images: butterflies and snowflakes (Fig. 1). Using a single image for this category would be methodologically incorrect since possible Spider vs. Nonspider differences could not be exclusively due to their different emotional meaning but to other factors (e.g., physical characteristics, cognitive categorization, familiarity, etc.). On the other hand, creating a control category formed by different images ensures that neural reactions to the specific characteristics of each of these stimuli are neutralized, while reactions to their common characteristic (i.e., their nonfrightening condition) stand out.¹ Thus, one of the two Nonspider images (butterflies) had more physical complexity (spatial frequency variability) than Spiders (snowflakes) and the other had less complexity.² Moreover, since these stimuli combined animals (butterflies) and nonanimals (snowflakes), the influence of concept- or category-related cognitive differences with respect to Spiders was also minimized. Other important nonemotional factors such as familiarity probably differ, also, between butterflies and snowflakes.

We combined four different strategies to ensure that subjects were unaware of spiders and nonspider elements (Fig. 1). First, stimuli were presented briefly (50 ms). Second, while subjects were required to look at the center of the screen, these elements appeared peripherally, forming a frame on the screen (4° wide; the size of the inner part of the frame was 34.4° × 24.7°). Third, they were partially hidden by uniform black noise (129.63% on the Adobe Photoshop 7.0® scale). The effect of this noise was the elimination of high spatial frequencies in the frame elements: edges

¹ In ERP terms, when responses to two (or more) different stimuli are averaged jointly, the correct signal-to-noise ratio is achieved only by those processes which are common to both stimuli (which appear in 100% of trials), but not by those specific (irrelevant in this study) for each stimuli (50% of trials).

² The analysis on the physical complexity of these stimuli is available at <http://www.uam.es/carretie/nimg05.htm>.

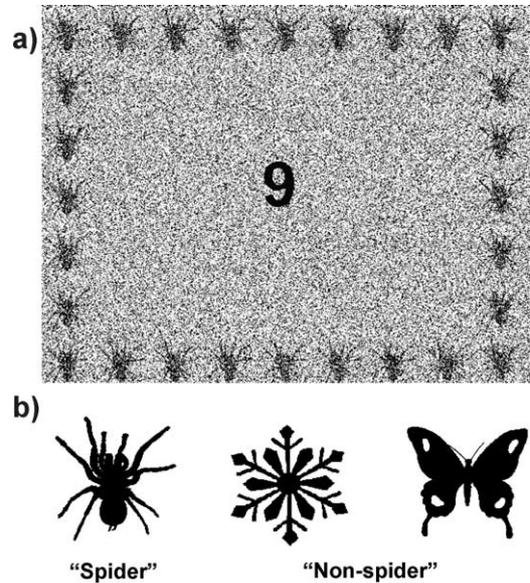


Fig. 1. (a) Example of stimulus: spider-framed stimulus with a digit over 5. (b) Discrete elements forming the frames in each type of stimuli (spider and nonspider framed).

or fine details were 'blurred.' And fourth, they were unattended (lack of attention to a stimulus, or "inattention blindness," hinders its conscious perception; Mack and Rock, 1998): the task required participants to attend to a (noise-free) number, 3.7° high, that appeared in the center of the screen (2, 4, 7, or 9). Participants had to press a key with the right hand when this central number was under 5, and a different key, also with the right hand, when it was over 5.

All subjects were indeed subjectively unaware of the elements forming the frames (spiders, butterflies, or snowflakes). At the end of the experiment, participants were asked "Did you see any frame around the number?" Seventeen out of the 31 giving a negative response. For those answering affirmatively, the second question was "Did you see any particular element in it?" Six participants responded negatively. The rest of the subjects (eight) were asked to describe what they saw, though none of them reported having detected any of the three critical elements: "I don't know" ($n = 2$), dots ($n = 2$), geometrical patterns ($n = 2$), plants ($n = 1$), and lines ($n = 1$). The advantages and validity of using subjective indices of awareness have been repeatedly defended (see Chalmers, 2001; Dehaene and Naccache, 2001; Merikle and Daneman, 2000; Merikle et al., 2001; Weiskrantz, 1997 on the comparison of subjective and objective methods; there are no reports of significant differences between the two). In order to avoid the task becoming an oddball paradigm,³ spiders, butterflies, and snowflakes each represented 1/3 of the 96 presentations. Within each of these three types, the proportion of stimuli with each of the four numbers (2, 4, 7, or 9) was the same (25%). Intertrial interval was 3000 ms. Order of presentation of Spider- and Non-spider-framed images was random.

³ The oddball paradigm consists of the unequal presentation of different discrete (not meta-categorical, as present 'nonspiders') stimuli: some of them (called 'standards') are presented more times than others 'odds' or 'deviants'. Typically, deviants elicit higher amplitudes than standards in some ERP components, a phenomenon that would constitute an interference in the present study.

After the recording sessions, and with the aim of analyzing whether the emotional charge of Spider and Nonspider images was that supposed a priori (i.e., frightening and nonfrightening, respectively), each subject filled out a bidimensional scaling test for each type of picture, assessing its levels of valence (−2, negative to 2, positive, being the extremes) and arousal (−2, calming to 2, arousing), two affective dimensions that are widely considered to explain the principal variance of emotional meaning (Lang et al., 1993; Osgood et al., 1957; Russell, 1979; Smith and Ellsworth, 1985). Results and analyses of these questionnaires will be described below.

Recording and data analysis

Electroencephalographic data were recorded using an electrode cap (ElectroCap International) with tin electrodes. A total of 60 scalp locations homogeneously distributed all over the scalp were used. All scalp electrodes, as well as one electrode at the left mastoid (M1), were originally referenced to one electrode at the right mastoid (M2). For the entire sample of electrodes, originally M2-referenced data were rereferenced offline using the average of the mastoids (M1 and M2) method.

Electrooculographic (EOG) data were recorded supra- and infra-orbitally (vertical EOG) and from the left versus right orbital rim (horizontal EOG). Electrode impedances were always kept below 3 k Ω . A band-pass of 0.1–50 Hz (3 dB points for −6 dB/octave roll-off) was used for the recording amplifiers. The channels were continuously digitizing data at a sampling rate of 250 Hz for the duration of complete recording session. The continuous recording was divided into 960 ms epochs for each trial, beginning 200 ms before the target onset. A visual inspection was also carried out, eliminating epochs with eye movements or blinks. Additionally, trials in which participants pressed the wrong key were deleted for analyses. This artifact and error rejection led to the average elimination of 5.387 spider-framed trials (SEM = 0.507) and 6.560 non-spider-framed trials (SEM = 0.419). ERP averages were categorized according to each type of stimulus (Spider and Nonspider framed).

Results

Fig. 2 shows six grand averages for each stimulus condition once the baseline (prestimulus recording) had been subtracted from each ERP. These grand averages correspond to a selection of frontal and posterior sites, were experimental effects (described later) showed the highest significance. Though the conscious elements of the stimulation did not vary across stimulus categories (the ERPs showing, consequently, an expectable similarity), these averages show effects (signaled as ‘P150’ and ‘N500’) related to the different, subjectively unconscious elements of the stimuli. As explained below, statistical analyses confirm the significance of these effects. In statistical tests involving analyses of variance (ANOVAs), the Greenhouse–Geisser (GG) epsilon correction was applied to adjust the degrees of freedom of the F ratios where necessary. In all cases, ANOVAs involved fully balanced factorial designs.

Detection and quantification of ERP components: temporal principal component analysis

Components explaining most ERP variance were detected and quantified through a covariance-matrix-based temporal principal

component analysis (tPCA). This technique has been repeatedly recommended for these tasks since the exclusive use of traditional visual inspection of grand averages and voltage computation may lead to several types of misinterpretation (Chapman and McCrary, 1995; Coles et al., 1986; Donchin and Heffley, 1978; Fabiani et al., 1987). The main advantage of tPCA is that it presents each ERP component with its ‘clean’ shape, extracting and quantifying it free of the influences of adjacent or subjacent components (traditional grand averages often show components in a distorted way and may even fail to show some of them). The decision on the number of components to select was based on the scree test (Cliff, 1987). Extracted components were submitted to varimax rotation. Following this selection criterion, nine components were extracted from ERPs (Fig. 3).

Analyses on the experimental effects

The next task was to detect any effect of the unconscious elements of the stimuli (Spiders and Nonspiders) on the nine components extracted by tPCA. For this purpose, ANOVAs on temporal factor scores were carried out. Factor scores, the parameter (resulting from the PCA) in which temporal factors or components are quantified, are calculated for each individual ERP, and reflect the amplitude of each component. Factors were Stimuli (two levels: spiders and nonspiders) and Recording channels (58 levels). The effect of Stimuli alone was significant in Factor 6 [$F(1,30) = 5.06$, $P < 0.05$], and Factor 5 showed a significant effect of the interaction Stimuli by Recording channels [$F(57,1710) = 5.69$, GG epsilon = 0.60, $P < 0.0025$]. In both cases, amplitudes were higher in response to Spider than in response to Nonspider stimuli. Fig. 4 shows mean factor scores of Factors 5 and 6 for each electrode location in the form of scalp maps. Factor peak latency and topography characteristics (see Figs. 3 and 4) associate Factor 6 (peaking at 152 ms) with the wave labeled “P150” in grand averages (Fig. 2) and Factor 5 (peaking at 504 ms) with that labeled “N500”. These labels will be employed hereafter to make the results easier to understand.

Fig. 4 suggests that these components have two regions of distribution, one anterior and the other posterior (positive or red in the case of P150, negative or blue in the case of N500). In order to test which of these regions contributed more to explaining the experimental effects, separate ANOVAs were carried out for each of these scalp regions. Spatial PCAs (sPCAs) were carried out on P150 and N500 temporal factor scores (directly related to amplitudes, as already explained) in order to configure and quantify these regions. This system is preferable to the traditional, a priori subdivision into geometrically defined scalp regions (Carretié et al., 2003; Spencer et al., 1999), since sPCA demarcates them according to the real behavior of each scalp-point recording (basically, each region or spatial factor is formed with the scalp points where recordings tend to covary). As a result, the shape of the sPCA-configured regions is functionally based and scarcely resembles the shape of the traditional, geometrically configured regions. Moreover, each spatial factor can be quantified through the spatial factor scores, a single parameter that reflects the amplitude of the whole spatial factor. As illustrated in Fig. 5, sPCAs extracted both a frontal and a posterior spatial factor for each component (P150 and N500; Fig. 6).

Repeated-measures ANOVAs on these P150 and N500 spatial factors with respect to Stimuli were carried out (two levels: Spiders and Nonspiders). For P150, results indicated that it is the frontal

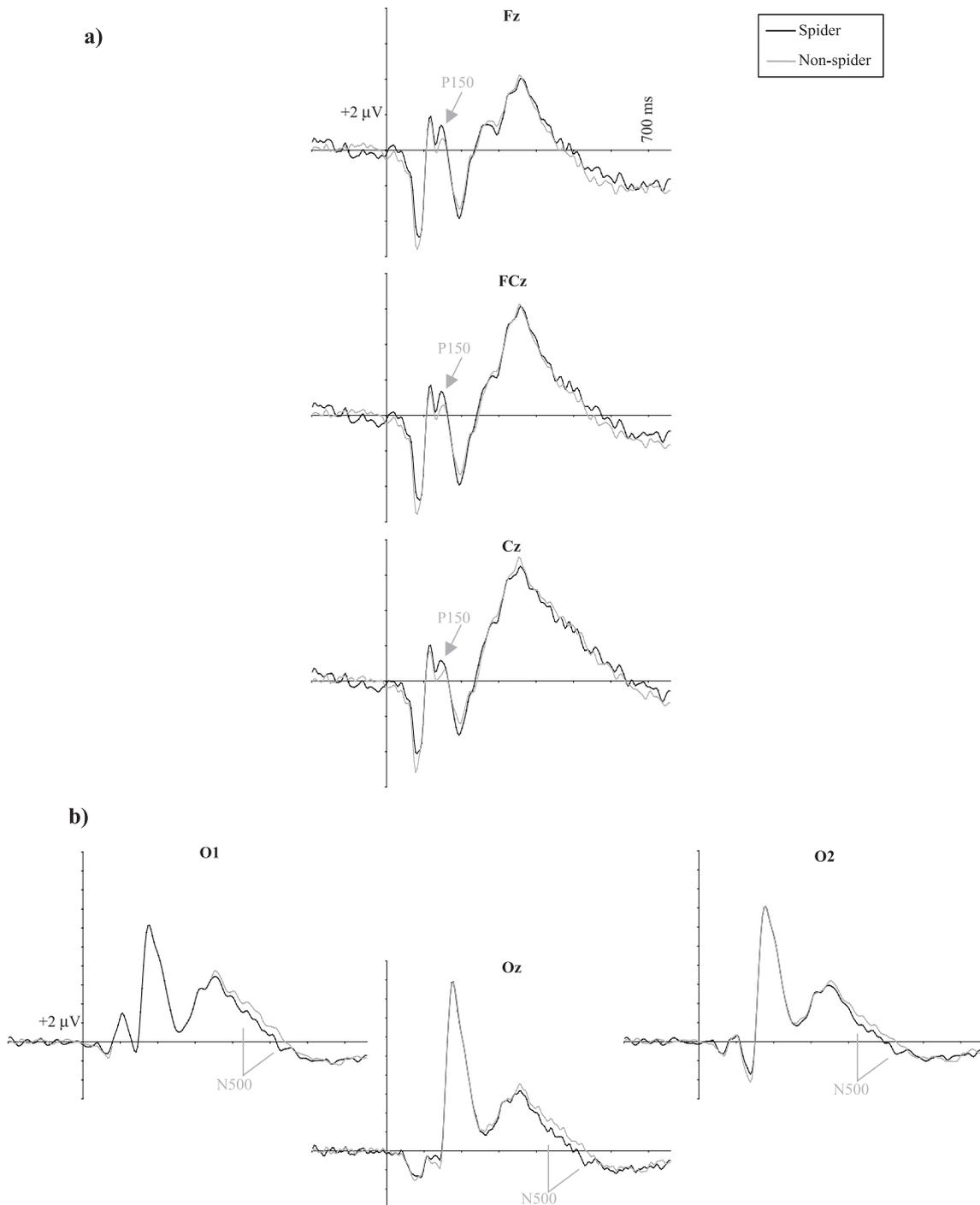


Fig. 2. Mean responses to the two types of stimuli at a selection of frontal (a) and posterior (b) sites were the experimental effects (described in the text) are easily distinguishable. Scales appear in Fz and O1, respectively.

spatial factor [$F(1,30) = 4.659, P < 0.05$], not the posterior factor ($P > 0.05$), that is sensitive to factor Stimuli. For N500, analyses showed the opposite trend: the posterior factor is sensitive to factor Stimuli [$F(1,30) = 7.93, P < 0.01$] but not the frontal factor ($P > 0.05$). Spiders elicit higher amplitudes than Nonspiders in both P150 (Spiders = 0.072, SEM = 0.185; Nonspiders = -0.072, SEM = 0.176) and N500 (in this negative component, amplitude increases as negativity increases: Spiders = -0.165, SEM = 0.193; Nonspiders = 0.165, SEM = 0.163).

Source localization analyses

Next step was to three-dimensionally localize the cortical regions that are sensitive to the experimental effects (it should be frontally located for P150, and posterior located for N500, according to the analyses described above). Low-resolution brain electromagnetic tomography (LORETA) was applied for P150 and N500 factor scores (directly related to amplitudes, as already explained). LORETA is a 3D, discrete linear solution for the EEG

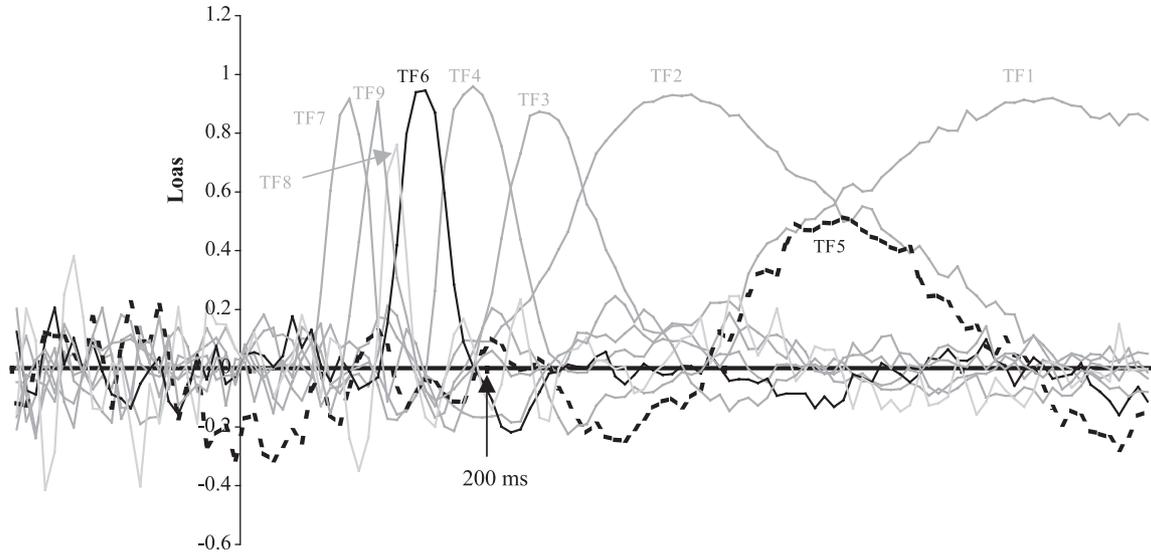


Fig. 3. tPCA: factor loadings after varimax rotation. Temporal Factors 6 (P150) and 5 (N500), which are sensitive to the experimental effects, is drawn in black.

inverse problem (Pascual-Marqui, 1999; Pascual-Marqui et al., 1994). Though, in general, solutions provided by EEG-based source-localization algorithms should be interpreted with caution due to their potential error margins, LORETA solutions have shown significant correspondence with those provided by functional magnetic resonance imaging in the same tasks (Vitacco et al., 2002), their error margin being modest (14 mm; Pascual-Marqui, 1999; Pascual-Marqui et al., 1994). Moreover, the large sample size employed in the present study ($n = 31$) contributes to diminish this error margin. In its current version, LORETA refers to a three-shell spherical model registered to the Talairach human brain atlas (Talairach and Tournoux, 1988). The solution is given, therefore, in

three coordinates: ‘x’ is the distance in millimeters to the right (+) or left (–) of midline, ‘y’ is the distance anterior (+) or posterior (–) to the anterior commissure, and ‘z’ is the distance above (+) or below (–) a horizontal plane through the anterior and posterior commissures.

In order to diminish the influence of noisy, irrelevant activity in calculations, LORETA was applied on the Spider minus Nonspider differential factor scores. Table 1 and Fig. 6 show the main sources of activity for P150 and N500. As may be appreciated, P150 presents a ventromedial prefrontal source together with a visual association cortex source. As explained (see previous section), ANOVAs suggest that the prefrontal source, but not the visual cortex source, is sensitive to the emotional content of the unconscious stimulation. On the other hand, main sources of N500 are all posterior located, and according to ANOVAs they are responsible of the sensitivity of this component to the experimental treatment.

Behavior and control analyses

Firstly, number of errors (i.e., incorrect button presses) and reaction times (RTs)⁴ for correct answers were analyzed in order to test whether the subjectively unconscious elements affected execution in the distracting task (i.e., categorization of the central numbers; see Table 2). Paired *t* tests were carried out in both cases, the results being nonsignificant ($P > 0.05$) for both RTs ($t = -1.63$) and errors ($t = -1.19$). Secondly, statistical analyses were carried out on valence and arousal assessments (see Stimuli and procedure section) in order to confirm that Spider stimuli presented higher emotional arousal and more negativity than Nonspider stimuli. Table 3 shows the means and standard error of means of both dimensions for each type of image. One-way repeated measures ANOVAs were computed, using Stimuli (two levels: Spiders, Nonspiders) as factor. These ANOVAs yielded significant differences in both valence and arousal [$F(1,39) = 409.06$,

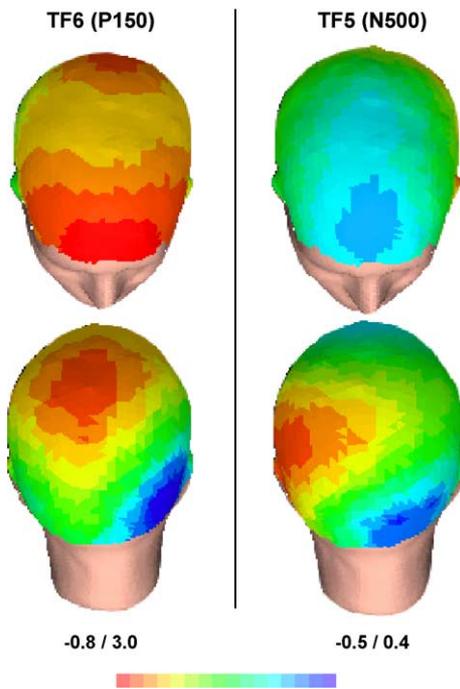


Fig. 4. Temporal factors 6 (P150) and 5 (N500): mean factor scores (directly related to amplitudes) for each of the 58 electrode locations in the form of scalp maps.

⁴ Fortuitous responses (i.e., accidental button presses: RTs < 100 ms) were not taken into account. This occurred in one single trial of three different subjects. No RTs surpassing 1500 ms from the stimulus onset were produced.

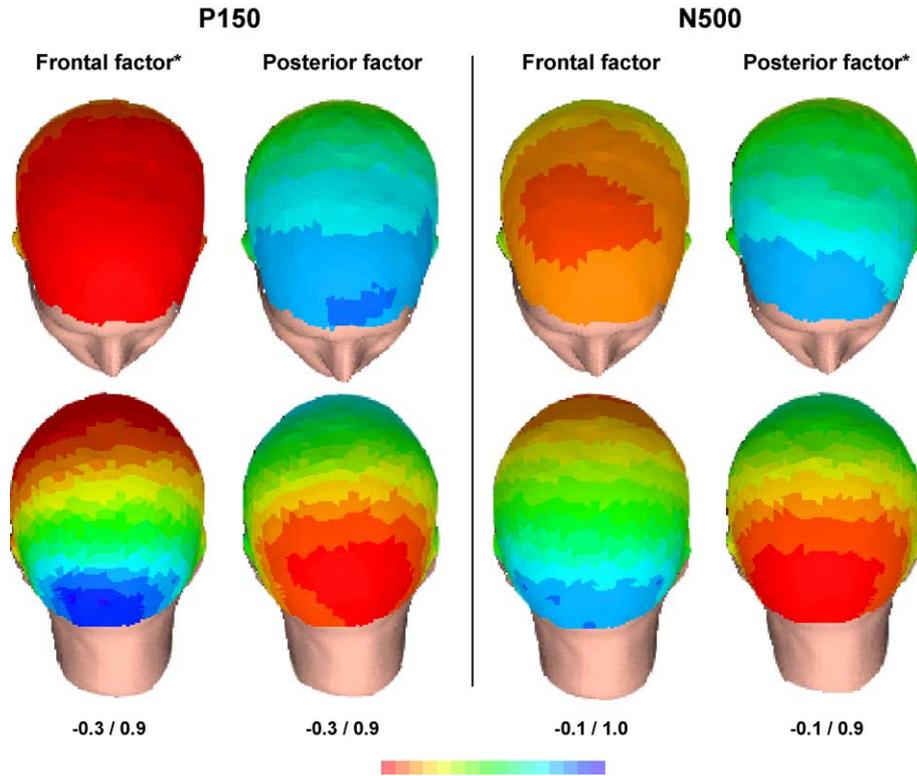


Fig. 5. Spatial factors extracted for P150 and N500 through sPCA. An asterisk signals those spatial factors sensitive to the experimental treatment.

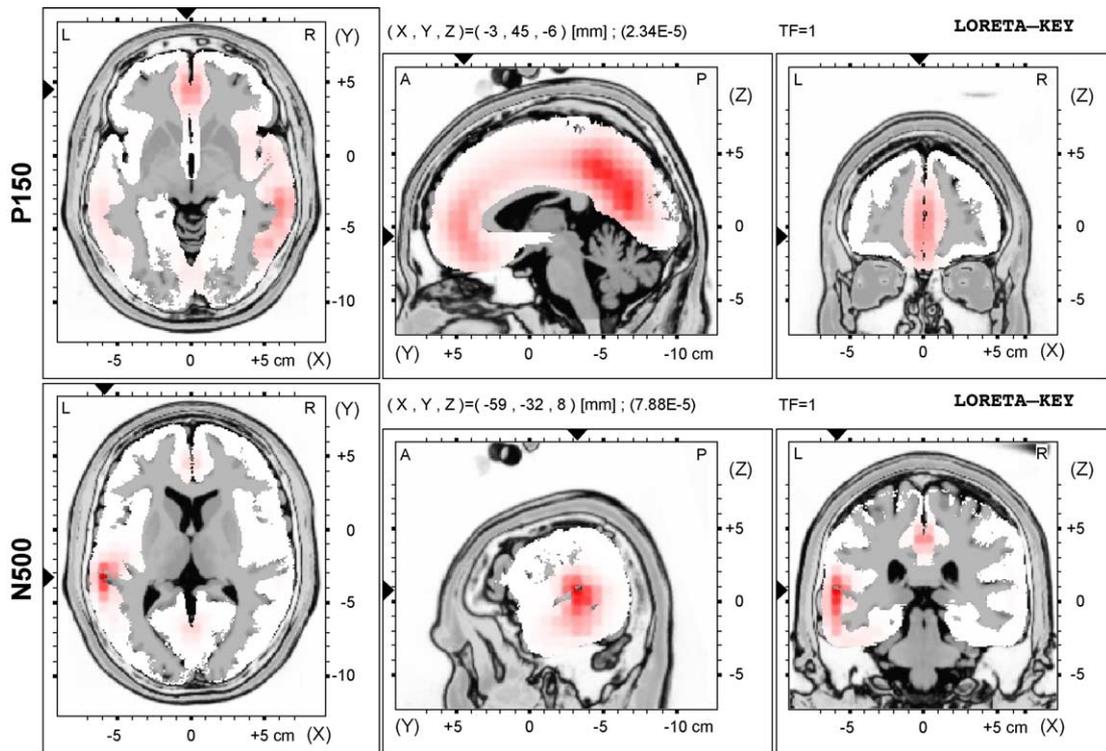


Fig. 6. Images of neural activity computed with LORETA for spider minus nonspider P150 and N500 factor scores. The main focuses are represented through three orthogonal brain views in Talairach space, sliced through the region of the maximum activity. Left slice: axial, seen from above, nose up; center slice: sagittal, seen from the left; right slice: coronal, seen from the rear. Talairach coordinates: x from left (L) to right (R); y from posterior (P) to anterior (A); z from inferior to superior.

Table 1

Main focuses provided by LORETA for spider minus nonspider P150 and N500 factor scores

	Talairach x, y, z	Anatomical location
P150	–3, 45, –6	Ventromedial prefrontal cortex
	4, –67, 22	Visual association cortex (precuneus)
N500	–59, –32, 8	Visual association cortex (superior temporal gyrus)
	–3, –39, 43	Posterior cingulate cortex

Talairach coordinates: x from left to right, y from posterior to anterior, z from inferior to superior.

$P < 0.001$ and $F(1,30) = 231.42$, $P < 0.001$, respectively], confirming that Spiders were more arousing and more negative than Nonspider stimuli.

Finally, differences in frontal P150 and posterior N500 amplitudes (where the experimental effects were significant) in response to the two Nonspider stimuli (butterflies and snowflakes) were tested. If these differences were significant in any of both components, then it could be concluded that, at least, part of the observed Spider vs. Nonspider differences were due to nonemotional factors (such as physical complexity or cognitive category). These analyses required new tPCA and sPCA including butterflies and snowflakes separately. ANOVAs on frontal P150 and posterior N500 factor scores showed no differences between butterfly and snowflake conditions [$F(1,30) = 0.82$, $P > 0.05$ and $F(1,30) = 0.27$, $P > 0.05$, respectively]. Therefore, nonemotional factors such as physical complexity or cognitive category are not influencing the observed experimental effects.

Discussion

Temporal, spatial (even assuming the already mentioned greatest margin of error), and statistical analyses show that the activation of the ventromedial prefrontal cortex (VMPFC; the junction area of medial prefrontal and orbitofrontal cortices) is greater in response to unconsciously perceived danger than in response to nonnegative unconscious stimulation. This differential prefrontal activation is produced around 150 ms after stimulus onset. Some previous studies using consciously perceived stimulation have also found rapid reactions (100–150 ms) of VMPFC to emotionally negative stimuli (Kawasaki et al., 2001; Northoff et al., 2000; Simpson et al., 2000). Interestingly, VMPFC response to negative stimuli is specifically associated with danger-related stimuli, such as anger faces, and not with other emotionally negative stimuli, such as sad faces (Blair et al., 1999). These data suggest that this prefrontal area is involved in the automatic response to danger that, as explained in the Introduction, facilitates survival. However, what is the particular role of the VMPFC in the reaction to danger?

Table 2

Means and standard error of means (in brackets) of arousal number of errors (incorrect button presses; percentages in square brackets) and reaction times (RTs; in milliseconds)

	Spider	Nonspider
Errors	0.581 (0.166) [1.816%]	0.823 (0.132) [2.572%]
RTs	461.935 (12.322)	467.322 (11.974)

Table 3

Means and standard error of means (in brackets) of arousal (–2, calming to 2, arousing) and valence (–2, negative to 2, positive) assessments given by the 31 subjects to the three types of stimulation

	Spider	Nonspider
Arousal	1.710 (0.083)	–0.690 (0.150)
Valence	–1.710 (0.095)	1.274 (0.113)

Several previous studies and the present results suggest that it is related to the top-down regulation of attention, through the VMPFC's capability to increase parietal and visual cortex activation (Armony and Dolan, 2002; Bar, 2003; Hopfinger et al., 2000; Sarter et al., 2001). The term 'top-down' may be applied to those neural mechanisms triggered by nonsensory, high-level neural circuits (such as prefrontal cortex) designed to enhance the processing of relevant inputs by sensory, low-level cortical areas (such as visual cortex). Reciprocally, neuroanatomical studies show that VMPFC receives inputs both from early stages of visual cortex (e.g., V2; see a review in Bar, 2003) and from danger-specialized subcortical structures such as the amygdala (e.g., Vuilleumier, 2002). Thus, key, significant elements of the visual scene can be rapidly extracted and detected by the VMPFC. This prefrontal area may consequently 'decide' to increase the level of attention. The initial visual information that reaches the VMPFC may be poor in details (i.e., lacking high spatial frequencies, as in the unconscious stimuli of the present experiment) but sufficient for triggering attentional facilitation where necessary (Bar, 2003). These early visual inputs to the VMPFC may explain its capability to respond quickly (from 100 to 150 ms, as already indicated) to danger-related stimulation (see also prefrontal ERP data obtained by Eimer and Holmes, 2002; Holmes et al., 2003).

Is the VMPFC capable of triggering an increase in visual cortex activation even when danger is perceived in conditions of restricted awareness? The present results suggest an affirmative response. Thus, 350 ms after activation of the VMPFC, several areas of posterior cortex [involving the posterior cingulate cortex (PCC) and the visual association cortex (VAC)] respond in the same direction to the stimulation: they show their highest activation in response to unconsciously perceived danger. Other studies have also demonstrated the capability of visual cortices to respond to unconscious (though nonemotional) stimulation (see reviews in Dehaene and Naccache, 2001; Kanwisher, 2001). The particular VAC area activated in this phase, the superior temporal gyrus, has been reported to participate in visual categorization (Culham, 2001), nonword reading (Wydell et al., 2003), and number comparison (Dehaene et al., 1996), processes needed in the present categorization task. The involvement of PCC in visual attention has been reported in several studies (Bussey et al., 1997; Turak et al., 2002). Particularly, some authors (Mesulam, 1981; Vuilleumier and Schwartz, 2001) have proposed that the role of PCC in attentional processes is to evaluate the affective valence of sensory events. In fact, and in line with the present data, PCC increases its activation in response to aversive visual stimuli (Fredrikson et al., 1995).

It may be concluded, firstly, that the present study supports the idea, raised by several studies previously mentioned, that VMPFC contribute to top-down regulation of attention. Secondly, present data suggest that such a VMPFC top-down regulation may be purely automatic and unconscious and that one of the results of this mechanism, probably the most conspicuous from an evolutionary point of view, is the facilitation of danger processing. It is

important to indicate that though this automatic mechanism may be triggered by unconscious danger, it should also be activated by conscious danger in order to better facilitate survival. In fact, its sensitivity to conscious danger is suggested by studies already mentioned (Blair et al., 1999; Kawasaki et al., 2001; Northoff et al., 2000; Simpson et al., 2000). The failure to find behavioral indices (error rates and reaction times) of better conscious target detection during Spider presentations does not necessarily contradict this conclusion. First, the visual detection task, designed primarily to restrict the awareness with which the critical elements were processed, was concurrent with the presentation of threatening elements. Studies showing danger-associated increase in the detection of targets present them after, and not simultaneously with, the threatening stimuli (Bradley et al., 2000; Mogg and Bradley, 1999). Second, the presentation of emotional information outside the spatial location where targets are being presented does not facilitate their detection (Vuilleumier and Schwartz, 2001). Further studies employing a wide range of experimental tasks and designs, and recording methodologies that improve the spatial resolution of EEG data, are necessary to advance in the definition of the ‘automatic system’ of response to danger.

Acknowledgments

This work was supported by the grants BSO2002-01980 from the Ministerio de Ciencia y Tecnología of Spain and 06/0091/2002 from the Comunidad de Madrid.

References

- Armony, J.L., Dolan, R.J., 2002. Modulation of spatial attention by fear-conditioned stimuli: an event-related fMRI study. *Neuropsychologia* 40, 817–826.
- Bar, M., 2003. A cortical mechanism for triggering top-down facilitation in visual object recognition. *J. Cogn. Neurosci.* 15, 600–609.
- Berridge, K.C., Winkielman, P., 2003. What is an unconscious emotion? (The case for unconscious “liking”). *Cogn. Emot.* 17, 181–211.
- Blair, R.J., Morris, J.S., Frith, L.D., Perrett, D.I., Dolan, R.J., 1999. Dissociable neural responses to facial expressions of sadness and anger. *Brain* 122, 883–893.
- Bradley, B.P., Mogg, K., Millar, N.H., 2000. Covert and overt orienting of attention to emotional faces in anxiety. *Cogn. Emot.* 14, 789–808.
- Bussey, T.J., Muir, J.L., Everitt, B.J., Robbins, T.W., 1997. Triple dissociation of anterior cingulate, posterior cingulate, and medial frontal cortices on visual discrimination tasks using a touchscreen testing procedure for the rat. *Behav. Neurosci.* 111, 920–936.
- Carretié, L., Martín-Loeches, M., Hinojosa, J.A., Mercado, F., 2001. Attention and emotion interaction studied through event related potentials. *J. Cogn. Neurosci.* 13, 1109–1128.
- Carretié, L., Hinojosa, J.A., Mercado, F., 2003. Cerebral patterns of attentional habituation to emotional visual stimuli. *Psychophysiology* 40, 381–388.
- Carretié, L., Hinojosa, J.A., Martín-Loeches, M., Mercado, F., Tapia, M., 2004. Automatic attention to emotional stimuli: neural correlates. *Hum. Brain Mapp.* 22, 290–299.
- Chalmers, D.J., 2001. *The Conscious Mind*. Oxford University Press, Oxford.
- Chapman, R.M., McCrary, J.W., 1995. EP component identification and measurement by principal components analysis. *Brain Cogn.* 27, 288–310.
- Cliff, N., 1987. *Analyzing Multivariate Data*. Harcourt Brace Jovanovich, New York.
- Coles, M.G.H., Gratton, G., Kramer, A.F., Miller, G.A., 1986. Principles of signal acquisition and analysis. In: Coles, M.G.H., Donchin, E., Porges, S.W. (Eds.), *Psychophysiology: Systems, Processes and Applications*. Elsevier, Amsterdam, pp. 183–221.
- Culham, J., 2001. There’s Waldo! *Trends Cogn. Sci.* 5, 231.
- Dehaene, S., Naccache, L., 2001. Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition* 79, 1–37.
- Dehaene, S., Tzourio, N., Frak, V., Raynaud, L., 1996. Cerebral activations during number multiplication and comparison: a PET study. *Neuropsychologia* 34, 1097–1106.
- Dimberg, U., Thunberg, M., Elmehed, K., 2000. Unconscious facial reactions to emotional facial expressions. *Psychol. Sci.* 11, 86–89.
- Donchin, E., Heffley, E.F., 1978. Multivariate analysis of event-related potential data: a tutorial review. In: Otto, D. (Ed.), *Multidisciplinary Perspectives in Event Related Brain Potential Research*. U.S. Government Printing Office, Washington, DC, pp. 555–572.
- Eimer, M., Holmes, A., 2002. An ERP study on the time course of emotional face processing. *NeuroReport* 13, 427–431.
- Esteves, F., Öhman, A., 1993. Masking the face: recognition of emotional facial expressions as a function of the parameters of backward masking. *Scand. J. Psychol.* 34, 1–18.
- Fabiani, M., Gratton, G., Karis, D., Donchin, E., 1987. Definition, identification, and reliability of measurement of the P300 component of the event related brain potential. In: Acles, P.K., Jennings, J.R., Coles, M.G.H. (Eds.), *Advances in Psychophysiology*, vol. 2. JAI Press, London, pp. 1–78.
- Fredrikson, M., Wik, G., Fischer, H., Anderson, J., 1995. Affective and attentive neural networks in humans: a PET study of Pavlovian conditioning. *NeuroReport* 7, 97–101.
- Holmes, A., Vuilleumier, P., Eimer, M., 2003. The processing of emotional facial expression is gated by spatial attention: evidence from event related brain potentials. *Cognit. Brain Res.* 16, 174–184.
- Hopfinger, J.B., Buonocore, M.H., Mangun, G.R., 2000. The neural mechanisms of top down attentional control. *Nat. Neurosci.* 3, 284–291.
- Kanwisher, N., 2001. Neural events and perceptual awareness. *Cognition* 79, 89–113.
- Kawasaki, H., Adolphs, R., Kaufman, O., Damasio, H., Damasio, A.R., Granner, M., Bakken, H., Hori, T., Howard, M.A., 2001. Single neuron responses to emotional visual stimuli recorded in human ventral prefrontal cortex. *Nat. Neurosci.* 4, 15–16.
- Lang, P.J., Greenwald, M.K., Bradley, M.M., Hamm, A.O., 1993. Looking at pictures: affective, facial, visceral, and behavioral reactions. *Psychophysiology* 30, 261–273.
- LeDoux, J., 1998. Fear and the brain: where have we been, and where are we going? *Biol. Psychiatry* 44, 1229–1238.
- Mack, A., Rock, I., 1998. *Inattentional Blindness*. MIT Press, Cambridge, MA.
- Merikle, P.M., Daneman, J.D., 2000. Conscious vs. unconscious perception. In: Gazzaniga, M.S. (Ed.), *The New Cognitive Neurosciences*. MIT Press, Cambridge, MA, pp. 1295–1303.
- Merikle, P.M., Smilek, D., Eastwood, J.D., 2001. Perception without awareness: perspectives from cognitive psychology. *Cognition* 79, 115–134.
- Mesulam, M.M., 1981. A cortical network for directed attention and unilateral neglect. *Ann. Neurol.* 4, 309–325.
- Mogg, K., Bradley, B.P., 1999. Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. *Cogn. Emot.* 13, 713–740.
- Morris, J.S., Öhman, A., Dolan, R.J., 1998. Conscious and unconscious emotional learning in the human amygdala. *Nature* 393, 467–470.
- Mourao-Miranda, J., Volchan, E., Moll, J., Oliveira-Souza, R., Oliveira, L., Bramati, I., Gattass, R., Pessoa, L., 2003. Contributions of stimulus valence and arousal to visual activation during emotional perception. *NeuroImage* 20, 1955–1963.
- Murphy, S.T., Zajonc, R.B., 1993. Affect, cognition, and awareness: affective priming with optimal and suboptimal stimulus exposures. *J. Pers. Soc. Psychol.* 64, 723–739.
- Northoff, G., Richter, A., Gessner, M., Schlagenhaut, F., Fell, J., Baumgart,

- F., Kaulisch, T., Kötter, R., Stephan, K.E., Leschinger, A., Hagner, T., Bargel, B., Witzel, T., Hinrichs, H., Bogerts, B., Scheich, H., Heinze, H.J., 2000. Functional dissociation between medial and lateral prefrontal cortical spatiotemporal activation in negative and positive emotions: a combined fMRI/MEG study. *Cereb. Cortex* 10, 93–107.
- Öhman, A., Soares, F., 1993. On the automaticity of phobic fear: conditioned skin conductance responses to masked phobic stimuli. *J. Abnorm. Psychol.* 102, 121–132.
- Osgood, C., Suci, G., Tannenbaum, P., 1957. *The Measurement of Meaning*. University of Illinois, Urbana, IL.
- Pascual-Marqui, R.D., 1999. Review of methods for solving the EEG inverse problem. *Int. J. Bioelectromagn.* 1, 75–86.
- Pascual-Marqui, R.D., Michel, C.M., Lehman, D., 1994. Low resolution electromagnetic tomography: a new method for localizing electrical activity in the brain. *Int. J. Psychophysiol.* 18, 49–65.
- Russell, J.A., 1979. Affective space is bipolar. *J. Pers. Soc. Psychol.* 37, 345–356.
- Sarter, M., Givens, B., Bruno, J.P., 2001. The cognitive neuroscience of sustained attention: were top down meets bottom up. *Brain Res. Rev.* 35, 146–160.
- Simpson, J.R., Öngür, D., Akbudak, E., Conturo, T.E., Ollinger, J.M., Snyder, A.Z., Gusnard, D.A., Raichle, M.E., 2000. The emotional modulation of cognitive processing: an fMRI study. *J. Cogn. Neurosci.* 12, 157–170.
- Smith, C.A., Ellsworth, P.C., 1985. Patterns of cognitive appraisal in emotion. *J. Pers. Soc. Psychol.* 48, 813–838.
- Spencer, K.M., Dien, J., Donchin, E., 1999. A componential analysis of the ERP elicited by novel events using a dense electrode array. *Psychophysiology* 36, 409–414.
- Talairach, J., Tournoux, P., 1988. *Co-planar Stereotaxic Atlas of the Human Brain*. Thieme, Stuttgart.
- Turak, B., Louvel, J., Buser, P., Lamarche, M., 2002. Event related potentials recorded from the cingulate gyrus during attentional tasks: a study in patients with implanted electrodes. *Neuropsychologia* 40, 99–107.
- Vitacco, D., Brandeis, D., Pascual-Marqui, R.D., Martín, E., 2002. Correspondence of event-related potential tomography and functional magnetic resonance imaging during language processing. *Hum. Brain Mapp.* 17, 4–12.
- Vuilleumier, P., 2002. Facial expression and selective attention. *Curr. Opin. Psychiatr.* 15, 291–300.
- Vuilleumier, P., Schwartz, S., 2001. Emotional facial expressions capture attention. *Neurology* 56, 153–158.
- Weiskrantz, L., 1997. *Conscious Lost and Found: A Neuropsychological Exploration*. Oxford University Press, Oxford.
- 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. *J. Neurosci.* 18, 411–418.
- Wydell, T.N., Vuorinen, T., Helenius, P., 2003. Neural correlates of letter-string length and lexicality during reading in a regular orthography. *J. Cogn. Neurosci.* 15, 1052–1062.