



**Memòria justificativa de recerca de les convocatòries BCC, BE, BP, CTP-
AIRE, DEBEQ, FI, FI-ICIP, INEFC i PIV**

La memòria justificativa consta de les dues parts que venen a continuació:

- 1.- Dades bàsiques i resums
- 2.- Memòria del treball (informe científic)

Tots els camps són obligatoris

1.- Dades bàsiques i resums

Nom de la convocatòria
BP

Llegenda per a les convocatòries:

BCC	Convocatòria de beques per a joves membres de comunitats catalanes a l'exterior
BDH	Beques i ajuts postdoctorals del Programa DGR-Henkel KGaA
BE	Beques per a estades per a la recerca fora de Catalunya
BP	Convocatòria d'ajuts postdoctorals dins del programa Beatriu de Pinós
CTP-AIRE	Ajuts per accions de cooperació en el marc de la comunitat de treball dels Pirineus. Ajuts de mobilitat de personal investigador.
DEBEQ (Modalitat A3)	Beques de Cooperació Internacional i Desenvolupament
FI	Beques predoctorals per a la formació de personal investigador
FI-ICIP	Beques i ajuts per a l'etapa de formació i de recerca de personal investigador novell en els àmbits d'interès de l'Institut Català Internacional per la Pau
INEFC	Beques predoctorals i de col·laboració, dins de l'àmbit de l'educació física i l'esport i les ciències aplicades a l'esport
PIV	Beques de recerca per a professors i investigadors visitants a Catalunya

Títol del projecte: ha de sintetitzar la temàtica científica del vostre document.
Emotional attention as a modulatory system of perception

Dades de l'investigador o beneficiari

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Paraules clau: cal que esmenteu cinc conceptes que defineixin el contingut de la vostra memòria.
emotion, attention, multisensory processing, retinal spikes, fMRI

Data de presentació de la justificació
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Nom i cognoms i signatura
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Vist i plau del/de la responsable de la
sol·licitud

Resum del projecte: cal adjuntar dos resums del document, l'un en anglès i l'altre en la llengua del document, on s'esmenti la durada de l'acció



Resum en la llengua del projecte (màxim 300 paraules)

(El resum es fa directament en anglès, per indicacions de la pròpia administració)

Resum en anglès (màxim 300 paraules)

Abundant evidence suggests that negative emotional stimuli are prioritized in the perceptual systems, eliciting enhanced neural responses in early sensory regions as compared with neutral information. This facilitated detection is generally paralleled by larger neural responses in early sensory areas, relative to the processing of neutral information. In this sense, the amygdala and other limbic regions, such as the orbitofrontal cortex, may play a critical role by sending modulatory projections onto the sensory cortices via direct or indirect feedback. The present project aimed at investigating two important issues regarding these mechanisms of emotional attention, by means of functional magnetic resonance imaging. In Study I, we examined the modulatory effects of visual emotion signals on the processing of task-irrelevant visual, auditory, and somatosensory input, that is, the intramodal and crossmodal effects of emotional attention. We observed that brain responses to auditory and tactile stimulation were enhanced during the processing of visual emotional stimuli, as compared to neutral, in bilateral primary auditory and somatosensory cortices, respectively. However, brain responses to visual task-irrelevant stimulation were diminished in left primary and secondary visual cortices in the same conditions. The results also suggested the existence of a multimodal network associated with emotional attention, presumably involving mediofrontal, temporal and orbitofrontal regions.

Resum en anglès (màxim 300 paraules) – continuació –.

Finally, Study II examined the different brain responses along the low-level visual pathways and limbic regions, as a function of the number of retinal spikes during visual emotional processing. The experiment used stimuli resulting from an algorithm that simulates how the visual system perceives a visual input after a given number of retinal spikes. The results validated the visual model in human subjects and suggested differential emotional responses in the amygdala and visual regions as a function of spike-levels. A list of publications resulting from work in the host laboratory is included in the report.

2.- Memòria del treball (informe científic sense limitació de paraules). Pot incloure altres fitxers de qualsevol mena, no més grans de 10 MB cadascun d'ells.

GENERAL INTRODUCTION

Over the past century, a large body of evidence has shown that emotional stimuli, such as faces with an emotional expressions, pictures with emotional content, or sounds with emotional displays, have a status of priority in the processing systems, eliciting stronger and faster attention capture than non-emotional stimuli (e.g., Öhman et al., 2001; Carretié et al., 2004; Anderson, 2005; Vuilleumier, 2005; see Domínguez-Borràs & Vuilleumier, 2012 and Domínguez-Borràs et al., 2012 for a review). Such a mechanism of attentional bias arises from the limited processing capacity of sensory systems, while attending to adaptive and evolutionary advantages, that is, the obvious necessity of rapidly reacting to crucial information for survival. This effect, in addition, may be especially pronounced with negative or threat-related stimuli (Lang et al., 2000). This facilitated detection of emotional stimuli observed in behavioral studies is generally paralleled by larger neural responses in sensory areas, relative to the processing of neutral information. This enhancement has been observed in early sensory cortices, including the primary visual area in the occipital lobe (V1; Lang et al., 1998; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Pourtois et al., 2004), or the primary auditory cortex in the temporal lobe (Ethofer et al., 2012; Grandjean et al., 2005), as well as in higher level cortical regions associated with object recognition (Keil et al., 2011; Morris et al., 1998; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005). On the other hand, studies using time-resolved techniques, such as event-related brain potentials (ERPs) and

magneto-encephalography (MEG) in humans, give support to the idea that an emotional modulation of perception may take place at early stages of stimulus processing. Early components associated with visual attention ~100–200 ms after stimulus onset show increased amplitudes to emotional faces, emotional scenes, or fear-conditioned stimuli (Dolan, Heinze, Hurlmann, & Hinrichs, 2006; Pourtois et al., 2004). Less frequent modulations are reported for components associated with object-categorization processes, such as the occipitotemporal N170, which may code for face features or configuration more than emotion information. Accordingly, direct intracranial recordings of fusiform responses to faces have shown an emotional enhancement starting only after the N170 peak (Pourtois, Spinelli, Seeck, & Vuilleumier, 2010a). In some cases, even earlier increases may occur for the C1 (a component arising ~80–90 ms poststimulus and presumably generated in the primary visual cortex) when fearful or threat-conditioned faces are presented in the peripheral visual field (Pourtois et al., 2004; Stolarova et al., 2006). In the auditory domain, fearful vocalizations or sounds conditioned with pleasant and unpleasant scenes may also elicit larger ERPs relative to neutral stimuli already ~150 ms after onset. Finally, later modulations of brain responses are also frequent (i.e., 300–400 ms), including larger P3 or sustained late positive potentials (LPPs; e.g. Sabatinelli, Lang, Keil, & Bradley, 2007), which might reflect more elaborate affective and cognitive evaluations, as well as memory. Moreover, the face-responsive fusiform cortex may show sustained activation to fearful expressions (> 700–800 s), clearly outlasting stimulus duration itself (Pourtois et al., 2010a).

Emotional processing does not elicit a general boosting of visual or auditory processing, but rather modulates cortical areas that are selectively responsive to the stimulus type (Peelen et al., 2007). This is similar to the effects typically produced by endogenous or exogenous attention mechanisms mediated by frontoparietal systems, leading to more robust neural representation of attentionally relevant stimuli, with a remarkable category specificity (Driver, 2001). However, emotional and attentional mechanisms seem relatively independent, involving partly distinct neural circuits, and showing additive effects to each other (Amting et al., 2010; Brosch, Pourtois, Sander, & Vuilleumier, 2011; Keil, Moratti, Sabatinelli, Bradley, & Lang, 2005; Lucas & Vuilleumier, 2008). Emotional biases cannot be simply designated as top-down or bottom-up, because they share components with both attentional systems. These biases might rather be understood as reflecting specialized neural mechanisms for *emotional attention* (Vuilleumier, 2005) or *motivated attention* (Lang et al., 1998), contributing to select sensory information in parallel with other top-down and bottom-up attentional mechanisms.

Thus, perception can be modulated by multiple sources simultaneously, including not only endogenous, exogenous, or object-based attention but also emotional feedback signals. In this vein, converging evidence from anatomy, imaging, and neuropsychology suggests that, the amygdala, a nuclear complex located in the medial temporal lobe, may play an important role in this modulatory effect (see Vuilleumier, 2005, Pourtois et al., 2012; Domínguez-Borràs

& Vuilleumier, 2012). In the visual modality, one hypothesis suggests that rudimentary visual signals might be extracted through subcortical-visual (perhaps magnocellular) pathways including the superior colliculus, and pulvinar nucleus of the thalamus, then projecting directly to the amygdala (Tamietto & de Gelder, 2010). This subcortical route was postulated based on residual emotional processing in patients with *blindsight* after destruction of the occipital cortex (Tamietto & de Gelder, 2010) and on preserved fear conditioning in animals without the sensory cortex (Romanski & LeDoux, 1992). Direct connections between visual pulvinar and amygdala remain questionable in humans (Pessoa & Adolphs, 2010), but exist in lower primates (Day-Brown, Wei, Chomsung, Petry, & Bickford, 2010). Other subcortical visual pathways from the brainstem to the amygdala were also reported in rodents (although unknown in humans; Usunoff, Itzev, Rolfs, Schmitt, & Wree, 2006). Alternatively, blindsight may depend on direct inputs from the lateral geniculate nucleus to extrastriate temporal cortex (Schmid et al., 2010) or from the pulvinar to fusiform in humans (Clarke, Riahi-Arya, Tardif, Eskenasy, & Probst, 1999), providing another route bypassing early occipital cortex, potentially projecting to the amygdala and other brain regions. This subcortical route would correspond to a more unconscious, rather automatic, route of emotional attention. However, emotional attention in healthy subjects may also be achieved through cortico-cortical pathways, through which unconscious and conscious or attentive processing may converge, yet with different latencies, oscillatory frequencies, or amplitudes (Pourtois et al., 2012; Vuilleumier, 2005). The orbitofrontal cortex (OFC) may also be critically involved in this modulatory effect (see Domínguez-Borràs & Vuilleumier, 2012). It is plausible that both the amygdala and other limbic regions involved in affective appraisal, such as the OFC, might activate at early latencies through an initial volley of feedforward inputs (Vuilleumier, 2005), before or in parallel with the recruitment of exogenous or endogenous attentional systems. Thus, the early activation of the amygdala (or other areas such as the OFC) would then modulate sensory cortices via direct feedback (Amaral et al., 2003; Vuilleumier, 2005) or indirect projections to the dorsal attention system in prefrontal and parietal areas (Vuilleumier, 2005). In any case, the effects and neural substrates of emotional attention on perception are still poorly understood.

AIMS OF THE PROJECT

1. To explore the intramodal, crossmodal and multimodal effects of visual emotional attention on auditory, visual and tactile processing (Study I).
2. To examine the relative timing, in terms of retinal spikes, of visual and limbic regions during emotional processing, defining their role in the neural networks subserving visual *emotional attention* (Study II).

STUDY I

Introduction

We have seen that sensory information is differently processed when it is affectively loaded in relation to when it is neutral, that is, that the emotional load of a given stimulus modulates its subsequent processing. Of recent interest, on the other hand, is the question of whether the processing of negative emotional stimuli extends this modulatory effect to the whole perceptual field, and even to other sensory pathways. In this sense, psychophysiological studies yielded that visualizing aversive pictures intensifies blink reflexes towards sudden auditory stimuli (e.g. Bradley et al., 2006). Recent experiments, in addition, showed that novel environmental sounds elicited larger novelty P3, a positive ERP associated with the evaluation of these novel events, while subjects responded to emotionally negative pictures in relation to when responding to the neutral ones (e.g. Domínguez-Borràs et al., 2008a, b). This modulation was observed as early as 200 ms after the occurrence of the sounds (Domínguez-Borràs et al., 2008b), increasing phase-synchronization of EEG gamma-band oscillations even at 100 ms after sound onset (Garcia-Garcia et al., 2009). Likewise, hemodynamic responses in superior temporal gyri showed enhanced activation to these novel events when responding to negative emotional faces (Domínguez-Borràs, 2009). Similarly, auditory cues containing emotional prosody enhanced N1-responses to visual targets, although possibly through facilitated spatial attention to either side of the screen (Brosch et al., 2008). All these results suggest that unexpected auditory events, irrelevant in neutral environmental conditions *per se*, may have become more available to the attentional set in a threatening environment, providing thus, if necessary, useful information for survival.

However, the underlying neural circuitry originating this modulatory effect is still unknown. One remaining question is, for instance, whether emotion modulates the processing of task-irrelevant information specifically in primary sensory cortices. Examining this aspect would help us to determine whether the processing of task-irrelevant information is modulated at the very primary stage of cortical processing or, on the contrary, it occurs on later phases. Recent unpublished results, for instance, showed that visual emotional inputs enhanced the processing of complex tones at N1 stage (thus, plausibly in primary sensory cortices, as corroborated with subsequent dipole modelling), in relation to the visual neutral ones, when these sounds were presented 100-150ms after picture onset (Selinger, L., Domínguez-Borràs, J., Escera, C., in preparation). A second question would be whether this modulation is a real multisensory effect. That is, if negative emotional processing may be able to modulate the processing of other stimuli that occur concomitantly, regardless of the sensory modality through which they are presented. If so, it should extend its effects to auditory, visual and somatosensory stimuli. Olfaction and taste, although robustly connected to the limbic system (e.g. Buck, 2000), should be considered differently due to the fact that their underlying

circuitry is phylogenetically more primitive (Buck, 2000). Finally, a third question would be if the subcortical pathways originating this modulatory effect on concomitant stimuli are similar to those enhancing activations for direct emotional processing (see General Introduction). Given, for instance, the connections between the amygdala and the visual (Freese & Amaral, 2005), auditory (LeDoux, 2000) and somatosensory pathways (Friedman et al., 1986), it is therefore plausible that, after a short stimulation by the visual emotional input, regions involved in emotional attention would potentiate the excitability, either directly or indirectly, of these sensory areas. Another possible model would give rise to direct modulation of multisensory integration circuits.

The present study aimed at investigating the modulatory effects of visual emotion on the processing of auditory, visual and somatosensory task-irrelevant stimuli at hemodynamic levels in humans.

Methods

Subjects

Nineteen subjects (Mean age: 22.21; StDev: 4.10), right-handed, with no neurological or psychiatric history, normal hearing, normal or corrected-to-normal vision and normal somatosensory processing, participated in the present study.

Stimuli

Visual task-relevant stimuli were 26 neutral and 26 fearful faces from the NimStim database (Tottenham et al., 2009) and the Karolinska Directed Emotional Faces set (Lundqvist, D., Flykt, A., Öhman, A. -1998. Department of Neurosciences, Karolinska Hospital, Stockholm, Sweden). All pictures were of similar size and luminance.

Auditory task-irrelevant stimuli were a complex tone, presented binaurally, consisting of a fundamental frequency of 500 Hz and two harmonics of 1000 Hz, and 1500 Hz. The amplitude of every subsequent harmonic tone was decreased in a scale of 50% of the intensity of the fundamental tone. The volume was manually set to 40dB sensation level for each individual subject. Visual task-irrelevant stimuli were two flickering checkerboards presented on each side of the screen (vertical size: 150; horizontal size: 150; 10 cycles/100pixels). Finally, tactile task-irrelevant stimuli consisted of a static single tap, presented to both lower cheeks with an MR-compatible pneumatic plastic cylinder, especially developed for the study. All task-irrelevant stimuli were presented with a duration of 100 ms.

Task, conditions and procedure

Faces (task-relevant stimuli) appeared in the middle of the screen for 400 ms. Then, one task-irrelevant stimulus appeared, which followed the faces by 125 ± 25 ms, according to the

"optimal window" established in previous unpublished results (Selinger et al., in preparation). Thus, trials could consist of a neutral face with a task-irrelevant auditory (NEU-Aud condition, $n=26$), visual (NEU-Vis condition, $n=26$) or tactile (NEU-Touch condition, $n=26$) stimulus, of a fearful face with a task-irrelevant auditory (NEG-Aud condition, $n=26$), visual (NEG-Vis condition, $n=26$) or tactile (NEG-Touch condition, $n=26$) stimulus, of a neutral face alone (NEU-Alone condition, $n=78$) or of a negative face alone (NEG-Alone condition, $n=78$), being the two latter conditions the experimental controls. The trial length ranged from 3600 to 4400 ms (mean 4000 ± 400 ms). A unique sequence was designed (with counterbalanced order across subjects) alternating the emotional conditions (NEU or NEG) in pseudorandomized blocks of different lengths, where the shortest emotional block lasted 10.5-seconds. Finally, subjects had to respond whether the face corresponded to a male or a female by pressing a response button with their right hand (buttons counterbalanced across subjects), while ignoring the task-irrelevant stimuli.

Scan parameters

MRI data were acquired on a 3T whole body MRI scanner (Trio TIM, Siemens, Germany), using a 12-channel head coil. Structural images were acquired with a T1-weighted 3D MPRAGE sequence (TR/TI/TE=1900/900/2.27ms, flip angle = 9 degrees, voxel dimensions: 1 mm isotropic, $256 \times 256 \times 192$ voxel). Functional images were obtained using a susceptibility weighted EPI sequence, optimized for blood oxygenation level dependency (BOLD) contrast. The EPI sequence comprised 36 slices (TR/TE = 2100/30 ms, flip angle = 80 degrees, PAT factor = 2, 64×64 pixel, 3.2×3.2 mm, 3.2 mm slice thickness, 20% slice gap), with non-interleaved sequential descending acquisitions. Functional images were slice time corrected, realigned, normalized spatially to the Montreal Neurological Institute (MNI) template and smoothed with an 8-mm FWHM gaussian kernel using SPM8 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK, <http://www.fil.ion.uncl.ac.uk/spm>).

Peripheral measures

Indirect measures of arousal consisted of pupil diameter (EyeTrac 6, Applied Science Laboratories, USA).

Analysis

Only those trials with a correct subject behavioral response were analyzed. At the first level, 9 event types were modeled, referred to each experimental condition (8) and 1 for trials with errors and 6 additional regressors referred to the movement parameters, which would be regressed out later. Data were high-pass filtered (1/128 Hz), corrected for intrinsic autocorrelations, and convolved with a standard HRF. Second-level analysis was performed on single-subject statistical parametric maps, which served as random effects. Three

contrasts of interest were defined, by means of voxel-referred t-tests, to compare BOLD signal for the following conditions: $[(\text{NEG-Aud} > \text{NEG-Alone}) > (\text{NEU-Aud} > \text{NEU-Alone})]$ as "emotional enhancement of auditory processing", $[(\text{NEG-Vis} > \text{NEG-Alone}) > (\text{NEU-Vis} > \text{NEU-Alone})]$ as "emotional enhancement of visual processing" and $[(\text{NEG-Touch} > \text{NEG-Alone}) > (\text{NEU-Touch} > \text{NEU-Alone})]$ as "emotional enhancement of somatosensory processing". Furthermore, emotional enhancement of visual processing was replaced by the opposite contrast, due to the absence of surviving voxels in the first one: $[(\text{NEG-Vis} > \text{NEG-Alone}) < (\text{NEU-Vis} > \text{NEU-Alone})]$, as "emotional suppression of visual processing". Moreover, subsequent ROI analyses were carried out using anatomical masks from the Anatomy toolbox (Eickhoff et al., 2005) and "WFU Pickatlas" (Maldjian et al., 2003), were only voxels surviving a p-value threshold of 0.05 (FWE-corrected) were considered significant. In a subsequent analysis, values of pupil diameter (accounting for arousal), as well as time values (accounting for habituation effects), were used as parametric modulators of every condition regressor in the General Linear Model. Finally, a conjunction analysis of all three contrasts of interest was performed, as well as Psychophysiological Interactions (PPI) using the peak of activation for each contrast of interest as seed region.

Results

As seen in Figure 1, brain responses to task-irrelevant stimuli were isolated from those to the faces, by contrasting each Aud/Vis/Touch-condition to the corresponding Face Alone condition (e.g. $\text{NEU-Aud} > \text{NEU-Alone}$, $\text{NEG-Aud} > \text{NEG-Alone}$, see Methods). As expected, activations associated to the auditory, visual and somatosensory task-irrelevant stimuli were observed in corresponding primary and secondary auditory, visual and somatosensory regions. Furthermore, those sensory-specific activations processed during the presentation of an emotional face (NEG-Aud , NEG-Vis and NEG-Touch , with NEG-Alone contrasted out) were compared to those during the presentation of a neutral face (NEU-Aud , NEU-Vis and NEU-Touch , with NEU-Alone contrasted out). In this sense, hemodynamic responses associated to the NEG-Aud condition were stronger than those for the Aud-NEU condition in bilateral primary auditory cortices, as well as left area of Wernicke (Fig. 2), indicating that the processing of task irrelevant sounds was enhanced during the processing of fearful faces, as compared to neutral. This effect was more prominent during the beginning of the experimental session, fading progressively over time, as it was only evident when accounting for time habituation effects. On the other hand, brain responses in the NEG-Touch condition were stronger than those for the Touch-NEU condition in bilateral primary (SI) and secondary (SII) somatosensory cortices (Fig. 3), indicating that the processing of task irrelevant touch stimulation was enhanced during the processing of fearful faces, as compared to neutral. However, brain responses in the NEG-Vis condition were indeed weaker than those for the NEU-Vis condition in bilateral primary and secondary (V1/V2) visual cortices (Fig. 4),

indicating that the processing of task irrelevant visual stimulation was suppressed during the processing of fearful faces, as compared to neutral.

Interestingly, conjunction analysis across all three (Aud, Vis and Touch) contrasts of interest revealed bilateral inferofrontal (bilateral Rolandic operculum and bilateral frontal inferior operculum) as well as left insula, associated with these attentional modulations by emotion. Subsequent PPIs using left and right Rolandic operculum as seed regions (i.e. those showing the peak values in the conjunction analysis) yielded a common modulatory network covarying for all three sensory modalities, which includes right middle frontal regions and right superior temporal gyrus (with the left hemisphere seed), and right middle frontal regions (with the right hemisphere seed). Finally, when pupil size was introduced in the model for conducting the same conjunction analysis of the three contrasts of interest, as it is a reliable index of arousal (Sterpenich et al., 2009; see Kreibig, 2010 for a review), an activation was observed in left orbitofrontal cortex.

Conclusions

The present results provide an interesting insight on how emotional attention modulates perception and attention. On one hand, they replicate the previous studies showing that a context of visual emotion modulates the processing of concomitant sounds (Domínguez-Borràs et al., 2008a,b, 2009), while extending the conclusions towards other sensory modalities. In fact, the results suggest that emotional processing modulates perception both within and across sensory pathways, albeit with a different impact as a function of the intra- or cross-modality relationship between stimuli. Thus, emotional processing enhances the perception of concomitant stimuli when these are crossmodal (e.g. visual emotion vs auditory/tactile concomitant stimulus), but suppresses the perception of those stimuli coming from the same sensory modality as the emotional stimulus (e.g. visual emotion vs visual concomitant stimulus). The latter effect is likely to reflect a mechanism of sensory competition between the emotional and the task-irrelevant stimulus (e.g. Schwartz et al., 2005), in favor of the emotional one. Furthermore, the results demonstrate that emotion modulates the processing of task-irrelevant information specifically in primary and secondary sensory cortices. Thus, the processing of task-irrelevant information is modulated at the very primary stage of cortical processing. Finally, the present results also point to the existence of a multisensory network associated with emotional attention in the human brain, presumably involving mediofrontal, temporal and orbitofrontal regions, the latter highly related to mechanisms of arousal (see Domínguez-Borràs & Vuilleumier, 2012).

STUDY II

Introduction

Regarding the neural networks underlying emotional processing, commented in the General Introduction, there is still much controversy around the latency of the responses within the limbic system, as well as in cortical sensory areas, during emotional processing in the visual domain (see Pessoa & Adolphs, 2010). For instance, the latency of amygdala responses to emotional cues remains poorly known. Differential amygdala activations to emotional faces have been reported around 40–140 ms poststimulus onset in humans with MEG (Luo et al., 2010), but around 140 ms (Pourtois et al., 2010b) or 200 ms poststimulus onset with intracranial recordings (e.g., Krolak-Salmon et al., 2004). These effects may thus arise just before, or in parallel with, the neural signature of stimulus identification in the cortex. Early activations in the orbitofrontal cortex have also been reported around 120 ms after onset, using intracranial (Kawasaki et al., 2001) and scalp recordings (Pourtois et al., 2005; Pourtois, et al., 2004). Furthermore, intracranial recordings revealed similar amygdala responses up to 140 ms after onset when fearful faces are presented at attended or unattended locations, but a later and prolonged response after 600 ms that is enhanced by overt attention to faces. Scalp recordings using the same task also found an early emotional effect around 100 ms over frontal sites, but at top-down attentional effects starting around 200 ms (Holmes et al., 2003). Therefore, it is plausible that both the amygdala and other limbic regions involved in affective appraisal, such as the OFC, might activate at early latencies through an initial volley of feedforward inputs (Vuilleumier, 2005), before or in parallel with the recruitment of exogenous or endogenous attentional systems (see Domínguez-Borràs & Vuilleumier, 2012).

In this sense, more work is needed to clarify the timing of emotion and attention effects in different brain regions, and to test the causality of interactions between them. Some of the reasons for the current controversy are the technical difficulties to properly localize and register, for instance, responses of the amygdala and other subcortical nuclei with virtually all main techniques used in humans, such as electroencephalography (EEG), magnetoencephalography (MEG; in terms of proper localization), functional magnetic resonance imaging (fMRI; in terms of timing) and even intra-cranial recordings (in terms of interpretation of the results). Given these factors, indirect timing measures, such as simply manipulating the nature of the stimuli used, combined with neuroimaging and electrophysiological techniques that provide good spatial and timing resolution, respectively, may become very helpful. The aims of the present study were to examine, with fMRI and behavioural measures, the variation of responses, linear or not, of different brain regions along the low-level visual pathways and limbic regions, such as the amygdala, as a function of the amount of spikes occurring in the retina during visual emotional processing. The experiment followed Van Rullen and Thorpe's model of temporal spike coding in the low-level visual system (e.g. VanRullen & Thorpe, 2001; Thorpe et al., 2001). Thorpe's group

developed an algorithm that simulates how the visual system perceives a visual input after a given amount of spikes in different processing stages such as in the retina (Perrinet et al., 2004). We used the images generated with this algorithm in order to, on one hand, validate the visual model in human subjects, and, on the other hand, address the abovementioned questions about emotion.

Methods

Subjects

Sixteen subjects (8 males; Mean age 26.06; StDev: 5.07), right-handed, with no neurological or psychiatric history, normal hearing, normal or corrected-to-normal participated in the present study.

Stimuli

Visual task-relevant stimuli were 25 neutral and 25 fearful faces; all in grayscale, from the NimStim database (Tottenham et al., 2009) and the Karolinska Directed Emotional Faces set (Lundqvist, D., Flykt, A., Öhman, A. -1998. Department of Neurosciences, Karolinska Hospital, Stockholm, Sweden). All pictures were of similar size and luminance (within each spike level). From these stimuli, a set of images was created simulating the outputs of 8 different degradations (i.e. "spike levels") according to how every image would be perceived by the visual system after 50, 100, 500, 1000, 5000, 10000, 50000 and 100000 retinal spikes, chosen after preliminary piloting.

Task, conditions and procedure

Faces (task-relevant stimuli) appeared in the middle of the screen for 200 ms. Trials could consist of a neutral face with a resolution of 50 retinal spikes (Face50_NEU condition), 100, (Face100_NEU condition), 500 (Face500_NEU condition), 1000 (Face1000_NEU condition), 5000 (Face5000_NEU condition), 10000 (Face10000_NEU condition), 50000 (Face50000_NEU condition) and 100000 (Face100000_NEU condition), or a fearful face with a resolution of 50 retinal spikes (Face50_NEG condition), 100, (Face100_NEG condition), 500 (Face500_NEG condition), 1000 (Face1000_NEG condition), 5000 (Face5000_NEG condition), 10000 (Face10000_NEG condition), 50000 (Face50000_NEG condition) and 100000 (Face100000_NEG condition). Total trial duration was of 3500 ± 800 ms. A sequence was designed (with counterbalanced order across subjects) alternating the emotional conditions (NEU or NEG) randomly. Subjects had to respond whether the face corresponded to a male or a female, or they were not sure, by pressing a response button with their right hand (all 3 buttons counterbalanced across subjects).

Scan parameters

MRI data were acquired on a 3T whole body MRI scanner (Trio TIM, Siemens, Germany), using a 12-channel head coil. Structural images were acquired with a T1-weighted 3D TR:

1900; Echo Time: 2.27; sequence voxel dimensions: 1 mm isotropic, in a 256 mm field of view). Functional images were obtained using a susceptibility weighted EPI sequence, optimized for blood oxygenation level dependency (BOLD) contrast. The EPI sequence comprised 40 slices (TR/TE = 2000/20 ms, flip angle = 80 degrees, base resolution: 64, 3.2 x 3.2 mm, 2.5 mm slice thickness, 0.8mm slice gap), with non-interleaved sequential descending acquisitions. Functional images were slice time corrected, realigned, normalized spatially to the Montreal Neurological Institute (MNI) template and smoothed with an 8-mm FWHM gaussian kernel using SPM8 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK, <http://www.fil.ion.uncl.ac.uk/spm>).

Analysis

Behavioral responses (Response Time –RT, Hit Rate –HR, Error Rate –ER, and Omissions). At the first level, 22 or 14 event types were modeled in 2 different analyses: 16 or 8 (Spike Level conditions pooled into half the original amount) referred to each experimental condition, respectively, and 6 additional regressors referred to the movement parameters, which would be regressed out later. Data were high-pass filtered (1/128 Hz), corrected for intrinsic autocorrelations, and convolved with a standard HRF. Second-level analysis was performed on single-subject statistical parametric maps, which served as random effects. Contrasts of interest were “Face visibility”, based on the behavioral results (all Spike Levels from 5000 onwards > all Spike Levels from 50 to 1000), “Emotional effect” (all NEG Spike Levels > all NEU Spike Levels), “Emotional effect in INvisible faces” (all NEG conditions for Spike Level 50 to 1000 > all NEU conditions for Spike Level 50 to 1000) and “Emotional effect in VISIBLE faces” (all NEG conditions for Spike Level 5000 to 100000 > all NEU conditions for Spike Level 5000 to 100000). An additional Full Factorial analysis was performed, with the factors Emotion (x2) and Spike Level (x8 or x4, respectively). ROI analyses were carried out using anatomical masks from the Anatomy toolbox (Eickhoff et al., 2005) and “WFU Pickatlas” (Maldjian et al., 2003), were only voxels surviving a p-value threshold of 0.05 (FWE-corrected) were considered significant.

Results and preliminary conclusions

Subjects responded faster as the Spike Level increased (Spikes: $F(7,63) = 19,884$; $p = 0.000002$). This effect was more pronounced for the emotional faces than the neutral ones (Emotion x Spikes: $F(7,63) = 3,759$; $p = 0,014$). Subjects responded more accurately as the Spike Level increased (Spikes: $F(7,63) = 100,26$; $p = 0.000000000006$) and when responding to the emotional faces, in relation to the neutral ones (Emotion: $F(1,9) = 61$; $p = 0.00002$). Similarly, the amount of “Not Sure” responses decreased as the Spike Level increased (Spikes: $F(7,63) = 42,506$; $p = 0,000002$), being almost absent from the Spike Level 5000 onwards. Omissions were also affected by Emotion and Spike Level (Emotion: $F(1,9) = 30.480$; $p = 0.0004$; Spikes: $F(7,63) = 19,414$; $p = 0,00000003$; Emotion x Spikes: $6,429$; $p =$

0,002; Fig. 5). Preliminary analysis of BOLD responses show a main effect of Spike Levels in bilateral fusiform, bilateral inferior temporal gyrus, bilateral inferior occipital cortex and bilateral orbitofrontal cortex, suggesting a linear response of main visual and face processing regions as a function of retinal spikes (Fig. 6). Finally, a trend of Spike Level x Emotion effect was observed in right amygdala and left inferior temporal gyrus, suggesting that the modulation by emotional processing expected in visual and limbic regions (see General Introduction) varies as a function of the retinal Spikes (Fig. 7). Subsequent analyses of "Emotional effect in Invisible faces" (that is, from 50 to 1000 Spikes) and Emotional effect in Visible faces" (that is, from 5000 to 100000 Spikes) revealed no emotional modulation of visual or limbic regions in the Invisible faces, but a stronger response of right fusiform, right insula and left temporal pole for the fearful faces, as compared to those neutral. In this analysis, no differential amygdala responses were observed. The present results provide a preliminary validation of the model by Perrinet et al. (2004) in humans. Further analyses will examine the specific progression of these activations, by means of parametric designs, and will try to establish the amount of retinal spikes needed for both limbic and visual processing regions during emotional processing.

Publications written in the host laboratory

- Domínguez-Borràs, J., Saj, A., Armony, J. L., Vuilleumier, P. (2012). Emotional processing and its impact on unilateral neglect and extinction. *Neuropsychologia*, 50(6), 1054-1071.
- Domínguez-Borràs, J., Vuilleumier, P. Affective biases in attention and perception. In: P. Vuilleumier and J. L. Armony (Eds.), *Handbook of Human Affective Neuroscience*. Cambridge University Press (*in press*).

UNDER REVIEW

- Domínguez-Borràs, J., Armony, J.L., Maravita, A., Driver, J., Vuilleumier, P. Partial recovery of visual extinction by Pavlovian conditioning in a patient with hemispatial neglect (*under second review*).

IN PREPARATION

- Domínguez-Borràs, J., Rieger, S. W., Vuilleumier, P. Intra, crossmodal and multimodal effects of emotional attention (*in preparation*).

Presentations in conferences of work conducted in the host laboratory

- Domínguez-Borràs, J., Vuilleumier, P., Escera, C. Crossmodal effects of visual emotional stimuli on the processing of task-irrelevant sounds: electrophysiological and hemodynamic evidence. Invited participation in symposium. Psychologie und Gehirn, Heidelberg, Germany, 2011. Organizers: Deutsche Gesellschaft für Psychologie (DGP) and Deutsche Gesellschaft für Psychologie und ihre Anwendung (DGPA).
- Rieger, S. W., Domínguez-Borràs, J., Vuilleumier, P. An MRI compatible somatosensory stimulation device for the investigation of crossmodal effects of emotion on the processing of tactile, visual, and auditory input. Poster presentation. 28th Annual Scientific Meeting, Leipzig, Germany, 2011. Organizers: European Society for Magnetic Resonance in Medicine and Biology (ESMRMB).
- Domínguez-Borràs, J., Rieger, S. W., Vuilleumier, P. Effects of visual emotional events on the processing of simultaneous auditory, visual, and somatosensory input. Poster presentation. Alpine Brain Imaging Meeting (ABIM), Champéry, Switzerland, 2012. Organizers: Patrik Vuilleumier, Sophie Schwartz, Dimitri Van De Ville, Ray Dolan.
- Domínguez-Borràs, J., Rieger, S. W., Vuilleumier, P. Effects of visual emotional events on the processing of simultaneous auditory, visual, and somatosensory input (Best poster presentation award). Affective Sciences Annual Research Forum, 2012. Organizers: National Center of Competence in Research (NCCR) in Affective Sciences.
- Domínguez-Borràs, J., Rieger, S. W., Vuilleumier, P. Intramodal, crossmodal and multimodal effects of emotional attention. Poster presentation. 18th Annual Meeting of the Organization for Human Brain Mapping (OHBM), Beijing, China, 2012. Organizers: Organization for Human Brain Mapping (OHBM).
- "Emotional processing and attention as modulatory systems of perception". Symposium organization. 8^o Congreso de la Sociedad Española de Psicofisiología y Neurociencia Cognitiva y Afectiva (SEPNECA), Barcelona, Spain, 2012. Organizer: Sociedad Española de Psicofisiología y Neurociencia Cognitiva y Afectiva (SEPNECA).
- Domínguez-Borràs, J., Rieger, S. W., Vuilleumier, P. Effects of visual emotion on the processing of auditory, visual and somatosensory input. Oral communication. 8^o Congreso de la Sociedad Española de Psicofisiología y Neurociencia Cognitiva y Afectiva (SEPNECA), Barcelona, Spain, 2012. Organizer: Sociedad Española de Psicofisiología y Neurociencia Cognitiva y Afectiva (SEPNECA).

- Domínguez-Borràs, J., Rieger, S. W., Vuilleumier, P. Intramodal, crossmodal and multimodal effects of emotional attention. Poster presentation. 8th FENS Forum of Neuroscience, Barcelona, Spain, 2012. Organizer: Federation of European Neuroscience Societies.
- Domínguez-Borràs, J., Rieger, S. W., Vuilleumier, P. Intramodal, crossmodal and multimodal effects of emotional attention. Invited oral communication in symposium. 52nd Annual Meeting of the Society for Psychophysiological Research (SPR), New Orleans (Louisiana) USA, 2012. Organizer: Society for Psychophysiological Research (SPR).

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