Biological Psychology 92 (2013) 492–512

Contents lists available at SciVerse ScienceDirect

Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

Brain mechanisms for emotional influences on perception and attention: What is magic and what is not

Gilles Pourtois[a,*], Antonio Schettino[a], Patrik Vuilleumier[b,c]

[a] *Department of Experimental-Clinical and Health Psychology, Ghent University, Belgium*
[b] *Department of Neuroscience, University Medical Center, Geneva, Switzerland*
[c] *Swiss Center for Affective Sciences, University of Geneva, Switzerland*

ARTICLE INFO

Article history:
Received 31 August 2011
Accepted 13 February 2012
Available online 21 February 2012

Keywords:
Emotion
Attention
Perception
Amygdala
Gain control

ABSTRACT

The rapid and efficient selection of emotionally salient or goal-relevant stimuli in the environment is crucial for flexible and adaptive behaviors. Converging data from neuroscience and psychology have accrued during the last decade to identify brain systems involved in emotion processing, selective attention, and their interaction, which together act to extract the emotional or motivational value of sensory events and respond appropriately. An important hub in these systems is the amygdala, which may not only monitor the emotional value of stimuli, but also readily project to several other areas and send feedback to sensory pathways (including striate and extrastriate visual cortex). This system generates saliency signals that modulate perceptual, motor, as well as memory processes, and thus in turn regulate behavior appropriately. Here, we review our current views on the function and properties of these brain systems, with an emphasis on their involvement in the rapid and/or preferential processing of threat-relevant stimuli. We suggest that emotion signals may enhance processing efficiency and competitive strength of emotionally significant events through gain control mechanisms similar to those of other (e.g. endogenous) attentional systems, but mediated by distinct neural mechanisms in amygdala and interconnected prefrontal areas. Alterations in these brain mechanisms might be associated with psychopathological conditions, such as anxiety or phobia. We conclude that attention selection and awareness are determined by multiple attention gain control systems that may operate in parallel and use different sensory cues but act on a common perceptual pathway.

Contents

1. Introduction: on the varieties of attention selection

Perception and awareness do not only result from the mere stimulation of our senses by external stimuli but are potently governed by internal processes and states that select and organize sensory inputs for goal-oriented behavior. Thus, perceptual processing reflects a dynamic interplay between the environment and the observer, with conscious detection being determined by both “objective” and more “subjective” factors. Even when sleeping, we may be deaf to many ordinary sounds but the personal significance and familiarity of one’s own name will make it more salient so as to break through and wake us up (Portas et al., 2000).

---

* Corresponding author at: Department of Experimental-Clinical and Health Psychology, Ghent University, Henri Dunantlaan 2, 9000 Gent, Belgium.
Tel.: +32 9 264 9144.
E-mail address: gilles.pourtois@ugent.be (G. Pourtois).

0301-0511/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
doi:10.1016/j.biopsycho.2012.02.007

The modulation of perception by both attention and emotion illustrates a similar interplay between some (external) stimulus properties and (internal) brain readiness to respond. On the one hand, we are surrounded by an overwhelmingly rich environment and a continuously changing flow of information, including a mixture of ordinary and novel or motivationally significant events. On the other hand, the speed and extent of information processing in perceptual pathways are inherently limited, in the sense that not all sensory stimuli can equally be processed in parallel and reach consciousness (Posner et al., 1980; Marois and Ivanoff, 2005). Attention has evolved in order to deal with this dilemma and subsumes multiple neural processes contributing to select the most relevant or useful information (Kastner and Ungerleider, 2000; Driver and Vuilleumier, 2001).

Which information gains access to more elaborate processing and consciousness is determined by both bottom–up (stimulus-driven) and top–down (goal-driven) factors (Egeth and Yantis, 1997; Theeuwes, 1994; Serences et al., 2005). A task-irrelevant stimulus may be processed preferentially or involuntarily because it is novel, unexpected (temporarily or spatially), or distinctively deviating in terms of its physical features relative to other competing stimuli (i.e. bottom–up or exogenous capture; see Theeuwes, 1994; Ranganath and Rainer, 2003; Wolfe and Horowitz, 2004). Alternatively, a weak or hidden stimulus will be picked out from a cluttered scene and undergo a privileged mode of processing when it meets with current goals and expectations (i.e. top–down or endogenous effect; see Posner, 1980; Folk et al., 1992), while other simultaneous but irrelevant events will fail to be noticed (as exemplified by the change blindness phenomena; see Simons and Levin, 1997; Pourtois et al., 2006a). However, these attentional effects are neither mutually exclusive, nor operating as monolithic and fully independent processes. Although exogenous attention is typically reflexive, operating rapidly and without voluntary control (Posner et al., 1980; Hopfinger and West, 2006), it can be modulated by top–down factors related to expectations and task demands (Folk et al., 1992; Hopfinger and Ries, 2005). Moreover, even subliminal (and hence unseen) exogenous cues can capture spatial attention (Mulckhuyse and Theeuwes, 2010), but such effects may nevertheless be contingent on current task goals and readiness to respond to particular stimulus features (Ansorge et al., 2009). Similarly, endogenous attention is usually associated with voluntary and effortful control (Posner et al., 1980; Kastner and Ungerleider, 2000), and yet it can also be influenced by automatic and unconscious activation of goals (Moskowitz, 2002; Dijksterhuis and Aarts, 2010). At the neuro-anatomical level, these two attention mechanisms (exogenous and endogenous) involve partly distinct brain circuits, including frontal and parietal cortex as well as subcortical structures (such as pulvinar and superior colliculus) (Posner and Dehaene, 1994), but also show substantial overlap and functional interactions (e.g. Corbetta and Shulman, 2002; Chica et al., 2011).

Another situation where selective attention is guided by an interplay between stimulus features and perceptual readiness of sensory pathways is illustrated by object-based attention (Driver et al., 2001; Yantis and Serences, 2003), whereby information that belongs to the same object is grouped into a whole (e.g. due to common contour or surface) and is processed preferentially, effortlessly and holistically, as compared to the same information presented in distinct objects. Object-based effects do not arise because a single stimulus feature is made more salient at a perceptual level, but because it is embedded in a coherent gestalt that constrains the distribution of attention (Driver et al., 1992; Downing et al., 2001). These effects reflect perceptual abilities that tend to organize sensory inputs and guide their selection for attention and awareness due to the intrinsic functional properties and "wiring" of our brain, and they rely on specific neural processes that are distinct from the fronto-parietal systems controlling exogenous or endogenous attention (such as visual grouping or segmentation mechanisms within occipito-temporal cortex; see Humphreys et al., 2004; Vuilleumier et al., 2001b; McMains and Kastner, 2011).

In this review, we argue that emotion signals provide yet another source of biases on perceptual processing. Abundant research suggests that besides influences from these three classic attention mechanisms (i.e. endogenous, exogenous, and object-based attention), the rapid and efficient selection of sensory information for deeper perceptual analysis can also depend on its emotional or motivational value for the organism (Öhman, 2001; Compton, 2003; Vuilleumier, 2005; Bradley, 2009). Like object-based attention, these effects reflect not only the specific features of external stimuli, but also the influence of internal factors or some stored "knowledge" on perceptual processing.

A central question about these effects, however, concerns which brain mechanisms are responsible for the preferential selection of emotionally salient stimuli in the environment, and whether they partly or fully overlap with those processes mediating bottom–up or top–down attention as described above (Vuilleumier, 2005, 2009; Shackman et al., 2011). As we will review hereafter, emotional effects on attention appear to share more similarities with a bottom–up than top–down process, although empirical data suggest that they may actually be better understood in terms of a separate, specialized control system (see Figs. 1 and 4) that does not share all its functional and anatomical components with classical attention mechanisms (Lucas and Vuilleumier, 2008; Brosch et al., 2011; Vuilleumier, 2009). Moreover, just like recent models of attention have emphasized a competitive integration between top–down and bottom–up effects on both exogenous (reflexive) and endogenous (voluntary) attention during stimulus processing (McMains and Kastner, 2011), it is likely that the effects of emotionally relevant stimuli may also involve a balance between bottom–up and top–down processes, or that "exogenous" emotional responses also partly depend on "endogenous" emotional signals (e.g. due to particular states or traits of the individual; see Fox, 1993; Koster et al., 2005; Bishop, 2007; Rossi and Pourtois, 2011; Cornwell et al., 2011). Thus, rather than arguing about the dominance of one attention mechanism over another, or the primacy between emotion and attention on perception (Zajonc, 1984; Lazarus, 1984; Pessoa et al., 2002a), it seems more important to better define the exact functional properties and neural substrates of the various processes that work together in order to control perception, through a convergence of both bottom–up and top–down signals.

To underscore the existence of different sources of attention effects and highlight how emotion might contribute to bias (visual) perception via specific neural mechanisms, we propose a general framework that we describe here as a "Multiple Attention Gain Control" (MAGiC) model. A main premise of this model is that emotion signals can shape perception by amplification mechanisms that do not overlap with other (e.g. endogenous or voluntary) attentional processes. But despite their different neural sources, the different gain control mechanisms might operate on the same sensory pathways and thus interact with each other. In this model, we also propose that the amygdala might play a pivotal (though not exclusive) role in generating emotional biasing signals. These premises are supported by a wide range of data (from neurophysiology, imaging, as well as neuropsychology) and integrate these results to account for the dynamic interplay between perception, emotion and attention.

Importantly, in this framework, emotional stimuli are "magic" and could be seen as "special" only to the extent that they have the propensity to engage dedicated neuronal systems relative to neutral stimuli, which are in turn capable of rapidly influencing perceptual or attentional systems (or both), such that these stimuli may gain additional "weight" in the competition for awareness

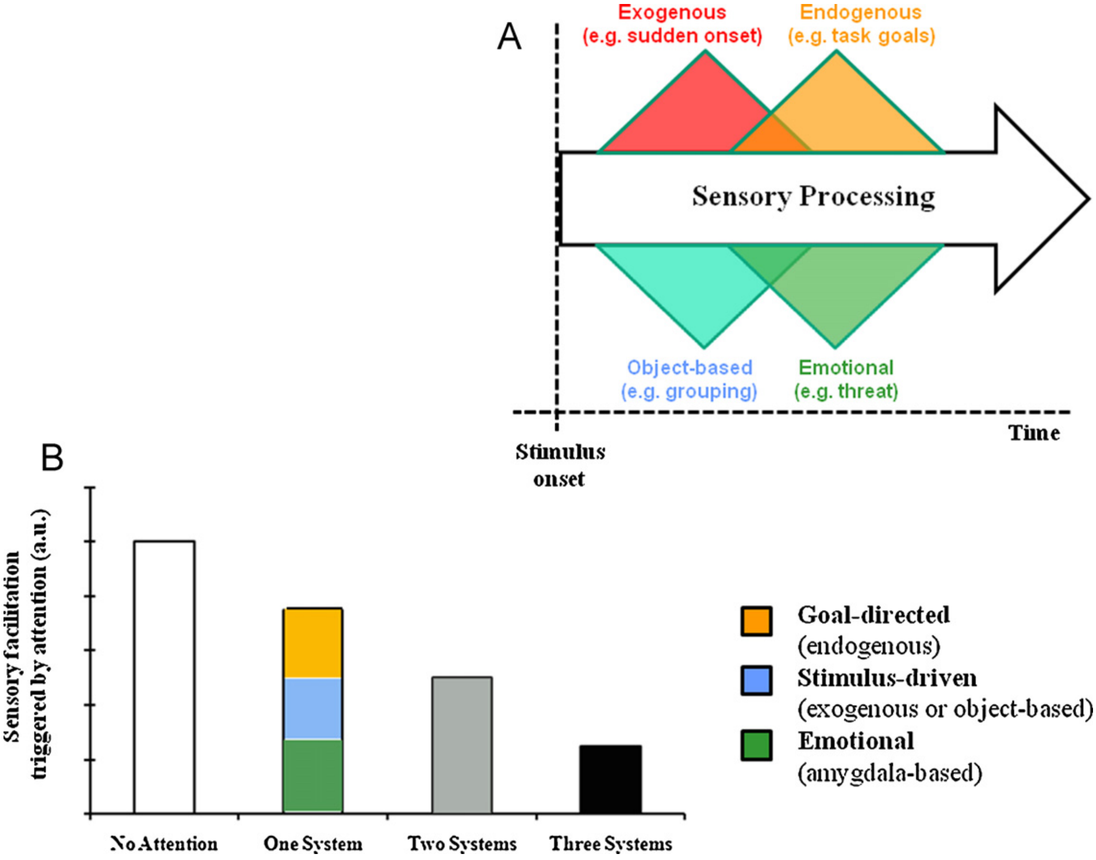

Fig. 1. Multiple brain systems are involved in gating perceptual processing, including endogenous, exogenous, object-based, and affective sources of biases. (A) These different systems can separately contribute to mechanisms of selection that govern attention and awareness, each driven by different sensory cues, mediated by distinct neural circuits with different time-course, but potentially acting on the same neural pathways (e.g. striate and extrastriate visual cortex) during partly overlapping time windows (e.g. P1 visual evoked potential). (B) According to this model, different task conditions may recruit each of these systems at different degrees and thus produce a graded facilitation of stimulus processing, possibly in an additive manner with a progressive gain as a function of the amount of modulation produced by each system (one, two or three), or instead in a competitive manner with an interference between different effects. In the schematic graph here, bars correspond to arbitrary units of “sensory responses” (referring either to brain activity in a specific region or behavioral effect, such as RT or accuracy). Depending on which systems (emotional, exogenous or endogenous) actually guide attention control (one, two, or three), sensory processing is facilitated, and the magnitude of sensory response is predicted by the number of systems engaged by the same stimulus, reflecting independent and additive contribution of each of the three kinds of biasing signals.

(Armony and Dolan, 2002; Pourtois et al., 2005b, 2006b). But this view does not imply that in order to spark off these effects, emotional stimuli must undergo a privileged route that neutral stimuli would not recruit. Whereas some neural responses and their subsequent impact on sensory processing might be unique to emotionally significant stimuli, their perceptual analysis and malleability to other attentional modulations is likely to be (at least partly) similar to emotionally neutral stimuli. However, to highlight that distinct (and potentially additive) attentional biases may govern the processing of emotional stimuli, it is useful to consider that these effects probably reflect specific mechanisms for “motivated attention” (Lang et al., 1992; Holland and Gallagher, 1999) or “emotional attention” (Vuilleumier, 2005). Below we present a general overview of the brain circuits and behavioral effects associated with these emotional influences on perception, as well as their relations to other attentional effects, and their modulations by various factors (Box 1).

2. Enhanced sensory processing for emotional stimuli

What is the hallmark of emotional attention effects in terms of brain activity and behavioral consequences? Three main functional properties are postulated. (i) First, the amplitude of neural responses to emotional relative to neutral stimuli is consistently enhanced in several areas along sensory pathways, including both specific (i.e. category-selective) and non-specific regions (i.e. early sensory cortex or fronto-parietal attention networks) (for recent meta-analytical evidence, see Lindquist et al., in press). This boosting is reminiscent of the typical gain control mechanism associated with endogenous or exogenous attention (Hillyard et al., 1998b), and thought to induce a more efficient mode of processing for emotionally salient stimuli. (ii) Second, the time-course of emotional effects suggests a distinctive spatio-temporal dynamic as compared with other attentional modulations (in fronto-parietal areas), with relatively early responses observed in some limbic regions, such as the amygdala (Krolak-Salmon et al., 2004; Luo et al., 2007, 2010; Pourtois et al., 2010b) or orbitofrontal cortex (Kawasaki et al., 2001), which might then act to gate sensory processing in distant regions at later latencies. (iii) Third, these emotional attention effects may occur in parallel to other gating effects mediated by fronto-parietal attention networks (see Amaral et al., 2003; Krolak-Salmon et al., 2001; Vuilleumier and Pourtois, 2007; Pourtois et al., 2010a,b; Rossi and Pourtois, in press), and thus be partly independent of (or even competing with) any concomitant modulation by the latter systems. Empirical evidence and theoretical interpretations for these three functional properties will be reviewed in detail separately, in this and the next two sections.

The amplification of sensory processing for specific objects or locations is considered as the major phenomenon underlying perceptual changes mediated by (bottom–up or top–down) attention mechanisms (Desimone and Duncan, 1995; Carrasco et al., 2006).

Box 1: Specificity of emotional attention brain mechanisms. How can emotional attention brain mechanisms be dissociated from brain systems involved in the control of non-emotional attention (either exogenous or endogenous)?

As described in the current review (see main text), emotional attention and amygdala-dependent circuits modulating perceptual processing have partly been dissociated using several different approaches. First, these effects can be pitted against one another (e.g. by manipulating independently attention and emotion) in behavioral tasks or neuroimaging experiments, although most previous studies concentrated on modulations of endogenous attention factors related to task goals (e.g. Vuilleumier et al., 2001a; Anderson et al., 2003; Keil et al., 2005) or perceptual load (Pessoa et al., 2002b). Fewer studies have compared emotional effects with those of exogenous attention (e.g. Pourtois et al., 2004; Brosch et al., 2011), which are known to depend on non-overlapping brain networks (Corbetta and Shulman, 2002). One recent study even manipulated three different factors (endogenous, exogenous and emotion) in the same task (Brosch et al., 2011; see also Keil et al., 2005), and found additive effects of each factor (see Fig. 1). In addition, dissociations between voluntary/endogenous attention and more "reflexive" effects of emotional attention have been found in studies of patients with focal brain lesions. For instance, patients with neglect or visual extinction suffer from selective damage to fronto-parietal networks controlling spatial (endogenous and/or exogenous) attention and show severe deficits in orienting their attention towards the contralesional side of space, but emotional biases in spatial orienting may still occur despite the overall neglect biases (Vuilleumier and Schwartz, 2001b; Fox, 2002; Grabowska et al., 2011), suggesting at least partly intact emotion influences despite the lesion. Conversely, impaired emotional effects have been observed in patients with selective damage to the amygdala (especially when bilateral), while spatial attention effects were preserved (Vuilleumier et al., 2004; Benuzzi et al., 2004; Anderson and Phelps, 2001; Rotshtein et al., 2010; but see Tsuchiya et al., 2009). These observations suggest that different sources of biases or gain control (emotional vs. endogenous vs. exogenous) might separately influence sensory processing and attention orienting during perception (Brosch et al., 2011; Keil et al., 2005), and that these systems might operate at partly different latencies following stimulus onset (see Pourtois et al., 2010b; Luo et al., 2010; Brosch et al., 2011; Ciesielski et al., 2010). Altogether, these results converge to support a multiple systems architecture responsible for attention control (Corbetta and Shulman, 2002; Vuilleumier, 2005), wherein the effects of emotional attention may flexibly add to those imposed by other bottom–up or top–down control processes. Ultimately, attention selection will thus result from the combined influences from all these neural sources (e.g. emotional vs. endogenous vs. exogenous), with different effects having different competitive strengths depending on the current task demands and affective context. Moreover, we suspect that even emotional attention might be further decomposed into more basic component processes, such as those mediated by the amygdala directly or those acting more indirectly via OFC, ACC, and cholinergic modulations.

Because of limitations in processing capacity, simultaneous stimuli cannot be fully analyzed in parallel and thus compete for processing resources in order to gain access to higher cognitive stages and awareness. Directing attention to the location or features of a given stimulus (through either endogenous or exogenous processes) will increase neural activity in brain regions representing this stimulus, at the expense of other concurrent stimuli. This phenomenon has been extensively demonstrated by neuronal recordings as well as imaging methods (EEG, PET, fMRI), and attributed to a gain control mechanism exerted by a fronto-parietal network (see Posner and Dehaene, 1994; Corbetta and Shulman, 2002) on lower-level sensory areas that can enhance the relevant/attended stimulus representation, while suppressing the irrelevant/unattended stimulus representation (see Fig. 4; Desimone and Duncan, 1995; Chelazzi et al., 1993; Hillyard et al., 1998b; Luck et al., 2000; Kastner and Ungerleider, 2000; Vuilleumier and Driver, 2007). Remarkably, a similar increase in the neural response of sensory cortical areas has commonly been observed for emotional compared to neutral stimuli across several imaging studies (PET or fMRI), in particular for signals of danger or threat-related stimuli (Lane et al., 1998; Lang et al., 1998; Vuilleumier et al., 2001a; Pessoa et al., 2002b; Surguladze et al., 2003; Sabatinelli et al., 2005). These effects may take place in the primary visual cortex (Lang et al., 1998; Halgren et al., 2000; Pourtois et al., 2004; Stolarova et al., 2006; Padmala and Pessoa, 2008) or involve category-selective regions of the inferotemporal cortex, including the fusiform face area (Morris et al., 1998; Vuilleumier et al., 2001a; Sabatinelli et al., 2005; Pourtois et al., 2010a) or the extrastriate body area (Peelen et al., 2007) depending on the nature of stimuli (e.g. facial or bodily expressions, respectively).

Whereas effects in primary visual cortex have been established by retinotopic mapping procedures in a few studies only (Padmala and Pessoa, 2008; Damaraju et al., 2009), there is abundant evidence for category-selective modulations. For example, fearful compared to neutral faces typically elicit an increased fMRI response in face-specific regions of fusiform cortex (Phan et al., 2002), even when the task does not require an explicit processing or judgment of facial expression (Morris et al., 1998; Critchley et al., 2000; Vuilleumier et al., 2001a), although explicit processing may further modulate these effects (producing either increases or decreases; e.g. see Gorno-Tempini et al., 2001). Likewise, the presentation of complex emotional scenes leads to greater fMRI responses in a widespread network of extrastriate visual regions (Sabatinelli et al., 2005, 2007, 2010). Similar results have been obtained in voice-selective areas of the lateral temporal cortex for emotionally salient auditory stimuli, such as angry or happy voices (Grandjean et al., 2005; Ethofer et al., 2012, 2009) as well as affective vocalisations or screams (Fecteau et al., 2007), suggesting that this boosting of sensory processing by emotion is not restricted to the visual modality/domain, but may reflect a more general property of emotional attention brain mechanisms. In analogy with the effect of attentional gain control, such increases in stimulus-specific activity have commonly been hypothesized to reflect increased processing efficiency for emotionally salient events (e.g. Vuilleumier, 2002, 2005), which may beneficially enhance attention towards them (Dennis and Chen, 2007; Bocanegra and Zeelenberg, 2009; Vuilleumier, 2009) and/or alter attention towards other concomitant stimuli in the same or different modalities (e.g. Zeelenberg and Bocanegra, 2010; Dominguez-Borras et al., 2008). Accordingly, greater responses to emotional faces correlate with better detection across different visual tasks (Vuilleumier et al., 2002; Lim et al., 2009; Kouider et al., 2009). Such increases in sensory processing may also play a role in the more efficient encoding and subsequent consolidation in memory of emotional events, although the link between these effects and subsequent changes in memory or plasticity induced by emotion has not been fully explored yet (LaBar and Cabeza, 2006; Buchanan, 2007) (Box 2).

A functional link between these neural responses and gains in perception or attention induced by emotion has also been supported at the behavioral level by several psychophysical studies, particularly in vision (Phelps et al., 2006; Bocanegra and Zeelenberg, 2009, 2011; Brosch et al., 2010). The brief presentation of a (task-irrelevant) upright fearful face (as opposed to either a neutral face or an inverted fearful face) enhances visual

Box 2: Methodology of emotional attention. How can the results from different research methodologies (different brain imaging techniques, clinical vs. healthy samples, animal models) be combined to develop and test models of emotional attention?

Many results showing activations of amygdala prior to or without attention/awareness have concluded that such effects reflect a rapid and effective response along sensory pathways that may be concomitant or even precede other effects imposed by voluntary attention control (e.g. Vuilleumier, 2005; Liddell et al., 2004; Williams et al., 2004; Tamietto and de Gelder, 2010). However, most of these findings were obtained using BOLD-fMRI (see Vuilleumier et al., 2001a, 2004; Bentley et al., 2003; Bishop et al., 2004a,b), whose temporal resolution is blurred due to the slow neuronal-hemodynamic coupling. Some techniques might improve these investigations, as shown by a recent fMRI study using a fast slice acquisition protocol (Sabatinelli et al., 2009) that confirmed a sequential two-stage activation from amygdala to fusiform cortex. Thus, this study could show that a differential emotional discrimination arose in the amygdala approximately 1 s before extrastriate occipital cortex (no differential effect was found in the striate cortex), consistent with a re-entrant organization of emotional inputs along visual pathways (Vuilleumier, 2005; Rudrauf et al., 2008; Sabatinelli et al., 2009). However, this timing difference is relatively long and somewhat hard to reconcile with responses latencies observed with other techniques (single neuron firing rate, EEG or MEG), and even fast fMRI might not have sufficient temporal resolution to establish a precise timing of information transmission. Yet, such delayed latencies are not inconsistent with intracranial recordings that found subliminal amygdala responses at 800 ms (Naccache et al., 2005) and sustained emotional modulations in fusiform cortex for more than 1 s (Pourtois et al., 2010a). Other imaging methods (such as arterial spin labeling or positron emission tomography) might also be usefully exploited to investigate changes in baseline activity that are potentially induced by anxiety, task difficulty, or higher error rates, but typically cancelled out in standard contrast with BOLD fMRI. Conversely, EEG and MEG studies can provide valuable information regarding the time-course of emotion-related and attention-related effects (Pourtois et al., 2004, 2005b; Keil et al., 2005; Luo et al., 2010; Rudrauf et al., 2008), but the anatomical sites of the effects remain difficult to establish with certainty even if sophisticated mathematical models can yield precious information on neural sources (e.g. Pourtois et al., 2005b). Therefore, a key method to obtain information about the exact location as well as timing of neural activity is provided by direct intracranial recordings in pharmaco-resistant epileptic patients during pre-surgery workup (Seeck et al., 1997; Halgren et al., 1994b,c; Allison et al., 1999). Recent work in such patients (see Kawasaki et al., 2001; Pourtois et al., 2010a,b) has clearly shown that some responses to emotional stimuli may start in amygdala and OFC at earlier or partly overlapping latencies than the category-selective and attention-dependent effects taking place in visual cortical areas, in keeping with the notion that sensory inputs might be broadcasted to different brain systems in parallel and then trigger distinct re-entrant signals modulating ongoing perceptual processes in the cortex. More research is needed to confirm and extend these findings, but these patients are rare due to medical advances in non-invasive diagnosis and unfortunately often suffer from an epilepsy disease that damages the medial-temporal lobe regions (e.g. amygdala and hippocampus), such that recordings are even rarer in cases with intact amygdalae (as in Pourtois et al., 2010b). More research is therefore needed in animal models where direct neuronal recordings can be combined with functional imaging, particularly in primates and for brain regions critically implicated in emotion attention (e.g. amygdala, OFC, pulvinar, and superior colliculus, as well as the various sensory cortices) (Armony et al., 1998; Gothard et al., 2007; Mosher et al., 2010). Overall, as in other neuroscience domains, a complete picture of emotion processing and its impact on attention will require a convergence of different methodologies.

sensitivity for the orientation of a subsequently presented low-spatial frequency stimulus (such as a Gabor patch; Phelps et al., 2006; Bocanegra and Zeelenberg, 2009). However, the same emotional cue can diminish orientation sensitivity for high-spatial frequency stimuli, suggesting that emotion may have a selective influence on low-level and early aspects of visual perception, and thus primarily modulates signal strength rather than causing a more general boosting effect (Bocanegra and Zeelenberg, 2009). Visual search (Eastwood et al., 2001; Öhman et al., 2001), attentional blink (Keil and Ihssen, 2004; Anderson, 2005), and spatial orienting tasks (Armony and Dolan, 2002; Pourtois et al., 2004) also tend to show better or faster detection for emotional (typically threat-related) targets, as compared with neutral stimuli. Crossmodal orienting effects have also been observed (e.g. visual orienting induced by emotional voices; see Brosch et al., 2009).

Interestingly, it is possible that similar attention gain control effects due to emotion could also explain other perceptual phenomena, including a distortion of time judgments by emotion. For instance, subjects usually tend to overestimate the actual duration of highly arousing pictures, including angry faces, relative to neutral pictures (Droit-Volet and Meck, 2007). Such effects might result from a stronger and quicker engagement of attention towards emotional stimuli (Shimojo et al., 1997). However, the functional significance of emotion-mediated increases in activity along different areas in sensory pathways as well as their exact impact on behavior still remain to be more fully explored.

3. Early vs. late modulations of neural response by emotion and attention

While fMRI and PET studies have pinpointed the anatomical loci of enhanced processing for emotional stimuli, converging results from electrophysiological methods such as EEG or MEG have also revealed distinctive increases in brain responses, and additionally shed light on the time-course of emotional attention effects. For example, enhanced event-related potentials (ERPs) are evoked by a variety of visual emotional stimuli, including negative emotional faces, aversively conditioned simple shapes or colors, as well as complex arousing emotional scenes (Halgren et al., 2000; Pizzagalli et al., 2002; Pourtois et al., 2004; Stolarova et al., 2006; Schupp et al., 2006; Sabatinelli et al., 2007). Depending on the task demands, and the actual stimuli used, these modulations by emotional signals can affect relatively early and/or late neural responses following stimulus onset and arise for distinct ERP components, including the classic C1, P1, or N1 visual responses, as well as the so-called EPN (Early Posterior Negativity) or LPP (Late Positive Potential) (Krolak-Salmon et al., 2001; Schupp et al., 2006; Sabatinelli et al., 2007; Olofsson et al., 2008; Wiens et al., 2010; Hajcak et al., this issue).

Remarkably, results showing increases in C1 amplitude for emotional stimuli suggest that, at least under some conditions, such emotional effects can affect the earliest cortical sweep of activity in the primary visual cortex (Jeffreys and Axford, 1972; Clark et al., 1995; Rossi and Pourtois, in press; see Rauss et al., 2011 for a recent review). The C1 arises around 80 ms post-stimulus onset and typically varies as a function of low-level visual characteristics, such as contrast or retinotopic position (Halgren et al., 2000), but the latter factors cannot explain emotional effects reported for faces (Pourtois et al., 2004; West et al., 2011), fear-conditioned gratings (Stolarova et al., 2006) or affective states (Rossi and Pourtois, in press). Recent ERP studies using source localization techniques have confirmed that the main generators of this early C1 component are located in the striate cortex (Pourtois et al., 2004, 2008; Rauss et al., 2009). Because the C1 component is thought to index the bottom–up retinotopic encoding of stimuli, and is typically impermeable to manipulations of endogenous or exogenous selective attention (see Martinez et al., 1999; Hillyard and Anllo-Vento, 1998; but see Kelly et al., 2008; Rauss et al., 2009), these findings suggest that emotion control systems may operate partly independently of and during an earlier time window than the more classical bottom–up or top–down attention mechanisms (see Fig. 1; see also Brosch et al., 2011). Moreover, these early emotion effects in primary visual cortex (triggered by the cue, i.e., a task-irrelevant fearful face) correlate with the degree of rapid spatial orienting towards the spatial location of emotional stimuli (as indexed by the amplitude of the P1 generated by the task-relevant target stimulus), suggesting a functional link between early neural increases in primary visual cortex and the subsequent deployment of spatial attention towards emotionally salient events (see Pourtois et al., 2004, 2005a).

A modulatory gain control of early visual ERPs produced by selective attention is typically observed for the subsequent P1 and/or N1 components (e.g. Heinze et al., 1990; Vogel and Luck, 2000), which reflect activity in extrastriate visual areas (Hillyard et al., 1998a; Di Russo et al., 2003; Martinez et al., 2001). Several studies have found that the extrastriate P1 response is also influenced by emotion (Batty and Taylor, 2003; Pourtois et al., 2004, 2005a; Rotshtein et al., 2010). Unlike the just preceding C1, the P1 component is mostly sensitive to the content or nature of the visual stimulus, more than its actual position in the visual field (see Martinez et al., 1999; Di Russo et al., 2003). It manifests as a bilateral occipito-temporal activity roughly 100–120 ms post visual stimulus onset, whose amplitude is typically increased for attended relative to unattended visual stimuli, especially in tasks requiring a rapid detection (as opposed to discrimination) of visual stimuli (see Hillyard and Anllo-Vento, 1998; Heinze et al., 1990; Pourtois et al., 2004). Similarly, larger amplitudes are evoked for negative/threat-related stimuli relative to neutral stimuli, including fearful faces, even when the attentional demands are balanced between conditions (see Batty and Taylor, 2003; Pourtois et al., 2005b). Increases in P1 amplitude are also observed for neutral stimuli whose location is cued by a preceding emotional stimulus, relative to a neutral cue (Pourtois et al., 2004, 2005b). Taken together, these emotional effects strongly resemble those of attention and suggest that both emotion and attention signals can eventually lead to more efficient sensory processing by acting at partly similar stages along the visual pathways (see Fig. 4; Desimone and Duncan, 1995; Hillyard et al., 1998b; Kastner and Ungerleider, 2000; Carrasco et al., 2006). Furthermore, the enhancement of P1 evoked by an emotional face has also been found to predict the magnitude of covert expression mimicry produced by the viewer (as indexed by facial EMG; Achaibou et al., 2008), a result indicating that this early perceptual enhancement might also contribute to the recognition of emotional expressions and influence motor behavior.

While abundant research has been conducted using emotional face stimuli, similar effects have been observed with other visual stimuli (see Sabatinelli et al., 2007 for complex visual scenes; Flaisch et al., 2009 for emotional gestures; Kissler et al., 2007 for emotional words) or different modalities (Brockelmann et al., 2011). Emotional effects evoked by faces are usually stronger and more resistant to other modulations by task demands than non-face stimuli (Rellecke et al., 2011). In addition, due to the complexity of emotional cues, some effects obtained with emotional scenes tend to occur later than those evoked by faces and show longer duration (and more sustained effects), such as the EPN and LPP (Schupp et al., 2006; Sabatinelli et al., 2007; Hajcak et al., this issue). Emotional stimuli can also modulate P3 responses which are generally associated with motivational processes, cognitive control and working memory (Krolak-Salmon et al., 2001; Olofsson et al., 2008; but see Carrétie et al., 1997).

Of note, not only the amplitude/strength of specific time-locked and phase-locked early ERP components is influenced by emotion, but early changes in the visual cortex as a function of the emotional content of the stimulus can also be identified in the EEG signal when looking at the frequency domain. More specifically, selective modulations of steady-state visual evoked potentials (SSVEPs) can be investigated with the presentation of task-irrelevant emotion-laden stimuli (Keil et al., 2005; Müller et al., 2008). In a recent study, such effects in SSVEPs were associated with activation of early visual areas, as well as a network of occipito-temporal and parietal structures (Keil et al., in press). In this paradigm, a visual stimulus flickering at a constant frequency (e.g. 10-Hz, but it can be lower or higher) can trigger a sensory-driven oscillatory activity originating from the striate and extrastriate visual cortex with exactly the same frequency band (e.g. 10 Hz). Interestingly, the amplitude of this SSVEP is not only influenced by manipulations of selective attention (i.e. larger for attended relative to unattended neutral stimuli) due to endogenous/voluntary or exogenous/reflexive orienting (see Müller et al., 1998), but a similar boosting of SSVEP amplitude is elicited when emotional (arousing) stimuli are presented in the flickering stimulus, reflecting an amplification of sensory processing in early visual cortex (Keil et al., 2005; Müller et al., 2008). In addition, such increases in SSVEPs to emotional stimuli may arise even when these are task-irrelevant distracters (Müller et al., 2008) or presented at an unattended location (Wieser et al., 2010). Likewise, SSVEP evoked by non-emotional targets may be reduced when presented together with emotionally engaging, task-irrelevant distractors (Müller et al., 2008). These findings suggest a source of modulation by emotion cues that is independent from voluntary attention and/or produces involuntary shifts in selective attention.

Collectively, these electrophysiological results again show that the emotional significance of stimuli can produce many effects that appear similar to the amplification by attention of task-relevant or behaviorally relevant stimuli, although several dissociations suggest the existence of partly distinct sources of influences on sensory processing. More direct evidence for additive effects comes from studies manipulating attention and emotion separately. For example, a recent study (Brosch et al., 2011) used a dot probe paradigm (see Posner et al., 1980) where a simple visual target (which could unpredictably appear on the right or left visual field) was preceded by three different types of cues: an endogenous/symbolic arrow pointing to one or the other side, an exogenous flash on one or the other side, and a face with either a fearful or neutral expression. Each of the three cueing effects was found to contribute to spatial orienting of attention and combined in an additive manner to facilitate target detection and reaction times (see Fig. 1B). Exogenous cueing was found to influence mainly cue-related activities (i.e. N2pc component; see Eimer, 1996). In contrast, the orthogonal emotional cueing effect (fearful vs. neutral face) mainly affected the processing of the subsequent neutral target, following the cue, as indicated by an augmented extrastriate P1 component for emotionally valid relative to invalid trials. This result is consistent with previous ERP findings (see Pourtois et al., 2004).

Other findings with EEG (Keil et al., 2005) or fMRI (Vuilleumier et al., 2001a) have also shown that emotional stimuli may still produce a relative increase in visual areas when presented at unattended locations, despite an overall reduction compared to attended stimuli (but see Pessoa et al., 2002b), a pattern suggesting a persistent emotionally driven bias in the competition for neural representation in the absence of selective attention. Overall, these effects support the notion that emotion and attention influences (i.e. “gain control”) on sensory processing are mediated by partly

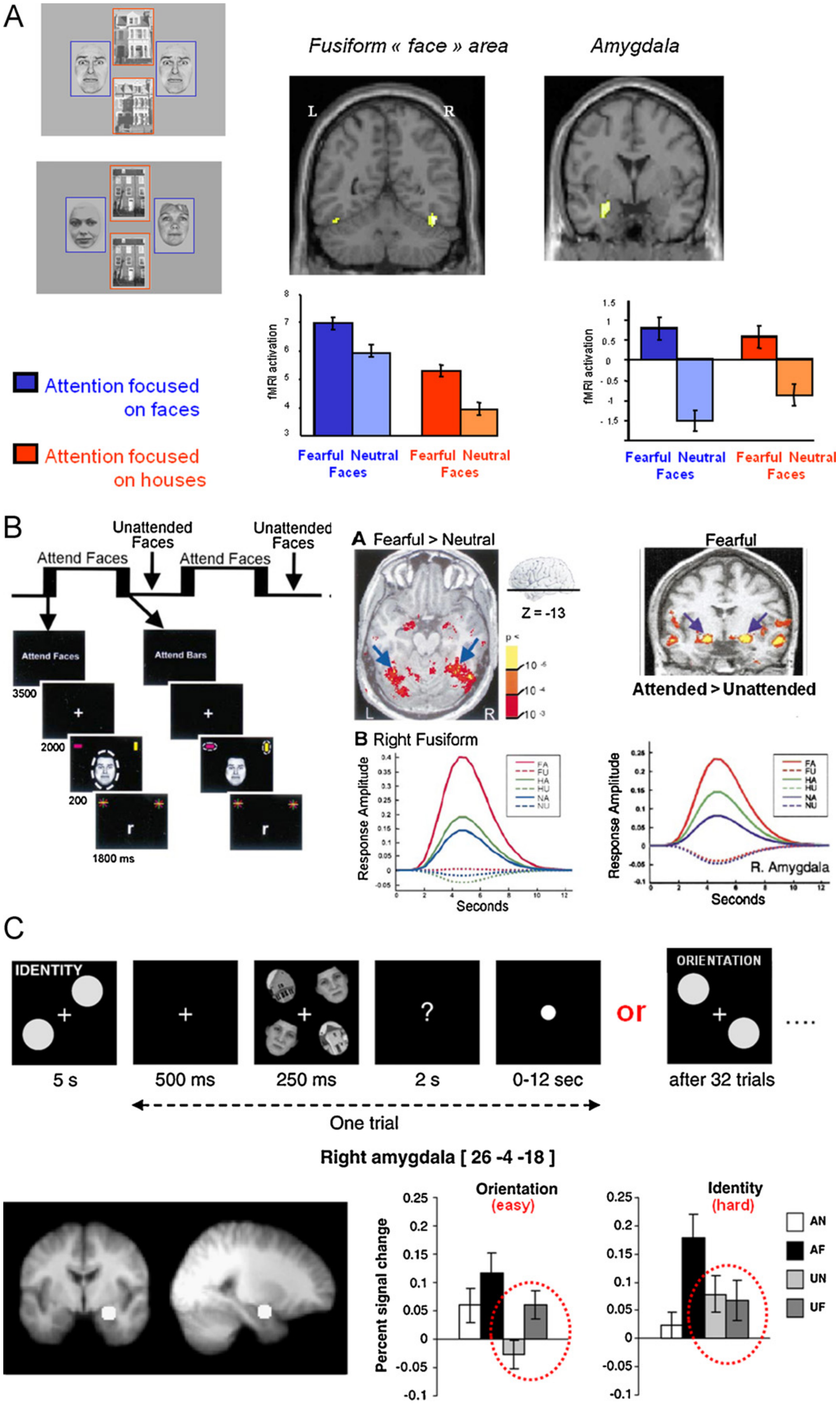

Fig. 2. Examples of different patterns of voluntary attention effects on the processing of emotional faces. (A) Data from Vuilleumier et al. (2001a). Participants had to judge (same/different) pictures shown at two pre-cued locations (vertical or horizontal pairs), while faces were briefly presented at the task-relevant or task-irrelevant locations (both fearful or both neutral, 200 ms, unpredictable order). Although ignored faces produced weaker responses in the fusiform cortex (irrespective of expression), responses were greater to fearful than neutral faces in the amygdala and fusiform cortex both when ignored and when attended, suggesting preserved amygdala reactivity despite reduced attentive processing. (B) Data from Pessoa et al. (2002b). Participants either made gender judgments on a central face (fearful, happy, or neutral) or

separate top–down signals, even when converging on the same sensory pathways.

4. Neural mechanisms for emotional attention

As we (Vuilleumier, 2005; Vuilleumier and Driver, 2007; Pourtois and Vuilleumier, 2006) and others (Lang and Davis, 2006; Amaral et al., 2003) have already argued elsewhere, a plausible source for emotion gain control on perceptual processing (e.g. visual cortex) is likely to implicate the amygdala and its strong bidirectional connections with sensory areas. In particular, anatomical studies in the monkey (Amaral et al., 2003), as well as recent DTI work in humans (Catani et al., 2003; Gschwind et al., in press), have demonstrated direct connections between the amygdala and early visual areas in both the striate and extrastriate cortex (presumably via the inferior longitudinal fasciculus). A similar pattern of bidirectional projections is likely to exist for the auditory and somatosensory modalities (Yukie, 2002), although the most abundant sensory inputs to the amygdala in primates appear to be visual.

The feedback connections from amygdala to visual areas are therefore likely to be responsible for the perceptual enhancement of emotionally relevant stimuli, in a stimulus-specific manner (Vuilleumier et al., 2001a; Peelen et al., 2007; Grandjean et al., 2005). Thus, even within the fusiform cortex, cortical voxels maximally responsive to faces are predominantly modulated by emotion expression in faces (but not bodies), whereas conversely cortical voxels maximally responsive to bodies are predominantly modulated by emotion expression in gestures rather than faces (see Peelen et al., 2007). Projections to early visual areas may also account for increased activations in V1/V2 (Lang et al., 1998; Pessoa et al., 2002b) and extrastriate areas in occipital cortex (Lane et al., 1997; Sabatinelli et al., 2005, 2007), with corresponding effects of the C1 and P1 components in early visual ERP. Hence, amygdala-dependent signals on visual areas might act in a very similar way as top–down signals associated with manipulations of spatial attention, which are instead primarily exerted by fronto-parietal regions (see Fig. 4; Corbetta and Shulman, 2002; Pourtois et al., 2005b).

At least two additional empirical observations corroborate this hypothesis. Firstly, lesions of the amygdala in humans have been shown to abolish the enhancement of neural responses to emotional faces in structurally intact visual cortex. One fMRI study (Vuilleumier et al., 2004) manipulated both emotional expression (fearful or neutral faces) and spatial attention (faces presented at task-relevant or irrelevant location) in a group of epileptic patients with unilateral lesions of the amygdala and/or hippocampus due to mesio-temporal lobe sclerosis, and found a preserved modulation of face-selective regions in fusiform cortex by spatial attention, but a loss of the emotional boost in patients with amygdala damage. Changes in early visual areas, medial prefrontal areas, and hypothalamus were also observed (Vuilleumier et al., 2004). By contrast, patients with temporal lobe sclerosis sparing the amygdala and affecting the hippocampus showed a normal pattern of emotional increases in fusiform cortex. Moreover, the loss of emotional effect predominated in visual areas on the same side as the amygdala lesions, suggesting a causal impact on distant visual areas caused by intra-hemispheric influences, in keeping with the direct feedback connections from amygdala established by anatomical studies (Amaral et al., 2003). Another fMRI study (Benuzzi et al., 2004) comparing responses to fearful and neutral faces in patients with epilepsy and temporal lobe sclerosis also found reduced activations in several occipito-temporal visual areas, and further reported a predominance of this deficit in patients with right-sided lesions.

Secondly, a recent ERP study (Rotshtein et al., 2010) also demonstrated that lesions of the amygdala in temporal lobe epilepsy patients may selectively impair the early neural responses associated with a perceptual enhancement of emotional faces. Remarkably, the presentation of fearful (compared to neutral) faces produced distinct increases in early visual responses corresponding to the P1 (around 100–150 ms) as well as later effects possibly related to memory encoding (P3, around 500–600 ms), that were both abolished in patients with amygdala sclerosis. By contrast, amygdala damage did not influence a third emotional increase seen at intermediate latencies (150–250 ms, corresponding to N1–N2 components) and possibly associated with explicit categorization of faces and expressions (Bentin et al., 1996). These data again suggest a causal link between the integrity of the amygdala and modulations of sensory processing taking place in the extrastriate visual cortex, at both early and later latencies following emotion stimulus onset (Rotshtein et al., 2010).

Collectively, these imaging results from EEG and fMRI converge to support the idea that the processing of emotional (at least fearful or threat-related) stimuli yields a gain control effect in the visual cortex (involving the fusiform and early visual areas in the time window of the P1), resembling the typical effect of selective attention (Heinze et al., 1990), but depending on (direct or indirect) inputs from the amygdala rather than attentional signals mediated by fronto-parietal regions (see Fig. 4; Desimone and Duncan, 1995; Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Woldorff et al., 2004). This emotional gain control effect may therefore account for the more efficient processing of threat-related stimuli, in addition to or in parallel with any concurrent modulation by other endogenous (task-dependent) or exogenous (stimulus-driven) mechanisms of attention (see above; see also Brosch et al., 2011).

Additional evidence for separate sources of influences from amygdala-mediated emotional processes and fronto-parietal attention systems is provided by a few imaging studies in brain-damaged patients with hemispatial neglect after parietal damage (Vuilleumier et al., 2002; Grabowska et al., 2011). These patients typically fail to orient to, detect, and/or respond to stimuli in the (usually left) space opposite to their (usually right) brain lesion, due to a destruction of brain networks controlling spatial attention towards that side (generally following stroke; Driver and Vuilleumier, 2001). Both exogenous and endogenous mechanisms of spatial attention are usually impaired, particularly in the acute stage (Bartolomeo et al., 2007; Corbetta and Shulman, 2011). Yet, emotional stimuli (such as fearful faces, pictures of spiders, aversive scenes, or angry voices) presented in the left space tend to be less severely neglected (i.e. better detected) relative to similar but neutral stimuli (Vuilleumier and Schwartz, 2001a; Fox, 2002; Lucas and Vuilleumier, 2008; Grandjean et al., 2008; Grabowska et al., 2011), suggesting that they may still grab attentional resources and preferentially compete for awareness despite the inability to voluntarily orient attention towards the contralesional side caused by fronto-parietal damage. In line with this, emotional stimuli presented in left neglected space may still

compared orientation of peripheral bars in brief visual displays that remained unchanged across conditions (200 ms, blocked design). Activations in fusiform and amygdala were totally flat when attention was focused on the bars, despite the presence of faces in the center of the display, suggesting that the orientation task difficulty consumed all processing resources and thus suppressed all visual inputs to both regions. (C) Data from Silvert et al. (2007). Participants performed a modified version of the task shown in (A) that could be either easy (right/left tilt judgment) or harder (same/different identity). In the easy task, ignored fearful faces produced stronger amygdala activation than ignored neutral faces, but this differential response was abolished in the hard task due to increase activation for the ignored neutral faces while activation to ignore fearful faces was unchanged. These studies illustrate that voluntary attention or inattention and task load can produce different patterns of effects for different brain regions, and affect responses evoked by both fearful and neutral faces.

produce increased activation in visual cortex and some prefrontal areas (e.g. orbitofrontal cortex, anterior cingulate cortex), relative to neutral stimuli, even when these are not consciously seen by the patient and evoke a reduced activity overall compared to consciously seen stimuli (Vuilleumier et al., 2002; Grabowska et al., 2011). Again, these findings suggest that emotional gain control mechanisms (presumably dependent on amygdala feedback; see Vuilleumier et al., 2002) can bias neural responses in favor of emotionally significant events and thus contribute to a greater capture of attention despite overall neglect. Note, however, that such effects do not reflect a "magic" immunity of emotional stimuli to attention deficits, since emotional stimuli are still more often missed in the left/contralesional than right/ipsilesional side in neglect patients; but rather the spatial biases in attention selection caused by unilateral/right parietal damage are combined and (at least partly) counteracted by concurrent emotional biases exerted from another emotion-responsive source (e.g. amygdala).

It should also be emphasized that besides the direct feedback connections from amygdala discussed here, emotional biases might also influence perception and attention via indirect pathways (Vuilleumier, 2005; Pessoa, 2009; Lim et al., 2009). For example, the amygdala also projects densely to basal nuclei of the forebrain, which in turn provide a major source of cholinergic inputs to many other brain areas including frontal, parietal, and sensory cortices. These cholinergic pathways can have a strong modulatory effect on attention by boosting and prolonging neuronal discharges (Parikh and Sarter, 2008). However, in one fMRI study where a cholinergic drug (physostigmine) was administered during a face processing task manipulating both attention and emotion (Bentley et al., 2003), no significant change was observed in the emotional modulation of fusiform cortex activity, confirming that these effects are mediated by direct amygdala feedback (Amaral et al., 2003; Vuilleumier et al., 2004). No change was observed in amygdala either. By contrast, physostigmine (a cholinergic enhancer) modulated activity in orbitofrontal cortex (OFC) and posterior parietal cortex (PPC) selectively in response to emotional face distracters, a pattern that was taken to suggest that cholinergic projections might act to interrupt current attention focus and promote efficient shifts towards emotional information (Vuilleumier, 2005, 2009). Moreover, indirect effects of emotion on attention via OFC and PPC are consistent with imaging studies that investigated spatial orienting towards threat-related stimuli in target detection tasks. These studies (Fredrikson et al., 1995; Armony and Dolan, 2002; Pourtois et al., 2006b) consistently found enhanced activations of fronto-parietal regions associated with attention control, including the frontal eye field and intraparietal sulcus, when orienting was triggered by emotional cues relative to neutral stimuli. Time-resolved imaging based on EEG and topographical segmentation (Pourtois et al., 2005b) also suggested that PPC activation might precede the sensory enhancement of target processing in occipital cortex (i.e. P1 effect) when orienting to the target is cued by a preceding emotional face at the same spatial location, and could thus mediate the spatially selective orienting of attention. Other indirect influences of amygdala responses on attention and perception are also possible through other neurotransmitter pathways implicated in arousal (e.g. via locus coerelus and noradrenaline).

Altogether, these data indicate that, due to the many output projections from the amygdala, emotional processing may have multiple ways to influence in a rapid and powerful manner a variety of cognitive functions at the perception, attention, and other (e.g. motor, see Sagaspe et al., 2011) levels. In addition, brain systems involved in other facets of affect and motivation might possibly also have distinct influences (Cardinal et al., 2002). However, much remains to be discovered about the exact role and interaction between these different pathways (Vuilleumier, 2005, 2009).

5. The impact and timing of voluntary attention control and tasks demands

A key assumption in this model is that the enhanced sensory processing of emotionally relevant stimuli (and the resulting biases in allocation of attention) relies on a distinct ventral attention system (Fig. 4) in which the amygdala plays a central causal role (rather than temporal-parietal junction, as proposed for exogenous spatial attention; see Corbetta and Shulman, 2002). Accordingly, as reviewed above, the emotional amplification of perceptual processing seen in fMRI and ERP studies may arise independently or even orthogonally from the more classical endogenous or exogenous attention control systems (Figs. 2 and 3), for which a cortical fronto-parietal network is predominantly implicated (Kastner and Ungerleider, 2000; Vuilleumier and Driver, 2007). However, a critical condition for emotional attention to operate efficiently is that the amygdala should not only activate, but also trigger the appropriate feedback signals, in response to emotionally significant stimuli that are not yet in the focus of attention, so as to allow attention to orient to them and adapt behavior accordingly.

In agreement with this idea, a number of results from neuropsychological studies in brain-damaged patients (see Vuilleumier and Schwartz, 2001a; Vuilleumier et al., 2002; Williams and Mattingley, 2004; Fox, 2002; Tamietto and de Gelder, 2010), as well as fMRI (Morris et al., 1999; Whalen et al., 1998), ERP (Williams et al., 2004; Liddell et al., 2004; Carretie et al., 2005) and MEG studies (Bayle et al., 2009) in healthy participants, indicate that emotional information is processed (at least to some extent and under certain circumstances) regardless of voluntary top–down attention and even without conscious awareness (but see Pessoa et al., 2002b and below). Again, unconscious processing by itself is not necessarily "magic" and specific to emotional stimuli, since substantial processing of complex, non-emotional information can also take place without conscious awareness and still recruit the corresponding "specialized" processing pathways (Merikle, 1992; Dehaene et al., 2006; Kouider and Dehaene, 2007; Vuilleumier and Righart, 2011). What is particular to the case of emotion processing is that neural substrates engaged without awareness or attention may include additional structures, relative to neutral stimuli, including the amygdala (and perhaps other regions), which have direct ouputs to influence sensory processing as well as many other brain systems controlling perception and behavior. Such effects on sensory processing are not shared with other unconscious (e.g. semantic) mechanisms.

However, the degree of amygdala activation to emotional or threat-related stimuli presented outside attention or awareness remains debated and appears to vary across experimental conditions or methods. On the one hand, there is abundant evidence that the amygdala responds to emotional information (e.g. facial expression) even when the task does not require explicit appraisal or judgments about the affective significance of stimuli (Vuilleumier and Pourtois, 2007). This may reflect a "default mode" of processing that is consistent with a role for the amygdala in monitoring the environment for potentially threatening or personally relevant events (Davis and Whalen, 2001; Sander et al., 2003; Armony et al., 1997). This does not preclude that different task demands or voluntary emotion regulation strategies can alter (increase or decrease) this readiness to respond (Ochsner and Gross, 2005; Vrticka et al., 2011), possibly through direct modulation of amygdala circuitry and/or indirect modulation of its inputs. Furthermore, there is also evidence that the amygdala may respond to emotional information presented outside the current focus of attention (Vuilleumier et al., 2001a, 2004; Bentley et al., 2003; Anderson et al., 2003; Williams et al., 2005a). This may in turn be sufficient to induce feedback signals to early sensory areas, and thus account for a smaller reduction in cortical activation (e.g. fusiform) for emotional

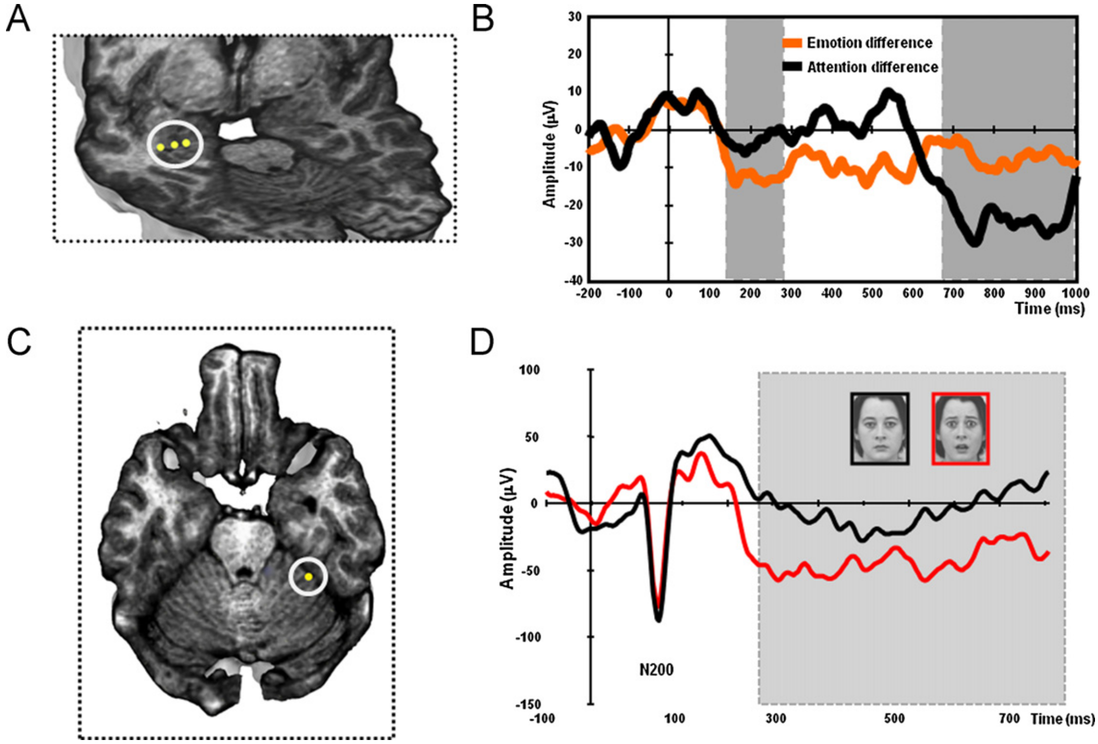

Fig. 3. Temporal dynamics of emotion and attention effects in amygdala and fusiform cortex. Data from Pourtois et al. (2010a,b) showing intracranial recordings in epileptic patients prior to temporal lobe surgery. (A) Location of electrodes in the left lateral amygdala of one patient. (B) Intracranial EEG results for the amygdala during a task where the patient was presented with pairs of faces (with fearful or neutral expression) at either task-relevant locations (attended condition) or task-irrelevant locations (unattended). Differential effects of emotion (fearful vs. neutral faces) started early after stimulus onset (150–200 ms, left-sided shaded area) and were similar for both attended and unattended faces. Differential effects of attention started later (650–700 ms, right-sided shaded). (C) Location of an electrode in the right lateral fusiform gyrus of another patient. (D) Intracranial EEG results for the fusiform cortex during a task where the patient performed a one-back repetition task with faces or houses. An early face-selective response (N200) was not modulated by the emotional expression of faces (fearful vs. neutral), but showed a strong and sustained amplitude modulation starting ~350 ms after stimulus onset and lasting more than 500 ms (shaded area). This pattern is consistent with feedback or re-entrant signals, presumably initiated by the amygdala which activated at a slightly preceding latency (see B).

compared to neutral unattended stimuli as well as their stronger competition for attention and awareness (Vuilleumier, 2005). For example, both the amygdala and fusiform may activate more to fearful than to neutral faces presented at task-irrelevant locations when participants perform a task on concurrent neutral visual stimuli (e.g. pictures of houses; see Fig. 2A). On the other hand, however, some studies found that directing attention away from emotion stimuli may reduce (or even abolish) amygdala responses when the perceptual demand of the task is higher (Pessoa et al., 2002a,b) and thus exhausts all attentional resources (see Lavie, 2005). For example, when participants have to perform a hard perceptual discrimination on peripheral visual targets, emotional faces presented at task-irrelevant locations evoke no differential activity compared to neutral faces, whereas they still do when target discrimination is easier (Pessoa et al., 2002a,b). The latter effect (at low attentional load) is by itself a demonstration that a differential emotional response does not depend on voluntary attentional focus and current task goals, whereas attentional influences related to task relevance or sensory competition (e.g. at high load) point to distinct modulatory sources, which could potentially attenuate amygdala reactivity or inputs to the amygdala at the cortical and/or subcortical (e.g. thalamic) level (Saalmann and Kastner, 2009). Thus, a strong attentional modulation in hard task conditions (e.g. under high perceptual load; Lavie, 2005; Schwartz et al., 2005) might sometimes override any apparent emotional response in amygdala and interconnected sensory areas. Indeed, it is striking that in such hard conditions, even sensory responses in cortical areas seem to be suppressed despite the presentation of otherwise highly visible stimuli (see Fig. 2B), precluding the possibility of any modulatory effect from other sources on the same (non-responsive) area.

However, these observations do not invalidate the notion that when task demands are properly balanced (or task load is not extreme; see Anderson and Phelps, 2001; Vuilleumier et al., 2001a; Pessoa et al., 2002b), there is more efficient processing and preferential attention selection of emotionally relevant stimuli relative to neutral stimuli, with distinctive early emotional effects in the amygdala (see Vuilleumier, 2005; Pourtois et al., 2010a,b). Nor does it contradict the assumption that multiple modulatory signals or attention systems may operate in parallel and each be flexibly engaged depending on the current task demands (Corbetta and Shulman, 2002; McMains and Kastner, 2011). Furthermore, the notions of "hard" tasks and "resources" are ill defined and may actually vary for different neural pathways, i.e., what is "hard" for some cortical areas (or some neurons) might not be so "hard" for the amygdala (or other neurons). Hence, in some task conditions (Vuilleumier et al., 2001a), weaker visual inputs to the extrastriate cortex due to top–down control by endogenous spatial attention can reduce fusiform responses to unattended faces, but still be sufficient to activate the amygdala to the same degree as stronger inputs (Fig. 2A), whereas even weaker inputs in other conditions (Pessoa et al., 2002b) might fail to activate both the cortex and amygdala. These effects are therefore not incompatible but rather suggest that the amygdala may have a different response threshold relative to other cortical responses, and that its activation does not directly depend on the magnitude of face processing in fusiform. Moreover, an attenuation of seemingly automatic processes by load or task demands is by no means specific to emotion processing but may also arise for other “bottom–up” processes, such as exogenous (Folk et al., 1992; Santangelo et al., 2008) and object-based attention (Xu, 2010; McMains and Kastner, 2011), which are typically thought to operate in a reflexive and involuntary manner.

In addition, note that a hard task may introduce other sources of modulation in neuroimaging results by changing the motivational state of participants. Because a hard task is usually associated with a higher rate of errors and/or higher reward value of correct responses, additional emotional effects may influence brain activity in certain regions, including the amygdala. In fact, error detection (Pourtois et al., 2010c) and event relevance (Sander et al., 2003) can modulate levels of amygdala activation. These factors could therefore contribute to blur a (weaker) differential response to emotional relative to neutral task-irrelevant pictures, when task demands are high. Likewise, expectations and affective states of the participants can influence the impact of attention of emotion processing and even abolish the effect of load (Cornwell et al., 2011; Bishop et al., 2004b; Rossi and Pourtois, in press). Furthermore, several studies found that when presented outside attention, neutral or positive faces may actually produce a “paradoxical” increase in amygdala response that did not occur when the same stimuli were attended (Vuilleumier et al., 2002; Anderson et al., 2003; Williams et al., 2005a; Silvert et al., 2007), suggesting a more broadly tuned (less selective) reactivity when cortical processing is diminished and thus leading to an apparent reduction in threat-specific responses (see Fig. 2C). Altogether, these and other factors might combine in various ways in different experiments and participants to produce different patterns of attentional effects on the response to emotional stimuli in the amygdala and interconnected brain areas.

In line with the notion that emotion processing may take place in parallel and independent from voluntary attention control, recent intracranial recordings from human amygdala provide evidence for early emotional responses following stimulus onset that precede the top–down effects of endogenous spatial attention (Fig. 3A and B; Pourtois et al., 2010b; see also Seeck et al., 1997; Halgren et al., 1994a; Holmes et al., 2003). In this study, intracranial ERPs were obtained from the structurally intact left lateral amygdala of a patient with refractory/pharmaco-resistant epilepsy (Pourtois et al., 2010b) while he performed a task previously designed to manipulate emotion (i.e. fearful vs. neutral faces) and attention (i.e. attending to faces vs. houses) independently (see Vuilleumier et al., 2001a, 2004). Early following stimulus onset (140–290 ms), fearful faces elicited a differential response in the amygdala relative to neutral faces (Fig. 3A and B), regardless of whether these face stimuli were at task-relevant locations or not (i.e. attending to houses). By contrast, directing spatial attention to faces (relative to houses) in the visual display modulated neural response in the same amygdala region, but at a much later latency (750–950 ms, see Fig. 3A and B). Note that these findings do not imply that spatial attention modulated visual cortex at the same delayed latency (but more likely around 200–300 ms, as typically shown by scalp EEG studies), rather they indicate that enhanced attentive processing differentially affected amygdala activity at a later stage only. Indeed, attention modulation in the amygdala was surprisingly delayed in this paradigm, as compared with the attentional effects that are usually observed in visual cortex and associated with the P1–N1 components in ERPs (Hillyard and Anllo-Vento, 1998; Pourtois and Vuilleumier, 2006). This pattern suggests that an early effect of emotion in the amygdala might arise prior to any gating by attention and influence perceptual processing through feedback on sensory areas in parallel or combination with modulatory effects of attention acting on the same areas during the P1–N1 latencies (Fig. 2A; see Vuilleumier, 2005). More generally, these results also suggest that both emotion and attention can influence amygdala processing, but at distinct (and non-overlapping) latencies following stimulus onset, with earlier effects for emotion relative to attention. Importantly, this dissociation in time-course cannot be resolved with fMRI due to the slow temporal resolution of this technique and may explain discrepancies between studies depending on the relative magnitude of emotion and attention effects (Box 2). Similar findings were obtained in healthy adult participants using MEG and source localization techniques (Luo et al., 2010). In the latter study, participants performed a line discrimination task (i.e. matching the orientation of two line flankers shown on each side of a central face) which was either easy (low load) or difficult (high load), while the central face could have either a fearful or neutral expression (Erthal et al., 2005). Results showed that the amygdala responded more to fearful relative to neutral faces early after stimulus onset (40–140 ms) regardless of task load, but this response was modulated by load during a later time interval only (280–410 ms; see also Fig. 2A and B).

Furthermore, as noted above, reciprocal anatomical connections between the amygdala and (striate and extrastriate) visual cortex (Amaral et al., 2003; Catani et al., 2003; Gschwind et al., in press) are thought to allow boosting sensory cortical processing in a stimulus-selective manner (see Vuilleumier et al., 2001a, 2004; Sabatinelli et al., 2005), including the fusiform face area for emotional faces (Kanwisher et al., 1997). Accordingly, in a another study, we had the opportunity to use intracranial recordings in an epileptic patient implanted with deep electrodes in a region of the right fusiform gyrus showing face-selective responses (likely corresponding to the fusiform face area, Fig. 3C and D; Pourtois et al., 2010a). The patient was shown either emotional (fearful or happy) or neutral faces, as well as other object categories (including houses), while performing a simple one-back repetition detection task. Results showed an early category-selective response (faces > houses; see Fig. 3C and D), peaking around 150 ms after onset, in agreement with previous neurophysiological results (i.e. N200 component; see Allison et al., 1999), but this response was not influenced by the emotional content of faces. By contrast, the same cortical site showed increased activity starting 320 ms after stimulus onset for emotional compared to neutral faces and this effect was sustained for ∼500 ms (see Fig. 3C and D; Pourtois et al., 2010a,b). This pattern is consistent with a feedback modulation arising from the amygdala (Matsumoto et al., 2005; Sugase et al., 1999; Vuilleumier et al., 2004; Vuilleumier, 2005) and beginning just after the differential emotional activity in this region (Pourtois et al., 2010b). Furthermore, the long-lasting enhancement of activity in fusiform cortex may be consistent with the delayed and sustained LPP component evoked by emotional stimuli in EEG recordings (Sabatinelli et al., 2007), and suggests that it might also serve to induce local neuronal changes related to memory traces.

Collectively, these intracranial and MEG results converge to suggest a two-stage model of emotional attention and interaction with task relevance. First, the amygdala appears to afford an early (∼120–140 ms) discrimination between emotional (threat-related) and neutral stimuli even when visual stimuli are weak because they are task-irrelevant (Luo et al., 2010, 2007) or outside the current focus of attention (Pourtois et al., 2010b). This early effect may take place in parallel to stimulus categorization in the visual cortex, and rely on an initial feedforward sweep of inputs throughout the visual pathways. Second, this early emotion response in the amygdala can trigger a modulation (i.e. increase) of the neural response in visual cortex (Vuilleumier et al., 2001a; Pourtois et al., 2010a), via both direct and indirect pathways projecting back to the cortex (Amaral et al., 2003; Vuilleumier, 2009, 2005; Sabatinelli et al., 2009). This boosting may thus increase processing efficiency and competitive biases for emotional relative to neutral stimuli, resembling an attention gain control effect that may add or combine with other modulatory influences, including those imposed by endogenous attention and perceptual load (Fig. 3C and D).

6. Neural routes to the amygdala

The fact that some emotional processing may take place in the amygdala without voluntary attention (or sometimes without awareness) has raised questions about the possible pathways conveying information to this region, prior to full cortical processing. Because animal work (LeDoux, 1996; Shi and Davis, 2001) and observations in human patients with blindsight after damage of area V1 (Morris et al., 2001; Anders et al., 2004; Pegna et al., 2005) showed that some emotional responses in amygdala and conditioning may still arise for visual stimuli despite damage to cortical relays, it has been hypothesized that sensory inputs might reach the amygdala through subcortical pathways that bypass cortical processing. In particular, for vision (e.g. face stimuli), a subcortical "quick and dirty" route via the superior colliculus and pulvinar has been proposed (Tamietto and de Gelder, 2010), in agreement with neuroimaging results showing activation in these two regions during unconscious processing of emotional stimuli (e.g. Morris et al., 1999; Pasley et al., 2004; Liddell et al., 2005). Furthermore, damage to human pulvinar may impair detection and spatial orienting to threat (Ward et al., 2007), and emotionally negative faces or scenes in a visual display may affect saccade trajectory (curvature) in a manner suggesting direct involvement of the superior colliculus (Nummenmaa et al., 2006, 2009; Devue et al., 2011). This subcortical pathway (and the exact pulvinar relay) has not been formally identified (Pessoa, 2005), but recent anatomical studies in primates have found robust projections from visual nuclei in pulvinar to the lateral amygdala (Day-Brown et al., 2010).

However, it has also been suggested that other subcortical visual roads might exist and project to higher-level extrastriate cortical areas (without passing through V1) rather than directly to the amygdala (Vuilleumier, 2005; Pessoa and Adolphs, 2010). For instance, in monkeys, the superior colliculus projects to V2 (Shipp, 2003) and visual pulvinar projects directly to V4 and V5 (Shipp and Zeki, 1995); whereas direct connections between pulvinar and fusiform cortex have also been found in humans in post-mortem studies (Clarke et al., 1999). Projections from the lateral geniculate nucleus (i.e. the main thalamus relay along the retino-cortical visual pathways) to extrastriate cortex have also been shown to mediate blindsight effects in monkeys (Schmid et al., 2010). Alternatively, subcortical relays in pulvinar might also be conceived to operate like the amygdala, and coordinate the activity of distant cortical networks involved in the evaluation of salient or biological relevant affective visual stimuli (see Pessoa and Adolphs, 2010).

As another alternative to this classic two-route model for "subliminal" and conscious emotion processing, a two-stage hypothesis has also been proposed (Vuilleumier, 2005), according to which the same cortical pathways (i.e. along occipito-temporal areas) might be recruited by an early and rapid feedforward sweep of inputs to various areas (e.g. frontal, parietal, and possibly amygdala), followed by feedback or "re-entrant" modulations exerted on sensory areas which may be necessary for full perceptual processing and access to conscious awareness (see Bullier, 2001; Lamme and Roelfsema, 2000; Lamme, 2003). There is abundant evidence that visual inputs propagate rapidly throughout the brain and reach high-level cortical regions such as FEF, PPC, and OFC in the range of 120 ms post-stimulus onset (Bullier and Nowak, 1995; Schmolesky et al., 1998; Kawasaki et al., 2001; Bar et al., 2006), allowing quick perceptual categorization and motor decision processes to be performed in less than 150 ms (Thorpe et al., 1996), that is, before the typical latency associated with voluntary attention control (Hillyard and Anllo-Vento, 1998; Hillyard et al., 1998a). This initial feedforward sweep of information might not only trigger top–down or re-entrant signals on sensory areas (which in turn are linked to exogenous orienting, object recognition, and awareness), but also spark off emotional evaluation processes in the amygdala prior to the impact of voluntary attention control (as suggested by intracranial recordings; see Pourtois et al., 2010b). Here again, there is no reason to assume that preattentive or unconscious emotion processing might be "magic" and benefit from an exclusive "low" route (Pessoa and Adolphs, 2010), just like evidence for subliminal perception of words or numbers (Dehaene et al., 1998, 2001; Kouider and Dehaene, 2007) or unconscious priming of motor processes (Eimer and Schlaghecken, 2002, 2003) does not require the existence of dedicated subcortical pathways to the corresponding cortical areas. The fact that the amygdala is located in the anterior temporal lobe, several synapses away from primary visual cortex, does not preclude rapid and unconscious activation since similar responses are observed in several other brain areas at a higher level in the processing hierarchy, including the hippocampus (Henke, 2010; Henke et al., 2003) or even motor cortex (Dehaene et al., 1998). In addition, recent DTI data in humans suggest that early occipital areas may project to anterior temporal lobe (including amygdala) through direct white-matter fibers in the inferior longitudinal fasciculus (Catani et al., 2003; Gschwind et al., in press). Moreover, MEG recordings and connectivity models of brain responses to visual emotional stimuli suggest that the latency and distribution of activity in occipito-temporal regions is best accounted for by a functional architecture involving *both* rapid inputs through a short-cut to the amygdala *and* subsequent feedback from amygdala to early cortical areas, rather than by a strictly sequential processing along the ventral visual stream (Rudrauf et al., 2008). These results support a dual route hypothesis, but a subcortical route or cortico-cortical long-range pathways appear equally plausible, and the exact anatomical substrates of these effects therefore remain to be clarified. Moreover, although a subcortical route is likely to explain amygdala activations and behavioral biases evoked by emotional stimuli presented in a blind visual field after V1 damage (de Gelder et al., 1999), either subcortical or cortical pathways (or even both) could potentially process emotional information prior or in parallel to selective attention.

In any case, both the two-pathway hypothesis (via subcortical or direct occipital inputs) and the two-stage hypothesis (via a fast cortico-cortical sweep) would allow for rapid emotion processing based on weak and rudimentary visual information. Indeed, both models predict that early amygdala responses to visual stimuli might primarily depend upon inputs from magnocellular visual pathways, which convey coarse information (low-spatial frequencies) and motion cues. Magnocellular inputs propagate rapidly throughout the visual system (both cortically and subcortically) and can initiate rapid object categorization processes (Bar, 2003; Schettino et al., 2011). By contrast, parvocellular inputs convey fine details such as edges and textures (low-spatial frequencies), as well as colors, but in a slower manner and only project to cortical areas within the occipito-temporal stream. Accordingly, it has been found that amygdala activation to fearful faces can be driven by crude visual information in the low-spatial frequency range (Vuilleumier et al., 2003) or just two high-contrast wide-open eyes (Whalen et al., 2004). Furthermore, whereas face and object processing in visual cortex is strongly dependent on high-spatial frequency cues provided by the parvocellular pathways, several fMRI (Vuilleumier et al., 2003; Winston et al., 2003) and EEG studies (Pourtois et al., 2005a; Alorda et al., 2007; Carretie et al., 2007; Vlamings et al., 2009; Schettino et al., 2011) have shown that the emotional enhancement of visual responses (e.g. in fusiform face area) is also selectively induced by low-spatial frequency cues in the stimuli. These coarse inputs are presumably conveyed by the magnocellular pathways, and thus able to activate the amygdala and then trigger secondary feedback prior to full cortical processing of parvocellular inputs (see also Rotshtein et al., 2007). In agreement with this view, detection and orienting to threat-related stimuli can be facilitated when these are presented in low rather than high-spatial frequencies (Holmes et al., 2005; Mermillod et al., 2010). Other recent behavioral results also confirm that emotion (e.g. seeing a fearful face) can improve fast temporal vision (via magnocellular channels) at the expense of fine-grained spatial vision (dependent on parvocellular channels; see Bocanegra and Zeelenberg, 2011). Hence, rapid emotional responses to visual stimuli might be evoked by coarse and imprecise information broadcasted throughout the visual systems at early latencies (though subcortical and/or cortical inputs), and thus influence ongoing perceptual processes, but these effects might not invariably or globally improve vision, and instead sometimes produce tradeoff phenomena that speed up processing but impair precision (Bocanegra and Zeelenberg, 2009, 2011).

7. Behavioral effects of emotion on attentional performance

There are numerous examples showing that visual detection and attention are boosted for emotional (e.g. threat) relative to neutral stimuli (Dominguez-Borras and Vuilleumier, in press). Such effects are manifested by faster RTs and/or enhanced accuracy in various tasks, including visual search (Eastwood et al., 2003; Fox et al., 2000; Williams et al., 2005b), attentional blink (Anderson and Phelps, 2001; Anderson, 2005), or spatial orienting (dot probe task; e.g. Brosch et al., 2011; Pourtois et al., 2004; Fox et al., 2001; for review, see Frischen et al., 2008). A role for the amygdala and emotional influences on attention in these tasks is supported by the convergence of these behavioral effects in healthy participants with patterns of neurophysiological responses in imaging studies, as well as observations in patients with lesions to the amygdala. Nonetheless, it must be noted that a direct link between changes in behavior (RT or accuracy) and the involvement of a specific brain region (amygdala) or circuit remains at best hypothetical. However, when combined with neuropsychology case studies and imaging work (EEG, MEG or fMRI), these behavioral data provide useful hints to interpret activations in specific brain systems and help to identify possible mechanisms underlying emotional attention.

Early reports concerning amygdala-damaged patients described emotional and social deficits, including a selective inability to recognize fear in face expressions and other signals of danger (Adolphs et al., 1994, 1995; Adolphs, 1999; LaBar et al., 1995), with no or less severe deficits in other emotions. This was initially interpreted as an impairment in the perceptual discrimination for fear expressions, but more recent studies have clarified the nature of this deficit by demonstrating an inability in directing attention towards the emotionally salient eye region in fearful faces, which could in turn produce a disproportionate deficit in fear recognition due to the "diagnostic" importance of these facial features in fear expressions (Adolphs et al., 2005; Kennedy and Adolphs, 2010). Hence, amygdala damage would not necessarily cause a perceptual deficit in recognizing fear per se, but instead lead to abnormal exploration or attention strategies when inspecting emotional (fearful) face expressions. This lack of attention to the eyes could in turn lead to a selective fear recognition deficit. In line with this interpretation, patient SM (with selective bilateral amygdala lesions; see Adolphs et al., 1994) fails to look to the eye region when freely attending to fearful faces, and as a result, shows a selective impairment in recognizing this specific facial expression (Adolphs et al., 2005; Kennedy and Adolphs, 2010). But critically, this impairment was totally reversed when SM was instructed to explicitly look at the eyes of faces. These data therefore suggest that amygdala damage may have an important impact on attention to salient face information, rather than on the recognition of fear cues per se.

Consistent with this view, another study (in another patient) elegantly demonstrated that bilateral lesions of the amygdala produced a selective impairment in emotional attention, as this patient did not show the normal facilitation of detection for emotionally arousing stimuli during an attentional blink task (Anderson and Phelps, 2001; Anderson, 2005). Whereas control participants showed a reduction of the attentional blink when confronted with a rapid serial visual presentation of words carrying an emotional meaning (such as taboo words), the patient with bilateral lesions of the amygdala did not (Anderson and Phelps, 2001). This result suggests that amygdala damage may cause an attentional allocation deficit towards emotionally relevant events (see also Sander et al., 2003) and hence hamper the normal generation of rapid orienting to cues of danger (LeDoux, 1996; Öhman and Mineka, 2001).

However, it must be noted that a recent study reported a preserved implicit emotion effect during a visual search task in patient SM (with bilateral and selective lesions of the amygdala), despite her deficit in reflexive orienting to the eyes and explicit fear recognition (Tsuchiya et al., 2009). Furthermore, in a binocular flash suppression paradigm, fearful faces tended to break through into awareness more frequently than happy faces, in SM like in controls (Tsuchiya et al., 2009). These findings suggest that the amygdala may not always be a necessary substrate for rapid and implicit influences of emotion on attention, although the reasons for discrepancy with other results in the same patient remain to be clarified. Likewise, in two other recent neuropsychology studies, a more efficient detection of emotional targets (e.g. pictures of snakes or spiders) relative to neutral targets (e.g. mushrooms or sprinklers) was still observed in a visual search (Piech et al., 2010) and attentional blink tasks (Bach et al., 2011) in patients with amygdala lesions (due to surgery for epilepsy). These discrepancies might be explained by the fact that these emotional attention mechanisms may rely on additional amygdala-independent processing capacities or strategies. For example, they might imply the involvement of other attention networks (see VanRullen et al., 2004), relative to brain systems recruited during spatial cueing or dot probe tasks, and/or relative to the effects observed with fewer items. Moreover, attention effects in the latter visual search or detection tasks could also potentially be explained by low-level features that contribute to discriminate faces with fearful expressions (e.g. big eyes) from other emotions (see Purcell et al., 1996; Öhman et al., 2001; Frischen et al., 2008).

Importantly, however, emotional biases in attention have also been found to be spared in patients with hemispatial neglect, a neurological disorder following damage to fronto-parietal brain areas implicated in endogenous and exogenous mechanisms of spatial orienting. For example, neglect patients show less severe extinction for emotional faces or voices relative to neutral stimuli presented in the contralesional/neglected space (though extinction is still present; Vuilleumier and Schwartz, 2001a,b; Fox, 2002; Grandjean et al., 2008) and faster detection of emotional than neutral targets among distractors in visual search tasks, even on the contralesional/neglected side (though performance is still slower and poorer as compared with the ipsilesional/intact side; Lucas and Vuilleumier, 2008; Grabowska et al., 2011). These findings accord with the notion of an additional competitive bias for emotional stimuli that is partly independent from fronto-parietal top–down mechanisms. Moreover, lesion analysis in neglect patients indicated that the strongest emotional biases were observed in patients with larger damage to fronto-parietal areas, whereas the weakest were observed in those with orbitofrontal damage, pointing to the involvement of different neural substrates for different sources of top–down biases on visual selective attention (Lucas and Vuilleumier, 2008; Grandjean et al., 2008). Faster detection of emotional compared to neutral faces has also been observed in a patient with severe prosopagnosia (i.e. impaired recognition of face identity) after occipito-temporal damage (Peelen et al., 2009), indicating that such emotion biases also persist after deficits in visual face processing abilities that depend on extrastriate visual cortex.

However, it remains to better understand what are the exact sensory cues (in faces and other stimuli) that drive emotional effects on perception and attention tasks (Vuilleumier and Huang, 2009). While the amygdala might be critical to learn the emotional significance of novel stimuli and respond to simple visual cues associated with emotional relevance (as can be conveyed by quick and coarse sensory pathways), differential reactions to some over-learned as well as more complex stimuli might require additional processes, possibly mediated by higher sensory (e.g. extrastriate) cortices or posterior orbitofrontal regions receiving inputs from both sensory regions and amygdala (Barbas et al., 2010).

8. Conclusions and perspectives

Data from neuroscience reviewed in this paper point to the existence of brain mechanisms centered on the amygdala and interconnected areas (OFC, cholinergic nuclei), whose main function is to assess the emotional value of sensory events and boost their perceptual processing in early sensory pathways, presumably allowing the organism to swiftly respond to emotionally relevant stimuli in the environment and extract relevant information about their nature and location (Vuilleumier, 2005; Vuilleumier and Huang, 2009). Within this system, the amygdala appears to play a central causal role both by being able to respond to relevant cues at early latencies post-stimulus onset (even based on coarse and partial information) and by exerting top–down influences on sensory processing in distant cortical regions, thanks to direct (as well as indirect) anatomical projections that provide feedback signals to these sensory areas (Amaral et al., 2003; Vuilleumier et al., 2004; Vuilleumier, 2005). These modulations of sensory cortices during emotion processing may arise just after the initial sweep of activation in the cortical visual pathways and influence ongoing competitive interactions between sensory inputs at early perceptual stages by increasing the representation of emotionally relevant stimuli (see Halgren et al., 2000; Pourtois et al., 2004; Stolarova et al., 2006). These modulatory effects of emotion closely resemble the typical enhancement produced in the same sensory regions by selective attention mechanisms, and normally associated with top–down signals from dorsal fronto-parietal networks (Desimone and Duncan, 1995; Kastner and Ungerleider, 2000; Posner and Dehaene, 1994; Corbetta and Shulman, 2002). Thus, both emotional influences from the amygdala and attentional influences from fronto-parietal areas seem to act as distinct gain control systems that can amplify emotion or task-relevant information in a stimulus-specific manner, producing similar increases in fMRI and EEG responses (Lang et al., 1998; Sabatinelli et al., 2009). Critically, because these emotion and attention effects have distinct sources, they may occur in a parallel or competitive manner and produce additive (or occasionally interactive) effects on sensory responses (Vuilleumier et al., 2001a; Keil et al., 2005; Brosch et al., 2011; Rossi and Pourtois, in press).

Hence, these affective biases in perception might be conceived as reflecting a distinct neural system for “emotional attention”, which help guide the selection of sensory stimuli for awareness and adaptive behavior, but based on their affective value rather than sensory or spatial attributes (Vuilleumier, 2005; Vuilleumier and Huang, 2009; Lang et al., 1997). Such effects are somewhat similar to those of object-based attention, which help organize sensory inputs into potentially relevant object parts based on internal processes capable of extracting surface and gestalt cues associated with objecthood or familiar configurations (Driver et al., 1992; Baylis and Driver, 1993). Like emotional effects, object-based attention can operate in the absence of voluntary attention and has distinct neuro-anatomical substrates within the ventral cortical visual stream (Vuilleumier et al., 2001b; McMains and Kastner, 2011), which act to increase the competitive strength of relevant information in the selection for attention (Driver et al., 1992; Baylis and Driver, 1993).

Furthermore, like object-based and exogenous mechanisms of attention, emotional influences on perception and attention appear to be “reflexive” (Hodsoll et al., 2011) in the sense that these effects are usually tacit, arising irrespective of the task demands, and triggered involuntarily or without conscious monitoring (Moors and De Houwer, 2006). However, as many other reflexive processes in the nervous system, this degree of involuntariness and automaticity does not imply that such effects are inflexible and resistant to contextual factors, including (in)compatibility with current goals or goal conduciveness (Vogt et al., 2010a,b), as well as modulations by perceptual load and expectations (Pessoa et al., 2002b; Hahn and Gronlund, 2007). For example, weaker inputs due to greater competition or endogenous attention might reduce the strength of emotional biases. It is also likely that the emotion feedback loops from amygdala to sensory areas can be regulated by top–down signals from other brain regions, particularly orbitofrontal and ventromedial prefrontal areas (Vuilleumier, 2009; see Fig. 4).

In particular, amygdala reactivity and emotional attention effects might depend on the current emotional context, as well as the participant’s emotional state and his/her personality dispositions (see Bishop, 2007; Cornwell et al., 2011). For example, the induction of acute stress or state anxiety can increase amygdala responses and reflexive enhancement of sensory cortices (Cornwell et al., 2011; van Marle et al., 2009; Rossi and Pourtois, in press), but also diminish threat-selectivity due to amplified responses to neutral or positive stimuli (van Marle et al., 2009). Thus, spontaneous anxiety associated with personal characteristics or incidental priming with threat information tend to reduce voluntary attentional filtering and increase amygdala responses to fearful face distractors at unattended locations (Bishop, 2007). Likewise, induced states of anxiety (e.g. threat of shock) can override the suppression of emotional effects normally caused by an augmented attentional load (Cornwell et al., 2011). Threat of shock also tends to increase neural responses in extrastriate visual cortex and the N1 component observed in ERPs, even for neutral visual stimuli (see Vogel and Luck, 2000; Shackman et al., 2011), reflecting a more general boost of perceptual discrimination processes due to arousal and acute anxiety, although a causal role for the amygdala in these latter effects remains to be determined. Moreover, motivational factors related to task difficulty and error monitoring in conditions of high load might further complicate response patterns in the amygdala (Pourtois et al., 2010c), and perhaps also contribute to diminish threat-selectivity of activations in this structure in some conditions (Williams et al., 2005a; see also Vuilleumier et al., 2002; Silvert et al., 2007; van Marle et al., 2009). Behaviorally, both state and trait anxiety have long been known to potentiate the impact of emotional (threat-related) biases in attention and perception across various tasks (Fox, 2002; Bar-Haim et al., 2007; Bradley et al., 1997; Mogg and Bradley, 1998), and the circuitry reviewed here provides plausible mechanisms to account for these effects (see Fig. 4).

In sum, therefore, there is no reason to assume that reflexive (i.e. automatic and involuntary) emotional responses in amygdala and subsequent influences on perception would imply a process that is totally encapsulated, “resource” free, and unaffected by changes in amount or duration of sensory inputs (e.g. Pessoa et al., 2002a; Pessoa, 2005). We believe that emotional stimuli have no “magic” or special intrinsic properties that make them immune to perceptual constraints imposed to other “regular” stimuli; but rather these stimuli can, under appropriate circumstances, spark off dedicated neural systems centered on the amygdala that can exert powerful influences on ongoing sensory processing and boost their representation and access to awareness relative to neutral information, through mechanisms partly independent of voluntary top–down attention control (Vuilleumier and Huang, 2009). Modulations by

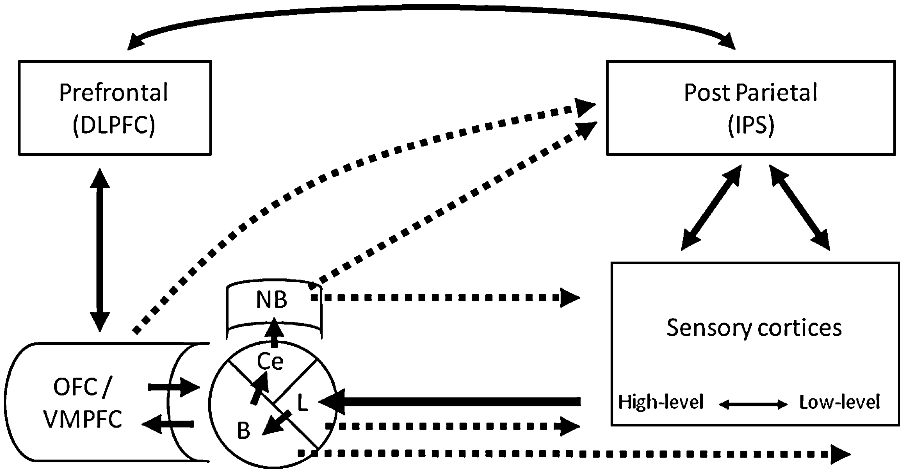

Fig. 4. Schematic diagram of neural pathways mediating interactions between emotional and attentional control. The amygdala mainly receives sensory information through the lateral nucleus (L) and sends feedback from both lateral (L) and basal (B) nuclei to different stages along sensory cortical areas. These projections may act to boost the representation and memory formation for emotionally relevant information. Amygdala output via the central nucleus (Ce) can also activate cholinergic projections from nucleus basalis (NB) in the forebrain that, in turn, modulate parietal as well as frontal and sensory cortical regions. These projections may promote alerting reactions and shifts of attention. Other output signals from the amygdala target ventral and medial prefrontal areas to guide behavior, decision making, and motor action. Projections to other systems in brainstem (noradrenergic) are not shown here. The strength of output signals and feedback loops may be modulated by signals from orbitofrontal cortex, as well as rostral regions in anterior cingulate (ACC) and dorsolateral prefrontal cortex (DLPFC). Top–down interactions between frontal, parietal, and sensory areas control the allocation of attentional resources to task-relevant locations or objects and mediate voluntary control. Altogether, these different regulatory systems provide multiple (additive or interactive) sources of modulations on sensory pathways that ultimately determine their access to awareness and memory systems. Functional alterations in regulatory mechanism exerted by prefrontal areas onto the amygdala may lead to the maintenance and vulnerability to negative affect or anxiety.

task load, expectations, or affective states are not inconsistent with reflexive mechanisms, as similar effects are also observed for exogenous mechanisms of attention that are typically considered to be automatic and involuntary (e.g. Folk et al., 1992; Santangelo et al., 2008). Likewise, pre-attentive or unconscious processing is not a privilege of emotional stimuli and can arise for complex (e.g. semantic) information without necessarily requiring a special (e.g. subcortical) route (e.g. Kouider and Dehaene, 2007), and preserved activation of the amygdala despite reduced cortical processing may simply reflect distinct categorization thresholds for different brain areas, perhaps operating at different latencies and based on partly different sensory information (Winston et al., 2003; Pourtois et al., 2005a). More importantly, the framework described here suggests that perception and attention are not governed by a single source of (top–down) modulatory signals, but instead emerge from competitive interactions between multiple factors that operate in parallel to increase the saliency and selection of behaviorally relevant information (Vuilleumier, 2005; Vuilleumier and Driver, 2007; McMains and Kastner, 2011). Emotion signals may thus act on perception via gain control mechanisms that have different sources than other (e.g. endogenous and voluntary) attentional processes, but similar targets in sensory pathways and similar effects on perceptual processing (Rossi and Pourtois, in press). Overall, this functional architecture is consistent with a “Multiple Attention Gain Control” (MAGiC) model, in which emotional biases in perception have many similarities with other classic attention mechanisms but also distinctive neural substrates and time-courses. In this model, the amygdala appears to play a key role in favoring attention towards emotional stimuli, though other brain areas or circuits (such as OFC, ACC, pulvinar, or brainstem neuromodulator systems) are likely to also contribute to this process. Like magic in art, this model does not invoke a “supernatural” power of emotion to influence sensation but instead rely on a set of several well-defined processes to “do the trick”.

Another important implication of this model is that it allows for distinct causes of modulations through both extrinsic and intrinsic factors, rather than just by the amount of inputs or resources allocated through endogenous attentional control. For example, the emotional attention system might be either amplified or attenuated by top–down modulations from higher-order regions in medial prefrontal/anterior cingulate/orbitofrontal regions involved in emotion regulation processes (see Fig. 4; Drevets and Raichle, 1998; Ochsner and Gross, 2005; Etkin et al., 2010a), but also through changes in the “firing threshold” settings of amygdala circuitry itself. These different kinds of modulations might produce different effects and be associated with different (e.g. psychopathological) conditions. A break-down in top–down “cognitive” control (resulting from functional alterations within prefrontal-amygdalar regulatory circuits, see Etkin et al., 2010b) might increase vulnerability to and maintenance of anxiety and negative affect (Bishop, 2007; Bishop et al., 2004a). This could in turn account for attention selection biases towards negative stimuli typically observed in some psychopathological conditions, such as general anxiety or depression (Fox, 2002; Mogg et al., 2000; Bar-Haim et al., 2007; Bishop, 2007; De Raedt and Koster, 2010). Alternatively, emotional attention could be exacerbated due to purely intrinsic changes in amygdala and hyper-reactivity of the sensory feedback loops (e.g. via learning or conditioning), a pattern possibly associated with specific phobias (such as snake or spider fears) rather than general anxiety (see Box 3).

Finally, we note that most of the empirical evidence supporting the framework reviewed here has been obtained with negative or threat-related stimuli. This focus of past research is understandable given the obvious and vital importance of efficient attention to threat (see Compton, 2003; Vuilleumier, 2005), as well as the crucial links with amygdala function (LeDoux, 1996; Amaral et al., 2003; Phelps and LeDoux, 2005) and the direct implications for psychopathology (Öhman and Mineka, 2001; Bar-Haim et al., 2007). However, it must be underscored that both human imaging studies (Phan et al., 2002; Kober et al., 2008) and neuronal recordings in primates (Paton et al., 2006; Baxter and Murray, 2002) have shown that the amygdala also activates to positive or arousing emotional stimuli, which sometimes also carry an important behavioral relevance (see Sander et al., 2003) and therefore may potentially induce similar emotional biases (e.g. see Schupp et al., 2006; Brosch et al., 2008). Moreover, reward learning can enhance perception and attention (Hickey et al., 2010), and also modulate the activity of parietal neurons that are usually related to attention (Maunsell, 2004; Platt and Glimcher, 1999). Although positive emotions have long been thought to produce distinctive effects of attention (e.g. broadening and shifting; see Fredrickson, 2004), more research is needed to determine the commonalities and specificities relative to emotional attention effects driven by fear-related information (see also Vuilleumier, 2005).

Box 3: Emotional attention in psychopathology. How can what we have learned about emotional attention in specific clinical, sub-clinical or healthy samples inform improved intervention strategies for relevant pathologies?

The amygdala-dependent circuits for emotional attention, as outlined here, may be considered as mediating a "reflexive" process whose amplitude is regulated by higher-order brain areas, involving mainly prefrontal and cingulate regions. There is abundant evidence that amygdala activity can be increased or decreased depending on explicit emotion regulation strategies, as well as personality factors, genetic makeup, and specific psychiatric disorders such as anxiety and depression (e.g. Drevets, 2003; Ochsner and Gross, 2005; Etkin et al., 2010a; Cornwell et al., 2011; Pezawas et al., 2005; Hariri et al., 2002; Canli et al., 2002). Moreover, in all these conditions, changes in amygdala activity have generally been associated with primary or secondary alterations in prefrontal areas. Our framework (see also Vuilleumier, 2005, 2009) provides a plausible neuroanatomical model to account for the behavioral attention effects that are observed in a wide range of psychopathological conditions, including anxiety. For example, anxious or depressed patients typically show maladaptive attentional biases towards negative information. Selective breakdowns in prefrontal top–down control mechanisms might account for heightened reactivity of the emotional attention systems, and perhaps reduced selectivity or overgeneralization, leading to the maintenance of and vulnerability to negative affect (Bishop, 2007). Other effects related to expectations, prior knowledge, past experience or affective predispositions may also shape and either up or down-regulate the normal functioning of emotional attention. For example, even though increasing the perceptual demands of a tasks (high load) may sometimes reduce activation of the amygdala to negative stimuli (see Pessoa et al., 2002b), experimental conditions involving a threat of shock (i.e. enhanced state anxiety) can attenuate the attention load effect and restore a greater amygdala activation to unattended fearful faces compared to neutral faces, likely reflecting an enhanced sensitivity to potential danger cues (Cornwell et al., 2011). These effects of expectations or affective states are unlike responses to shock or shock-associated stimuli themselves, which may be reduced under high load (Lim et al., 2008) or low stimulus visibility/awareness conditions (Lim et al., 2009). On the other hand, trait anxiety, which is characterized by attention control impairments (Eysenck et al., 2007; Derryberry and Reed, 2002) and a decreased or abnormal recruitment of prefrontal-cingulate performance monitoring regions (Bishop et al., 2004a), might produce distinct functional alterations within the amygdala that increase its output to other brain regions involved in autonomic control and stress regulation via projections from the central rather than basolateral amygdala (Bishop et al., 2004b). Moreover, state vs. trait anxiety may have a different impact on the emotional attention network, with state anxiety perhaps mainly influencing stimulus-driven responses within the amygdala, and trait anxiety more specifically altering the top–down control exerted by prefrontal regions onto the amygdala (see Bishop, 2007). Finally, phobia might implicate functional and/or structural changes primarily affecting the amygdala itself, rather than the regulatory prefrontal circuits (see Irle et al., 2010). Accordingly, recent meta-analyses of neuroimaging results for different categories of anxiety disorders suggest that each disorder tends to be associated with a distinctive pattern of changes in brain areas overlapping with those involved in emotional attention (see Etkin and Wager, 2007). These distinctions may in turn have important implications for remediation strategies or compensation mechanisms triggered by psychotherapeutic treatments. For example, one can speculate that if the anxiety results from a functional alteration within the prefrontal-amygdala network controlling amygdala responsiveness, then the use of explicit regulation strategies such as self-distancing or reappraisal (see Ochsner and Gross, 2005; Kalisch, 2009) may turn out to be difficult to implement, and therefore less effective than manipulations acting on "intact" part of the circuits; whereas conversely reinforcing top–down prefrontal modulation on the amygdala might be more appropriate for other anxiety disorders such as phobia.

To conclude, the "magic" of emotional influences on attention is to unveil the fact that affective appraisals do not only serve to add feelings to our senses, as simple colors or flavors added to objects perceived in the world. Indeed, emotion signals and motivational relevance appear to have a direct and causal impact on how sensory information is selected, and can thus strongly influence what is perceived and what is ignored. The past decade of research in cognitive neuroscience has witnessed tremendous advances in our understanding of the brain substrates underlying these effects, and the various sources of modulations that may affect them. Additional studies are still needed, however, to better characterize the exact neural pathways implicated in different stages of the emotional attention deployment, and to determine the exact degree of overlap vs. separation with other attention mechanisms, as well as their respective timing following stimulus onset. In addition, although past research has focused on the amygdala and direct connections to cortical and subcortical sensory pathways, this system is likely to form a more extended functional network with other brain regions, including subcortical nuclei in basal forebrain and brainstem, as well as the periaqueductal gray (PAG), thalamus, and several prefrontal areas in orbitofrontal (OFC), ventromedial prefrontal (VMPC), and anterior cingulate cortex (ACC) – all these regions being usually activated during rapid processing and response to emotionally relevant stimuli in the environment (Mobbs et al., 2009, 2007; see also Dominguez-Borras and Vuilleumier, in press). As a matter of fact, earlier animal work already suggested that, besides the amygdala, other structures (e.g. OFC or insula), may be involved in re-entrant processing during fear conditioning, startle modulation, as well as the modulation of visual processing (Shi and Davis, 2001). To fully understand this system, it will be important to dissect each of its components, and to define its specificities and connections with other brain mechanisms associated with attention gain control. By doing so, researchers should go beyond the traditional notions of a single attention system or binary (e.g. controlled vs. automatic) divisions, but instead redefine the corresponding psychological construct and behavioral phenomena in terms of their underlying neural processes.

Acknowledgements

GP is supported by grants from the European Research Council (Starting Grant #200758) and Ghent University (BOF Grant #05Z01708). The authors thank the organizers of the Emotional Attention international symposium held in Ghent in January 2011 for giving us the opportunity to contribute to this special issue, and the four reviewers for their comments and suggestions.

References

Achaibou, A., Pourtois, G., Schwartz, S., Vuilleumier, P., 2008. Simultaneous recording of EEG and facial muscle reactions during spontaneous emotional mimicry. Neuropsychologia 46 (4), 1104–1113.

Adolphs, R., 1999. Social cognition and the human brain. Trends Cogn. Sci. 3 (12), 469–479.

Adolphs, R., Gosselin, F., Buchanan, T.W., Tranel, D., Schyns, P., Damasio, A.R., 2005. A mechanism for impaired fear recognition after amygdala damage. Nature 433 (7021), 68–72.

Adolphs, R., Tranel, D., Damasio, H., Damasio, A., 1994. Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. Nature 372 (6507), 669–672.

Adolphs, R., Tranel, D., Damasio, H., Damasio, A.R., 1995. Fear and the human amygdala. J. Neurosci. 15 (9), 5879–5891.

Allison, T., Puce, A., Spencer, D.D., McCarthy, G., 1999. Electrophysiological studies of human face perception. I: potentials generated in occipitotemporal cortex by face and non-face stimuli. Cereb. Cortex 9 (5), 415–430.

Alorda, C., Serrano-Pedraza, I., Campos-Bueno, J.J., Sierra-Vazquez, V., Montoya, P., 2007. Low spatial frequency filtering modulates early brain processing of affective complex pictures. Neuropsychologia 45 (14), 3223–3233.

Amaral, D.G., Behniea, H., Kelly, J.L., 2003. Topographic organization of projections from the amygdala to the visual cortex in the macaque monkey. Neuroscience 118 (4), 1099–1120.

Anders, S., Birbaumer, N., Sadowski, B., Erb, M., Mader, I., Grodd, W., et al., 2004. Parietal somatosensory association cortex mediates affective blindsight. Nat. Neurosci. 7 (4), 339–340.

Anderson, A.K., 2005. Affective influences on the attentional dynamics supporting awareness. J. Exp. Psychol. Gen. 134 (2), 258–281.

Anderson, A.K., Christoff, K., Panitz, D., De Rosa, E., Gabrieli, J.D., 2003. Neural correlates of the automatic processing of threat facial signals. J. Neurosci. 23 (13), 5627–5633.

Anderson, A.K., Phelps, E.A., 2001. Lesions of the human amygdala impair enhanced perception of emotionally salient events. Nature 411 (6835), 305–309.

Ansorge, U., Kiss, M., Eimer, M., 2009. Goal-driven attentional capture by invisible colors: evidence from event-related potentials. Psychon. Bull. Rev. 16 (4), 648–653.

Armony, J.L., Dolan, R.J., 2002. Modulation of spatial attention by fear-conditioned stimuli: an event-related fMRI study. Neuropsychologia 40 (7), 817–826.

Armony, J.L., Quirk, G.J., LeDoux, J.E., 1998. Differential effects of amygdala lesions on early and late plastic components of auditory cortex spike trains during fear conditioning. J. Neurosci. 18 (7), 2592–2601.

Armony, J.L., Servan-Schreiber, D., Cohen, J.D., Ledoux, J.E., 1997. Computational modeling of emotion: explorations through the anatomy and physiology of fear conditioning. Trends Cogn. Sci. 1 (1), 28–34.

Bach, D.R., Talmi, D., Hurlemann, R., Patin, A., Dolan, R.J., 2011. Automatic relevance detection in the absence of a functional amygdala. Neuropsychologia 49 (5), 1302–1305.

Bar-Haim, Y., Lamy, D., Pergamin, L., Bakermans-Kranenburg, M.J., van Ijzendoorn, M.H., 2007. Threat-related attentional bias in anxious and nonanxious individuals: a meta-analytic study. Psychol. Bull. 133 (1), 1–24.

Bar, M., 2003. A cortical mechanism for triggering top-down facilitation in visual object recognition. J. Cogn. Neurosci. 15 (4), 600–609.

Bar, M., Kassam, K.S., Ghuman, A.S., Boshyan, J., Schmid, A.M., Dale, A.M., et al., 2006. Top-down facilitation of visual recognition. Proc. Natl. Acad. Sci. U.S.A. 103 (2), 449–454.

Barbas, H., Zikopoulos, B., Timbie, C., 2010. Sensory pathways and emotional context for action in primate prefrontal cortex. Biol. Psychiatry 69 (12), 1133–1139.

Bartolomeo, P., Thiebaut de Schotten, M., Doricchi, F., 2007. Left unilateral neglect as a disconnection syndrome. Cereb. Cortex 17 (11), 2479–2490.

Batty, M., Taylor, M.J., 2003. Early processing of the six basic facial emotional expressions. Brain Res. Cogn. Brain Res. 17 (3), 613–620.

Baxter, M.G., Murray, E.A., 2002. The amygdala and reward. Nat. Rev. Neurosci. 3 (7), 563–573.

Bayle, D.J., Henaff, M.A., Krolak-Salmon, P., 2009. Unconsciously perceived fear in peripheral vision alerts the limbic system: a MEG study. PLoS ONE 4 (12), e8207.

Baylis, G.C., Driver, J., 1993. Visual attention and objects: evidence for hierarchical coding of location. J. Exp. Psychol. Hum. Percept. Perform. 19 (3), 451–470.

Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. J. Cogn. Neurosci. 8 (6), 551–565.

Bentley, P., Vuilleumier, P., Thiel, C.M., Driver, J., Dolan, R.J., 2003. Cholinergic enhancement modulates neural correlates of selective attention and emotional processing. NeuroImage 20 (1), 58–70.

Benuzzi, F., Meletti, S., Zamboni, G., Calandra-Buonaura, G., Serafini, M., Lui, F., et al., 2004. Impaired fear processing in right mesial temporal sclerosis: a fMRI study. Brain Res. Bull. 63 (4), 269–281.

Bishop, S., 2007. Neurocognitive mechanisms of anxiety: an integrative account. Trends Cogn. Sci. 11 (7), 307–316.

Bishop, S., Duncan, J., Lawrence, A.D., 2004a. Prefrontal cortical function and anxiety: controlling attention to threat-related stimuli. Nat. Neurosci. 7 (2), 184–188.

Bishop, S., Duncan, J., Lawrence, A.D., 2004b. State anxiety modulation of the amygdala response to unattended threat-related stimuli. J. Neurosci. 24 (46), 10364–10368.

Bocanegra, B.R., Zeelenberg, R., 2009. Emotion improves and impairs early vision. Psychol. Sci. 20 (6), 707–713.

Bocanegra, B.R., Zeelenberg, R., 2011. Emotion-induced trade-offs in spatiotemporal vision. J. Exp. Psychol. Gen. 140 (2), 272–282.

Bradley, B., Mogg, K., Millar, N., BonhamCarter, C., Fergusson, E., Jenkins, J., et al., 1997. Attentional biases for emotional faces. Cogn. Emot. 11 (1), 25–42.

Bradley, M., 2009. Natural selective attention: orienting and emotion. Psychophysiology 46 (1), 1–11.

Brockelmann, A.K., Steinberg, C., Elling, L., Zwanzger, P., Pantev, C., Junghöfer, M., 2011. Emotion-associated tones attract enhanced attention at early auditory processing: magnetoencephalographic correlates. J. Neurosci. 31 (21), 7801–7810.

Brosch, T., Grandjean, D., Sander, D., Scherer, K.R., 2009. Cross-modal emotional attention: emotional voices modulate early stages of visual processing. J. Cogn. Neurosci. 21 (9), 1670–1679.

Brosch, T., Pourtois, G., Sander, D., 2010. The perception and categorization of emotional stimuli: a review. Cogn. Emot. 24 (3), 377–400.

Brosch, T., Pourtois, G., Sander, D., Vuilleumier, P., 2011. Additive effects of emotional, endogenous, and exogenous attention: behavioral and electrophysiological evidence. Neuropsychologia 49, 1779–1787.

Brosch, T., Sander, D., Pourtois, G., Scherer, K.R., 2008. Beyond fear: rapid spatial orienting toward positive emotional stimuli. Psychol. Sci. 19 (4), 362–370.

Buchanan, T.W., 2007. Retrieval of emotional memories. Psychol. Bull. 133 (5), 761–779.

Bullier, J., 2001. Integrated model of visual processing. Brain Res. Brain Res. Rev. 36 (2–3), 96–107.

Bullier, J., Nowak, L.G., 1995. Parallel versus serial processing: new vistas on the distributed organization of the visual system. Curr. Opin. Neurobiol. 5 (4), 497–503.

Canli, T., Sivers, H., Whitfield, S.L., Gotlib, I.H., Gabrieli, J.D., 2002. Amygdala response to happy faces as a function of extraversion. Science 296 (5576), 2191.

Cardinal, R.N., Parkinson, J.A., Hall, J., Everitt, B.J., 2002. Emotion and motivation: the role of the amygdala, ventral striatum, and prefrontal cortex. Neurosci. Biobehav. Rev. 26 (3), 321–352.

Carrasco, M., Loula, F., Ho, Y.X., 2006. How attention enhances spatial resolution: evidence from selective adaptation to spatial frequency. Percept. Psychophys. 68 (6), 1004–1012.

Carretie, L., Hinojosa, J.A., Lopez-Martin, S., Tapia, M., 2007. An electrophysiological study on the interaction between emotional content and spatial frequency of visual stimuli. Neuropsychologia 45 (6), 1187–1195.

Carretie, L., Hinojosa, J.A., Mercado, F., Tapia, M., 2005. Cortical response to subjectively unconscious danger. NeuroImage 24 (3), 615–623.

Carrétie, L., Iglesias, J., Garcia, T., Ballesteros, M., 1997. N300, P300 and the emotional processing of visual stimuli. Electroencephalogr. Clin. Neurophysiol. 103 (2), 298–303.

Catani, M., Jones, D.K., Donato, R., Ffytche, D.H., 2003. Occipito-temporal connections in the human brain. Brain 126 (Pt 9), 2093–2107.

Chelazzi, L., Miller, E.K., Duncan, J., Desimone, R., 1993. A neural basis for visual search in inferior temporal cortex. Nature 363 (6427), 345–347.

Chica, A.B., Bartolomeo, P., Valero-Cabre, A., 2011. Dorsal and ventral parietal contributions to spatial orienting in the human brain. J. Neurosci. 31 (22), 8143–8149.

Ciesielski, B.G., Armstrong, T., Zald, D.H., Olatunji, B.O., 2010. Emotion modulation of visual attention: categorical and temporal characteristics. PLoS ONE 5 (11), e13860.

Clark, V.P., Fan, S., Hillyard, S.A., 1995. Identification of early visual evoked potential generators by retinotopic and topographic analyses. Hum. Brain Mapp. 2, 170–187.

Clarke, S., Riahi-Arya, S., Tardif, E., Eskenasy, A.C., Probst, A., 1999. Thalamic projections of the fusiform gyrus in man. Eur. J. Neurosci. 11 (5), 1835–1838.

Compton, R.J., 2003. The interface between emotion and attention: a review of evidence from psychology and neuroscience. Behav. Cogn. Neurosci. Rev. 2 (2), 115–129.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3 (3), 201–215.

Corbetta, M., Shulman, G.L., 2011. Spatial neglect and attention networks. Annu. Rev. Neurosci. 34, 569–599.

Cornwell, B.R., Alvarez, R.P., Lissek, S., Kaplan, R., Ernst, M., Grillon, C., 2011. Anxiety overrides the blocking effects of high perceptual load on amygdala reactivity to threat-related distractors. Neuropsychologia 49 (5), 1363–1368.

Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., et al., 2000. Explicit and implicit neural mechanisms for processing of social information from facial expressions: a functional magnetic resonance imaging study. Hum. Brain Mapp. 9 (2), 93–105.

Damaraju, E., Huang, Y.M., Barrett, L.F., Pessoa, L., 2009. Affective learning enhances activity and functional connectivity in early visual cortex. Neuropsychologia 47 (12), 2480–2487.

Davis, M., Whalen, P.J., 2001. The amygdala: vigilance and emotion. Mol. Psychiatry 6 (1), 13–34.

Day-Brown, J.D., Wei, H., Chomsung, R.D., Petry, H.M., Bickford, M.E., 2010. Pulvinar projections to the striatum and amygdala in the tree shrew. Front. Neuroanat. 4, 143.

de Gelder, B., Vroomen, J., Pourtois, G., Weiskrantz, L., 1999. Non-conscious recognition of affect in the absence of striate cortex. Neuroreport 10 (18), 3759–3763.

De Raedt, R., Koster, E.H., 2010. Understanding vulnerability for depression from a cognitive neuroscience perspective: a reappraisal of attentional factors and a new conceptual framework. Cogn. Affect. Behav. Neurosci. 10 (1), 50–70.

Dehaene, S., Changeux, J.P., Naccache, L., Sackur, J., Sergent, C., 2006. Conscious, preconscious, and subliminal processing: a testable taxonomy. Trends Cogn. Sci. 10 (5), 204–211.

Dehaene, S., Naccache, L., Cohen, L., Bihan, D.L., Mangin, J.F., Poline, J.B., et al., 2001. Cerebral mechanisms of word masking and unconscious repetition priming. Nat. Neurosci. 4 (7), 752–758.

Dehaene, S., Naccache, L., Le Clec, H.G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., et al., 1998. Imaging unconscious semantic priming. Nature 395 (6702), 597–600.

Dennis, T.A., Chen, C.C., 2007. Neurophysiological mechanisms in the emotional modulation of attention: the interplay between threat sensitivity and attentional control. Biol. Psychol. 76 (1–2), 1–10.

Derryberry, D., Reed, M.A., 2002. Anxiety-related attentional biases and their regulation by attentional control. J. Abnorm. Psychol. 111, 225–236.

Desimone, R., Duncan, J., 1995. Neural mechanisms of selective visual attention. Annu. Rev. Neurosci. 18, 193–222.

Devue, C., Belopolsky, A.V., Theeuwes, J., 2011. The role of fear and expectancies in capture of covert attention by spiders. Emotion 11 (4), 768–775.

Di Russo, F., Martinez, A., Hillyard, S.A., 2003. Source analysis of event-related cortical activity during visuo-spatial attention. Cereb. Cortex 13 (5), 486–499.

Dijksterhuis, A., Aarts, H., 2010. Goals, attention, and (Un)consciousness. Annu. Rev. Psychol. 61, 467–490.

Dominguez-Borras, J., Garcia-Garcia, M., Escera, C., 2008. Emotional context enhances auditory novelty processing: behavioural and electrophysiological evidence. Eur. J. Neurosci. 28 (6), 1199–1206.

Dominguez-Borras, J., Vuilleumier, P. Affective biases in attention and perception. In: Vuilleumier, P., Armony, J. (Eds.), Handbook of Human Affective Neuroscience. Cambridge University Press, Cambridge, in press.

Downing, P., Liu, J., Kanwisher, N., 2001. Testing cognitive models of visual attention with fMRI and MEG. Neuropsychologia 39 (12), 1329–1342.

Drevets, W.C., 2003. Neuroimaging abnormalities in the amygdala in mood disorders. Ann. N. Y. Acad. Sci. 985, 420–444.

Drevets, W.C., Raichle, M.E., 1998. Reciprocal suppression of regional cerebral blood flow during emotional versus higher cognitive processes: implications for interactions between emotion and cognition. Cogn. Emot. 12 (3), 353–385.

Driver, J., Baylis, G.C., Rafal, R.D., 1992. Preserved figure-ground segregation and symmetry perception in visual neglect. Nature 360 (6399), 73–75.

Driver, J., Davis, G., Russell, C., Turatto, M., Freeman, E., 2001. Segmentation, attention and phenomenal visual objects. Cognition 80 (1–2), 61–95.

Driver, J., Vuilleumier, P., 2001. Perceptual awareness and its loss in unilateral neglect and extinction. Cognition 79 (1–2), 39–88.

Droit-Volet, S., Meck, W.H., 2007. How emotions colour our perception of time. Trends Cogn. Sci. 11 (12), 504–513.

Eastwood, J.D., Smilek, D., Merikle, P.M., 2001. Differential attentional guidance by unattended faces expressing positive and negative emotion. Percept. Psychophys. 63 (6), 1004–1013.

Eastwood, J.D., Smilek, D., Merikle, P.M., 2003. Negative facial expression captures attention and disrupts performance. Percept. Psychophys. 65 (3), 352–358.

Egeth, H.E., Yantis, S., 1997. Visual attention: control, representation, and time course. Annu. Rev. Psychol. 48, 269–297.

Eimer, M., 1996. The N2pc component as an indicator of attentional selectivity. Electroencephalogr. Clin. Neurophysiol. 99 (3), 225–234.

Eimer, M., Schlaghecken, F., 2002. Links between conscious awareness and response inhibition: evidence from masked priming. Psychon. Bull. Rev. 9 (3), 514–520.

Eimer, M., Schlaghecken, F., 2003. Response facilitation and inhibition in subliminal priming. Biol. Psychol. 64 (1–2), 7–26.

Erthal, F.S., de Oliveira, L., Mocaiber, I., Pereira, M.G., Machado-Pinheiro, W., Volchan, E., et al., 2005. Load-dependent modulation of affective picture processing. Cogn. Affect. Behav. Neurosci. 5 (4), 388–395.

Ethofer, T., Bretscher, J., Gschwind, M., Kreifelts, B., Wildgruber, D., Vuilleumier, P., 2012. Emotional voice areas: anatomic location, functional properties, and structural connections revealed by combined fMRI/DTI. Cereb. Cortex 22 (1), 191–200.

Ethofer, T., Van De Ville, D., Scherer, K., Vuilleumier, P., 2009. Decoding of emotional information in voice-sensitive cortices. Curr. Biol. 19 (12), 1028–1033.

Etkin, A., Egner, T., Kalisch, R., 2010a. Emotional processing in anterior cingulate and medial prefrontal cortex. Trends Cogn. Sci. 15 (2), 85–93.

Etkin, A., Prater, K.E., Hoeft, F., Menon, V., Schatzberg, A.F., 2010b. Failure of anterior cingulate activation and connectivity with the amygdala during implicit regulation of emotional processing in generalized anxiety disorder. Am. J. Psychiatry 167 (5), 545–554.

Etkin, A., Wager, T.D., 2007. Functional neuroimaging of anxiety: a meta-analysis of emotional processing in PTSD, social anxiety disorder, and specific phobia. Am. J. Psychiatry 164 (10), 1476–1488.

Eysenck, M.W., Derakshan, N., Santos, R., Calvo, M.G., 2007. Anxiety and cognitive performance: attentional control theory. Emotion 7 (2), 336–353.

Fecteau, S., Belin, P., Joanette, Y., Armony, J.L., 2007. Amygdala responses to nonlinguistic emotional vocalizations. NeuroImage 36 (2), 480–487.

Flaisch, T., Schupp, H.T., Renner, B., Junghöfer, M., 2009. Neural systems of visual attention responding to emotional gestures. NeuroImage 45 (4), 1339–1346.

Folk, C.L., Remington, R.W., Johnston, J.C., 1992. Involuntary covert orienting is contingent on attentional control settings. J. Exp. Psychol. Hum. Percept. Perform. 18 (4), 1030–1044.

Fox, E., 1993. Allocation of visual-attention and anxiety. Cogn. Emot. 7 (2), 207–215.

Fox, E., 2002. Processing emotional facial expressions: the role of anxiety and awareness. Cogn. Affect. Behav. Neurosci. 2 (1), 52–63.

Fox, E., Lester, V., Russo, R., Bowles, R.J., Pichler, A., Dutton, K., 2000. Facial expressions of emotion: are angry faces detected more efficiently? Cogn. Emot. 14 (1), 61–92.

Fox, E., Russo, R., Bowles, R., Dutton, K., 2001. Do threatening stimuli draw or hold visual attention in subclinical anxiety? J. Exp. Psychol. Gen. 130 (4), 681–700.

Fredrickson, B.L., 2004. The broaden-and-build theory of positive emotions. Philos. Trans. R. Soc. Lond. B Biol. Sci. 359 (1449), 1367–1377.

Fredrikson, M., Wik, G., Fischer, H., Andersson, J., 1995. Affective and attentive neural networks in humans: a PET study of Pavlovian conditioning. Neuroreport 7 (1), 97–101.

Frischen, A., Eastwood, J.D., Smilek, D., 2008. Visual search for faces with emotional expressions. Psychol. Bull. 134 (5), 662–676.

Gorno-Tempini, M.L., Pradelli, S., Serafini, M., Pagnoni, G., Baraldi, P., Porro, C., et al., 2001. Explicit and incidental facial expression processing: an fMRI study. NeuroImage 14 (2), 465–473.

Gothard, K.M., Battaglia, F.P., Erickson, C.A., Spitler, K.M., Amaral, D.G., 2007. Neural responses to facial expression and face identity in the monkey amygdala. J. Neurophysiol. 97 (2), 1671–1683.

Grabowska, A., Marchewka, A., Seniow, J., Polanowska, K., Jednorog, K., Krolicki, L., et al., 2011. Emotionally negative stimuli can overcome attentional deficits in patients with visuo-spatial hemineglect. Neuropsychologia 49, 3327–3337.

Grandjean, D., Sander, D., Lucas, N., Scherer, K.R., Vuilleumier, P., 2008. Effects of emotional prosody on auditory extinction for voices in patients with spatial neglect. Neuropsychologia 46 (2), 487–496.

Grandjean, D., Sander, D., Pourtois, G., Schwartz, S., Seghier, M.L., Scherer, K.R., et al., 2005. The voices of wrath: brain responses to angry prosody in meaningless speech. Nat. Neurosci. 8 (2), 145–146.

Gschwind, M., Pourtois, G., Schwartz, S., Van de Ville, D., Vuilleumier, P. While-matter connectivity between face-responsive regions in the human brain. Cereb. Cortex, doi:10.1093/cercor/bhr226, in press.

Hahn, S., Gronlund, S.D., 2007. Top-down guidance in visual search for facial expressions. Psychon. Bull. Rev. 14 (1), 159–165.

Hajcak, G., Macnamara, A., Foti, D., Ferri, J., Keil, A. The dynamic allocation of attention to emotion: simultaneous and independent evidence from the late positive potential and steady state visual evoked potentials. Biol. Psychol., doi:10.1016/j.biopsycho.2011.11.012, this issue.

Halgren, E., Baudena, P., Heit, G., Clarke, J.M., Marinkovic, K., Clarke, M., 1994a. Spatio-temporal stages in face and word processing. I. Depth-recorded potentials in the human occipital, temporal and parietal lobes [corrected]. J. Physiol. Paris 88 (1), 1–50.

Halgren, E., Baudena, P., Heit, G., Clarke, M., Marinkovic, K., 1994b. Spatiotemporal stages in face and word-processing. 1. Depth recorded potentials in the human occipital and parietal lobes. J. Physiol. Paris 88 (1), 1–50.

Halgren, E., Baudena, P., Heit, G., Clarke, M., Marinkovic, K., Chauvel, P., 1994c. Spatiotemporal stages in face and word-processing. 2. Depth-recorded potentials in the human frontal and rolandic cortices. J. Physiol. Paris 88 (1), 51–80.

Halgren, E., Raij, T., Marinkovic, K., Jousmaki, V., Hari, R., 2000. Cognitive response profile of the human fusiform face area as determined by MEG. Cereb. Cortex 10 (1), 69–81.

Hariri, A.R., Mattay, V.S., Tessitore, A., Kolachana, B., Fera, F., Goldman, D., et al., 2002. Serotonin transporter genetic variation and the response of the human amygdala. Science 297 (5580), 400–403.

Heinze, H.J., Luck, S.J., Mangun, G.R., Hillyard, S.A., 1990. Visual event-related potentials index focused attention within bilateral stimulus arrays. 1. Evidence for early selection. Electroencephalogr. Clin. Neurophysiol. 75 (6), 511–527.

Henke, K., 2010. A model for memory systems based on processing modes rather than consciousness. Nat. Rev. Neurosci. 11 (7), 523–532.

Henke, K., Mondadori, C.R., Treyer, V., Nitsch, R.M., Buck, A., Hock, C., 2003. Nonconscious formation and reactivation of semantic associations by way of the medial temporal lobe. Neuropsychologia 41 (8), 863–876.

Hickey, C., Chelazzi, L., Theeuwes, J., 2010. Reward changes salience in human vision via the anterior cingulate. J. Neurosci. 30 (33), 11096–11103.

Hillyard, S.A., Anllo-Vento, L., 1998. Event-related brain potentials in the study of visual selective attention. Proc. Natl. Acad. Sci. U.S.A. 95 (3), 781–787.

Hillyard, S.A., Teder-Salejarvi, W.A., Munte, T.F., 1998a. Temporal dynamics of early perceptual processing. Curr. Opin. Neurobiol. 8 (2), 202–210.

Hillyard, S.A., Vogel, E.K., Luck, S.J., 1998b. Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. Philos. Trans. R. Soc. Lond. B Biol. Sci. 353 (1373), 1257–1270.

Hodsoll, S., Viding, E., Lavie, N., 2011. Attentional capture by irrelevant emotional distractor faces. Emotion 11 (2), 346–353.

Holland, P.C., Gallagher, M., 1999. Amygdala circuitry in attentional and representational processes. Trends Cogn. Sci. 3 (2), 65–73.

Holmes, A., Green, S., Vuilleumier, P., 2005. The involvement of distinct visual channels in rapid attention towards fearful facial expressions. Cogn. Emot. 19 (6), 899–922.

Holmes, A., Vuilleumier, P., Eimer, M., 2003. The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials. Brain Res. Cogn. Brain Res. 16 (2), 174–184.

Hopfinger, J.B., Ries, A.J., 2005. Automatic versus contingent mechanisms of sensory-driven neural biasing and reflexive attention. J. Cogn. Neurosci. 17 (8), 1341–1352.

Hopfinger, J.B., West, V.M., 2006. Interactions between endogenous and exogenous attention on cortical visual processing. NeuroImage 31 (2), 774–789.

Humphreys, G.W., Riddoch, M.J., Forti, S., Ackroyd, K., 2004. Action influences spatial perception: neuropsychological evidence. Vis. Cogn. 11 (2–3), 401–427.

Irle, E., Ruhleder, M., Lange, C., Seidler-Brandler, U., Salzer, S., Dechent, P., et al., 2010. Reduced amygdalar and hippocampal size in adults with generalized social phobia. J. Psychiatry Neurosci. 35 (2), 126–131.

Jeffreys, D.A., Axford, J.G., 1972. Source locations of pattern-specific components of human visual evoked-potentials. 1. Component of striate cortical origin. Exp. Brain Res. 16 (1), 1–21.

Kalisch, R., 2009. The functional neuroanatomy of reappraisal: time matters. Neurosci. Biobehav. Rev. 33 (8), 1215–1226.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. 17 (11), 4302–4311.

Kastner, S., Ungerleider, L.G., 2000. Mechanisms of visual attention in the human cortex. Annu. Rev. Neurosci. 23, 315–341.

Kawasaki, H., Kaufman, O., Damasio, H., Damasio, A.R., Granner, M., Bakken, H., et al., 2001. Single-neuron responses to emotional visual stimuli recorded in human ventral prefrontal cortex. Nat. Neurosci. 4 (1), 15–16.

Keil, A., Costa, V., Smith, J.C., Sabatinelli, D., McGinnis, E.M., Bradley, M.M., et al. Tagging cortical networks in emotion: A topographical analysis. Hum Brain Mapp., doi:10.1002/hbm.21413, in press.

Keil, A., Ihssen, N., 2004. Identification facilitation for emotionally arousing verbs during the attentional blink. Emotion 4 (1), 23–35.

Keil, A., Moratti, S., Sabatinelli, D., Bradley, M.M., Lang, P.J., 2005. Additive effects of emotional content and spatial selective attention on electrocortical facilitation. Cereb. Cortex 15 (8), 1187–1197.

Kelly, S.P., Gomez-Ramirez, M., Foxe, J.J., 2008. Spatial attention modulates initial afferent activity in human primary visual cortex. Cereb. Cortex 18 (11), 2629–2636.

Kennedy, D.P., Adolphs, R., 2010. Impaired fixation to eyes following amygdala damage arises from abnormal bottom-up attention. Neuropsychologia 48 (12), 3392–3398.

Kissler, J., Herbert, C., Peyk, P., Junghöfer, M., 2007. Buzzwords: early cortical responses to emotional words during reading. Psychol. Sci. 18 (6), 475–480.

Kober, H., Barrett, L.F., Joseph, J., Bliss-Moreau, E., Lindquist, K., Wager, T.D., 2008. Functional grouping and cortical-subcortical interactions in emotion: a meta-analysis of neuroimaging studies. NeuroImage 42 (2), 998–1031.

Koster, E.H., De Raedt, R., Goeleven, E., Franck, E., Crombez, G., 2005. Mood-congruent attentional bias in dysphoria: maintained attention to and impaired disengagement from negative information. Emotion 5 (4), 446–455.

Kouider, S., Dehaene, S., 2007. Levels of processing during non-conscious perception: a critical review of visual masking. Philos. Trans. R. Soc. Lond. B Biol. Sci. 362 (1481), 857–875.

Kouider, S., Eger, E., Dolan, R., Henson, R.N., 2009. Activity in face-responsive brain regions is modulated by invisible, attended faces: evidence from masked priming. Cereb. Cortex 19 (1), 13–23.

Krolak-Salmon, P., Fischer, C., Vighetto, A., Mauguiere, F., 2001. Processing of facial emotional expression: spatio-temporal data as assessed by scalp event-related potentials. Eur. J. Neurosci. 13 (5), 987–994.

Krolak-Salmon, P., Henaff, M.A., Vighetto, A., Bertrand, O., Mauguiere, F., 2004. Early amygdala reaction to fear spreading in occipital, temporal, and frontal cortex: a depth electrode ERP study in human. Neuron 42 (4), 665–676.

LaBar, K.S., Cabeza, R., 2006. Cognitive neuroscience of emotional memory. Nat. Rev. Neurosci. 7 (1), 54–64.

LaBar, K.S., LeDoux, J.E., Spencer, D.D., Phelps, E.A., 1995. Impaired fear conditioning following unilateral temporal lobectomy in humans. J. Neurosci. 15 (10), 6846–6855.

Lamme, V.A., 2003. Why visual attention and awareness are different. Trends Cogn. Sci. 7 (1), 12–18.

Lamme, V.A., Roelfsema, P.R., 2000. The distinct modes of vision offered by feedforward and recurrent processing. Trends Neurosci. 23 (11), 571–579.

Lane, R.D., Reiman, E.M., Axelrod, B., Yun, L.S., Holmes, A., Schwartz, G.E., 1998. Neural correlates of levels of emotional awareness: evidence of an interaction between emotion and attention in the anterior cingulate cortex. J. Cogn. Neurosci. 10 (4), 525–535.

Lane, R.D., Reiman, E.M., Bradley, M.M., Lang, P.J., Ahern, G.L., Davidson, R.J., et al., 1997. Neuroanatomical correlates of pleasant and unpleasant emotion. Neuropsychologia 35 (11), 1437–1444.

Lang, P.J., Bradley, M.M., Cuthbert, B.N., 1992. A motivational analysis of emotion – reflex cortex connections. Psychol. Sci. 3 (1), 44–49.

Lang, P.J., Bradley, M.M., Cuthbert, B.N., 1997. Motivated attention: affect, activation, and action. In: Attention and orienting: sensory and motivational processes, pp. 97–135.

Lang, P.J., Bradley, M.M., Fitzsimmons, J.R., Cuthbert, B.N., Scott, J.D., Moulder, B., et al., 1998. Emotional arousal and activation of the visual cortex: an fMRI analysis. Psychophysiology 35 (2), 199–210.

Lang, P.J., Davis, M., 2006. Emotion, motivation, and the brain: reflex foundations in animal and human research. Prog. Brain Res. 156, 3–29.

Lavie, N., 2005. Distracted and confused? Selective attention under load. Trends Cogn. Sci. 9 (2), 75–82.

Lazarus, R.S., 1984. On the primacy of cognition. Am. Psychol. 39 (2), 124–129.

LeDoux, J., 1996. The Emotional Brain: the Mysterious Underpinnings of Emotional Life. Simon and Schuster, New-York.

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 (1), 235–243.

Liddell, B.J., Williams, L.M., Rathjen, J., Shevrin, H., Gordon, E., 2004. A temporal dissociation of subliminal versus supraliminal fear perception: an event-related potential study. J. Cogn. Neurosci. 16 (3), 479–486.

Lim, S.L., Padmala, S., Pessoa, L., 2008. Affective learning modulates spatial competition during low-load attentional conditions. Neuropsychologia 46 (5), 1267–1278.

Lim, S.L., Padmala, S., Pessoa, L., 2009. Segregating the significant from the mundane on a moment-to-moment basis via direct and indirect amygdala contributions. Proc. Natl. Acad. Sci. U.S.A. 106 (39), 16841–16846.

Lindquist, K.A., Wager, T.D., Kober, H., Bliss-Moreau, E., Feldman Barrett, L. The brain basis of emotion: a meta-analytic review. Behav. Brain Sci., doi:10.1098/rstb.2008.0310, in press.

Lucas, N., Vuilleumier, P., 2008. Effects of emotional and non-emotional cues on visual search in neglect patients: evidence for distinct sources of attentional guidance. Neuropsychologia 46 (5), 1401–1414.

Luck, S.J., Woodman, G.F., Vogel, E.K., 2000. Event-related potential studies of attention. Trends Cogn. Sci. 4 (11), 432–440.

Luo, Q., Holroyd, T., Jones, M., Hendler, T., Blair, J., 2007. Neural dynamics for facial threat processing as revealed by gamma band synchronization using MEG. NeuroImage 34 (2), 839–847.

Luo, Q., Holroyd, T., Majestic, C., Cheng, X., Schechter, J., Blair, R.J., 2010. Emotional automaticity is a matter of timing. J. Neurosci. 30 (17), 5825–5829.

Marois, R., Ivanoff, J., 2005. Capacity limits of information processing in the brain. Trends Cogn. Sci. 9 (6), 296–305.

Martinez, A., Anllo-Vento, L., Sereno, M.I., Frank, L.R., Buxton, R.B., Dubowitz, D.J., et al., 1999. Involvement of striate and extrastriate visual cortical areas in spatial attention. Nat. Neurosci. 2 (4), 364–369.

Martinez, A., DiRusso, F., Anllo-Vento, L., Sereno, M.I., Buxton, R.B., Hillyard, S.A., 2001. Putting spatial attention on the map: timing and localization of stimulus selection processes in striate and extrastriate visual areas. Vis. Res. 41 (10–11), 1437–1457.

Matsumoto, N., Okada, M., Sugase-Miyamoto, Y., Yamane, S., Kawano, K., 2005. Population dynamics of face-responsive neurons in the inferior temporal cortex. Cereb. Cortex 15 (8), 1103–1112.

Maunsell, J.H., 2004. Neuronal representations of cognitive state: reward or attention? Trends Cogn. Sci. 8 (6), 261–265.

McMains, S., Kastner, S., 2011. Interactions of top-down and bottom-up mechanisms in human visual cortex. J. Neurosci. 31 (2), 587–597.

Merikle, P.M., 1992. Perception without awareness. Critical issues. Am. Psychol. 47 (6), 792–795.

Mermillod, M., Droit-Volet, S., Devaux, D., Schaefer, A., Vermeulen, N., 2010. Are coarse scales sufficient for fast detection of visual threat? Psychol. Sci. 21 (10), 1429–1437.

Mobbs, D., Marchant, J.L., Hassabis, D., Seymour, B., Tan, G., Gray, M., et al., 2009. From threat to fear: the neural organization of defensive fear systems in humans. J. Neurosci. 29 (39), 12236–12243.

Mobbs, D., Petrovic, P., Marchant, J.L., Hassabis, D., Weiskopf, N., Seymour, B., et al., 2007. When fear is near: threat imminence elicits prefrontal-periaqueductal gray shifts in humans. Science 317 (5841), 1079–1083.

Mogg, K., Bradley, B.P., 1998. A cognitive-motivational analysis of anxiety. Behav. Res. Ther. 36 (9), 809–848.

Mogg, K., McNamara, J., Powys, M., Rawlinson, H., Seiffer, A., Bradley, B.P., 2000. Selective attention to threat: a test of two cognitive models of anxiety. Cogn. Emot. 14 (3), 375–399.

Moors, A., De Houwer, J., 2006. Automaticity: a theoretical and conceptual analysis. Psychol. Bull. 132 (2), 297–326.

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 (Pt 6), 1241–1252.

Morris, J.S., Friston, K.J., Buchel, C., Frith, C.D., Young, A.W., Calder, A.J., et al., 1998. A neuromodulatory role for the human amygdala in processing emotional facial expressions. Brain 121 (Pt 1), 47–57.

Morris, J.S., Öhman, A., Dolan, R.J., 1999. A subcortical pathway to the right amygdala mediating unseen fear. Proc. Natl. Acad. Sci. U.S.A. 96 (4), 1680–1685.

Mosher, C.P., Zimmerman, P.E., Gothard, K.M., 2010. Response characteristics of basolateral and centromedial neurons in the primate amygdala. J. Neurosci. 30 (48), 16197–16207.

Moskowitz, G.B., 2002. Preconscious effects of temporary goals on attention. J. Exp. Soc. Psychol. 38 (4), 397–404.

Mulckhuyse, M., Theeuwes, J., 2010. Unconscious attentional orienting to exogenous cues: a review of the literature. Acta Psychol. (Amst.) 134 (3), 299–309.

Müller, M.M., Andersen, S.K., Keil, A., 2008. Time course of competition for visual processing resources between emotional pictures and foreground task. Cereb. Cortex 18 (8), 1892–1899.

Müller, M.M., Teder-Sälejärvi, W., Hillyard, S.A., 1998. The time course of cortical facilitation during cued shifts of spatial attention. Nat. Neurosci. 1 (7), 631–634.

Naccache, L., Gaillard, R., Adam, C., Hasboun, D., Clemenceau, S., Baulac, M., et al., 2005. A direct intracranial record of emotions evoked by subliminal words. Proc. Natl. Acad. Sci. U.S.A. 102 (21), 7713–7717.

Nummenmaa, L., Hyona, J., Calvo, M.G., 2006. Eye movement assessment of selective attentional capture by emotional pictures. Emotion 6 (2), 257–268.

Nummenmaa, L., Hyona, J., Calvo, M.G., 2009. Emotional scene content drives the saccade generation system reflexively. J. Exp. Psychol. Hum. Percept. Perform. 35 (2), 305–323.

Ochsner, K.N., Gross, J.J., 2005. The cognitive control of emotion. Trends Cogn. Sci. 9 (5), 242–249.

Öhman, A., 2001. Nonconscious emotion: evolutionary, neural, and psychophysiologic perspectives. Psychophysiology 38, S5.

Öhman, A., Lundqvist, D., Esteves, F., 2001. The face in the crowd revisited: a threat advantage with schematic stimuli. J. Pers. Soc. Psychol. 80 (3), 381–396.

Öhman, A., Mineka, S., 2001. Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. Psychol. Rev. 108 (3), 483–522.

Olofsson, J.K., Nordin, S., Sequeira, H., Polich, J., 2008. Affective picture processing: an integrative review of ERP findings. Biol. Psychol. 77 (3), 247–265.

Padmala, S., Pessoa, L., 2008. Affective learning enhances visual detection and responses in primary visual cortex. J. Neurosci. 28 (24), 6202–6210.

Parikh, V., Sarter, M., 2008. Cholinergic mediation of attention: contributions of phasic and tonic increases in prefrontal cholinergic activity. Ann. N. Y. Acad. Sci. 1129, 225–235.

Pasley, B.N., Mayes, L.C., Schultz, R.T., 2004. Subcortical discrimination of unperceived objects during binocular rivalry. Neuron 42 (1), 163–172.

Paton, J.J., Belova, M.A., Morrison, S.E., Salzman, C.D., 2006. The primate amygdala represents the positive and negative value of visual stimuli during learning. Nature 439 (7078), 865–870.

Peelen, M.V., Atkinson, A.P., Andersson, F., Vuilleumier, P., 2007. Emotional modulation of body-selective visual areas. Soc. Cogn. Affect. Neurosci. 2, 274–283.

Peelen, M.V., Lucas, N., Mayer, E., Vuilleumier, P., 2009. Emotional attention in acquired prosopagnosia. Soc. Cogn. Affect. Neurosci. 4 (3), 268–277.

Pegna, A.J., Khateb, A., Lazeyras, F., Seghier, M.L., 2005. Discriminating emotional faces without primary visual cortices involves the right amygdala. Nat. Neurosci. 8 (1), 24–25.

Pessoa, L., 2005. To what extent are emotional visual stimuli processed without attention and awareness? Curr. Opin. Neurobiol. 15 (2), 188–196.

Pessoa, L., 2009. How do emotion and motivation direct executive control? Trends Cogn. Sci. 13 (4), 160–166.

Pessoa, L., Adolphs, R., 2010. Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. Nat. Rev. Neurosci. 11 (11), 773–783.

Pessoa, L., Kastner, S., Ungerleider, L.G., 2002a. Attentional control of the processing of neural and emotional stimuli. Brain Res. Cogn. Brain Res. 15 (1), 31–45.

Pessoa, L., McKenna, M., Gutierrez, E., Ungerleider, L.G., 2002b. Neural processing of emotional faces requires attention. Proc. Natl. Acad. Sci. U.S.A. 99 (17), 11458–11463.

Pezawas, L., Meyer-Lindenberg, A., Drabant, E.M., Verchinski, B.A., Munoz, K.E., Kolachana, B.S., et al., 2005. 5-HTTLPR polymorphism impacts human cingulate-amygdala interactions: a genetic susceptibility mechanism for depression. Nat. Neurosci. 8 (6), 828–834.

Phan, K.L., Wager, T., Taylor, S.F., Liberzon, I., 2002. Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. NeuroImage 16 (2), 331–348.

Phelps, E.A., LeDoux, J.E., 2005. Contributions of the amygdala to emotion processing: from animal models to human behavior. Neuron 48 (2), 175–187.

Phelps, E.A., Ling, S., Carrasco, M., 2006. Emotion facilitates perception and potentiates the perceptual benefits of attention. Psychol. Sci. 17 (4), 292–299.

Piech, R.M., McHugo, M., Smith, S.D., Dukic, M.S., Van Der Meer, J., Abou-Khalil, B., et al., 2010. Fear-enhanced visual search persists after amygdala lesions. Neuropsychologia 48 (12), 3430–3435.

Pizzagalli, D.A., Lehmann, D., Hendrick, A.M., Regard, M., Pascual-Marqui, R.D., Davidson, R.J., 2002. Affective judgments of faces modulate early activity (approximately 160 ms) within the fusiform gyri. NeuroImage 16 (3 Pt 1), 663–677.

Platt, M.L., Glimcher, P.W., 1999. Neural correlates of decision variables in parietal cortex. Nature 400 (6741), 233–238.

Portas, C.M., Krakow, K., Allen, P., Josephs, O., Armony, J.L., Frith, C.D., 2000. Auditory processing across the sleep-wake cycle: simultaneous EEG and fMRI monitoring in humans. Neuron 28 (3), 991–999.

Posner, M., Snyder, C.R.R., Davidson, B.J., 1980. Attention and the detection of signals. J. Exp. Psychol. Gen. 109 (2), 160–174.

Posner, M.I., 1980. Orienting of attention. Q. J. Exp. Psychol. 32, 3–25.

Posner, M.I., Dehaene, S., 1994. Attentional networks. Trends Neurosci. 17 (2), 75–79.

Pourtois, G., Dan, E.S., Grandjean, D., Sander, D., Vuilleumier, P., 2005a. Enhanced extrastriate visual response to bandpass spatial frequency filtered fearful faces: time course and topographic evoked-potentials mapping. Hum. Brain Mapp. 26 (1), 65–79.

Pourtois, G., De Pretto, M., Hauert, C.A., Vuilleumier, P., 2006a. Time course of brain activity during change blindness and change awareness: performance is predicted by neural events before change onset. J. Cogn. Neurosci. 18 (12), 2108–2129.

Pourtois, G., Grandjean, D., Sander, D., Vuilleumier, P., 2004. Electrophysiological correlates of rapid spatial orienting towards fearful faces. Cereb. Cortex 14 (6), 619–633.

Pourtois, G., Rauss, K., Vuilleumier, P., Schwartz, S., 2008. Perceptual learning modifies primary visual cortex activity in humans. Vision Res. 48 (1), 55–62.

Pourtois, G., Schwartz, S., Seghier, M.L., Lazeyras, F., Vuilleumier, P., 2006b. Neural systems for orienting attention to the location of threat signals: an event-related fMRI study. NeuroImage 31 (2), 920–933.

Pourtois, G., Spinelli, L., Seeck, M., Vuilleumier, P., 2010a. Modulation of face processing by emotional expression and gaze direction during intracranial recordings in right fusiform cortex. J. Cogn. Neurosci. 22 (9), 2086–2107.

Pourtois, G., Spinelli, L., Seeck, M., Vuilleumier, P., 2010b. Temporal precedence of emotion over attention modulations in the lateral amygdala: intracranial ERP evidence from a patient with temporal lobe epilepsy. Cogn. Affect. Behav. Neurosci. 10 (1), 83–93.

Pourtois, G., Thut, G., Grave de Peralta, R., Michel, C., Vuilleumier, P., 2005b. Two electrophysiological stages of spatial orienting towards fearful faces: early temporo-parietal activation preceding gain control in extrastriate visual cortex. NeuroImage 26 (1), 149–163.

Pourtois, G., Vocat, R., N'Diaye, K., Spinelli, L., Seeck, M., Vuilleumier, P., 2010c. Errors recruit both cognitive and emotional monitoring systems: simultaneous intracranial recordings in the dorsal anterior cingulate gyrus and amygdala combined with fMRI. Neuropsychologia 48 (4), 1144–1159.

Pourtois, G., Vuilleumier, P., 2006. Dynamics of emotional effects on spatial attention in the human visual cortex. Prog. Brain Res. 156, 67–91.

Purcell, D.G., Stewart, A.L., Skov, R.B., 1996. It takes a confounded face to pop out of a crowd. Perception 25 (9), 1091–1108.

Ranganath, C., Rainer, G., 2003. Neural mechanisms for detecting and remembering novel events. Nat. Rev. Neurosci. 4 (3), 193–202.

Rauss, K., Schwartz, S., Pourtois, G., 2011. Top-down effects on early visual processing in humans: a predictive coding framework. Neurosci. Biobehav. Rev. 35 (5), 1237–1253.

Rauss, K.S., Pourtois, G., Vuilleumier, P., Schwartz, S., 2009. Attentional load modifies early activity in human primary visual cortex. Hum. Brain Mapp. 30 (5), 1723–1733.

Rellecke, J., Palazova, M., Sommer, W., Schacht, A., 2011. On the automaticity of emotion processing in words and faces: event-related brain potentials evidence from a superficial task. Brain Cogn. 77 (1), 23–32.

Rossi, V., Pourtois, G., 2011. Transient state-dependent fluctuations in anxiety measures using STAI, POMS, PANAS or VAS: a comparative review. Anxiety Stress Coping, doi:10.1080/10615806.2011.582948.

Rossi, V., Pourtois, G. State-dependent attention modulation of human primary visual cortex: a high density ERP study. NeuroImage, doi:10.1016/j.neuroimage.2012.02.007, in press.

Rotshtein, P., Richardson, M.P., Winston, J.S., Kiebel, S.J., Vuilleumier, P., Eimer, M., et al., 2010. Amygdala damage affects event-related potentials for fearful faces at specific time windows. Hum. Brain Mapp. 31 (7), 1089–1105.

Rotshtein, P., Vuilleumier, P., Winston, J., Driver, J., Dolan, R., 2007. Distinct and convergent visual processing of high and low spatial frequency information in faces. Cereb. Cortex 17, 2713–2724.

Rudrauf, D., David, O., Lachaux, J.P., Kovach, C.K., Martinerie, J., Renault, B., et al., 2008. Rapid interactions between the ventral visual stream and emotion-related structures rely on a two-pathway architecture. J. Neurosci. 28 (11), 2793–2803.

Saalmann, Y.B., Kastner, S., 2009. Gain control in the visual thalamus during perception and cognition. Curr. Opin. Neurobiol. 19 (4), 408–414.

Sabatinelli, D., Bradley, M.M., Fitzsimmons, J.R., Lang, P.J., 2005. Parallel amygdala and inferotemporal activation reflect emotional intensity and fear relevance. NeuroImage 24 (4), 1265–1270.

Sabatinelli, D., Fortune, E.E., Li, Q., Siddiqui, A., Krafft, C., Oliver, W.T., et al., 2010. Emotional perception: meta-analyses of face and natural scene processing. NeuroImage 54 (3), 2524–2533.

Sabatinelli, D., Lang, P.J., Bradley, M.M., Costa, V.D., Keil, A., 2009. The timing of emotional discrimination in human amygdala and ventral visual cortex. J. Neurosci. 29 (47), 14864–14868.

Sabatinelli, D., Lang, P.J., Keil, A., Bradley, M.M., 2007. Emotional perception: correlation of functional MRI and event-related potentials. Cereb. Cortex 17 (5), 1085–1091.

Sagaspe, P., Schwartz, S., Vuilleumier, P., 2011. Fear and stop: a role for the amygdala in motor inhibition by emotional signals. NeuroImage 55 (4), 1825–1835.

Sander, D., Grafman, J., Zalla, T., 2003. The human amygdala: an evolved system for relevance detection. Rev. Neurosci. 14 (4), 303–316.

Santangelo, V., Finoia, P., Raffone, A., Belardinelli, M.O., Spence, C., 2008. Perceptual load affects exogenous spatial orienting while working memory load does not. Exp. Brain Res. 184 (3), 371–382.

Schettino, A., Loeys, T., Delplanque, S., Pourtois, G., 2011. Brain dynamics of upstream perceptual processes leading to visual object recognition: a high density ERP topographic mapping study. NeuroImage 55 (3), 1227–1241.

Schmid, M.C., Mrowka, S.W., Turchi, J., Saunders, R.C., Wilke, M., Peters, A.J., et al., 2010. Blindsight depends on the lateral geniculate nucleus. Nature 466 (7304), 373–377.

Schmolesky, M.T., Wang, Y., Hanes, D.P., Thompson, K.G., Leutgeb, S., Schall, J.D., et al., 1998. Signal timing across the macaque visual system. J. Neurophysiol. 79 (6), 3272–3278.

Schupp, H.T., Flaisch, T., Stockburger, J., Junghöfer, M., 2006. Emotion and attention: event-related brain potential studies. Prog. Brain Res. 156, 31–51.

Schwartz, S., Vuilleumier, P., Hutton, C., Maravita, A., Dolan, R.J., Driver, J., 2005. Attentional load and sensory competition in human vision: modulation of fMRI responses by load at fixation during task-irrelevant stimulation in the peripheral visual field. Cereb. Cortex 15 (6), 770–786.

Seeck, M., Michel, C.M., Mainwaring, N., Cosgrove, R., Blume, H., Ives, J., et al., 1997. Evidence for rapid face recognition from human scalp and intracranial electrodes. Neuroreport 8 (12), 2749–2754.

Serences, J.T., Shomstein, S., Leber, A.B., Golay, X., Egeth, H.E., Yantis, S., 2005. Coordination of voluntary and stimulus-driven attentional control in human cortex. Psychol. Sci. 16 (2), 114–122.

Shackman, A.J., Maxwell, J.S., McMenamin, B.W., Greischar, L.L., Davidson, R.J., 2011. Stress potentiates early and attenuates late stages of visual processing. J. Neurosci. 31 (3), 1156–1161.

Shi, C., Davis, M., 2001. Visual pathways involved in fear conditioning measured with fear-potentiated startle: behavioral and anatomic studies. J. Neurosci. 21 (24), 9844–9855.

Shimojo, S., Miyauchi, S., Hikosaka, O., 1997. Visual motion sensation yielded by non-visually driven attention. Vis. Res. 37 (12), 1575–1580.

Shipp, S., 2003. The functional logic of cortico-pulvinar connections. Philos. Trans. R. Soc. Lond. B Biol. Sci. 358 (1438), 1605–1624.

Shipp, S., Zeki, S., 1995. Segregation and convergence of specialised pathways in macaque monkey visual cortex. J. Anat. 187 (Pt 3), 547–562.

Silvert, L., Lepsien, J., Fragopanagos, N., Goolsby, B., Kiss, M., Taylor, J.G., et al., 2007. Influence of attentional demands on the processing of emotional facial expressions in the amygdala. NeuroImage 38 (2), 357–366.

Simons, D.J., Levin, D.T., 1997. Change blindness. Trends Cogn. Sci. 1, 261–267.

Stolarova, M., Keil, A., Moratti, S., 2006. Modulation of the C1 visual event-related component by conditioned stimuli: evidence for sensory plasticity in early affective perception. Cereb. Cortex 16 (6), 876–887.

Sugase, Y., Yamane, S., Ueno, S., Kawano, K., 1999. Global and fine information coded by single neurons in the temporal visual cortex. Nature 400 (6747), 869–873.

Surguladze, S.A., Brammer, M.J., Young, A.W., Andrew, C., Travis, M.J., Williams, S.C., et al., 2003. A preferential increase in the extrastriate response to signals of danger. NeuroImage 19 (4), 1317–1328.

Tamietto, M., de Gelder, B., 2010. Neural bases of the non-conscious perception of emotional signals. Nat. Rev. Neurosci. 11 (10), 697–709.

Theeuwes, J., 1994. Endogenous and exogenous control of visual selection. Perception 23 (4), 429–440.

Thorpe, S., Fize, D., Marlot, C., 1996. Speed of processing in the human visual system. Nature 381 (6582), 520–522.

Tsuchiya, N., Moradi, F., Felsen, C., Yamazaki, M., Adolphs, R., 2009. Intact rapid detection of fearful faces in the absence of the amygdala. Nat. Neurosci. 12 (10), 1224–1225.

van Marle, H.J., Hermans, E.J., Qin, S., Fernandez, G., 2009. From specificity to sensitivity: how acute stress affects amygdala processing of biologically salient stimuli. Biol. Psychiatry 66 (7), 649–655.

VanRullen, R., Reddy, L., Koch, C., 2004. Visual search and dual tasks reveal two distinct attentional resources. J. Cogn. Neurosci. 16 (1), 4–14.

Vlamings, P.H., Goffaux, V., Kemner, C., 2009. Is the early modulation of brain activity by fearful facial expressions primarily mediated by coarse low spatial frequency information? J. Vis. 9 (5), 1201–1213.

Vogel, E.K., Luck, S.J., 2000. The visual N1 component as an index of a discrimination process. Psychophysiology 37 (2), 190–203.

Vogt, J., De Houwer, J., Crombez, G., 2010a. Multiple goal management starts with attention: goal prioritizing affects the allocation of spatial attention to goal-relevant events. Exp. Psychol. 58 (1), 55–61.

Vogt, J., De Houwer, J., Moors, A., Van Damme, S., Crombez, G., 2010b. The automatic orienting of attention to goal-relevant stimuli. Acta Psychol. (Amst) 134 (1), 61–69.

Vrticka, P., Sander, D., Vuilleumier, P., 2011. Effects of emotion regulation strategy on brain responses to the valence and social content of visual scenes. Neuropsychologia 49 (5), 1067–1082.

Vuilleumier, P., 2002. Facial expression and selective attention. Curr. Opin. Psychiatry 15 (3), 291–300.

Vuilleumier, P., 2005. How brains beware: neural mechanisms of emotional attention. Trends Cogn. Sci. 9 (12), 585–594.

Vuilleumier, P., 2009. The role of the human amygdala in perception and attention. In: Whalen, P.J., Phelps, E.A. (Eds.), The Human Amygdala. Guilford Press, New York.

Vuilleumier, P., Armony, J.L., Clarke, K., Husain, M., Driver, J., Dolan, R.J., 2002. Neural response to emotional faces with and without awareness: event-related fMRI in a parietal patient with visual extinction and spatial neglect. Neuropsychologia 40 (12), 2156–2166.

Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001a. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. Neuron 30 (3), 829–841.

Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2003. Distinct spatial frequency sensitivities for processing faces and emotional expressions. Nat. Neurosci. 6 (6), 624–631.

Vuilleumier, P., Driver, J., 2007. Modulation of visual processing by attention and emotion: windows on causal interactions between human brain regions. Philos. Trans. R. Soc. Lond. B Biol. Sci. 362 (1481), 837–855.

Vuilleumier, P., Huang, Y.M., 2009. Emotional attention: uncovering the mechanisms of affective biases in perception. Curr. Dir. Psychol. Sci. 18 (3), 148–152.

Vuilleumier, P., Pourtois, G., 2007. Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. Neuropsychologia 45 (1), 174–194.

Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., Dolan, R.J., 2004. Distant influences of amygdala lesion on visual cortical activation during emotional face processing. Nat. Neurosci. 7 (11), 1271–1278.

Vuilleumier, P., Righart, R., 2011. Attention and automaticity in processing facial expressions. In: Calder, A., Rhodes, G., Johnson, M., Haxby, J.V. (Eds.), Oxford Handbook of Face Perception. Oxford University Press, Oxford.

Vuilleumier, P., Schwartz, S., 2001a. Beware and be aware: capture of spatial attention by fear-related stimuli in neglect. Neuroreport 12 (6), 1119–1122.

Vuilleumier, P., Schwartz, S., 2001b. Emotional facial expressions capture attention. Neurology 56 (2), 153–158.

Vuilleumier, P., Valenza, N., Landis, T., 2001b. Explicit and implicit perception of illusory contours in unilateral spatial neglect: behavioural and anatomical correlates of preattentive grouping mechanisms. Neuropsychologia 39 (6), 597–610.

Ward, R., Calder, A.J., Parker, M., Arend, I., 2007. Emotion recognition following human pulvinar damage. Neuropsychologia 45 (8), 1973–1978.

West, G.L., Anderson, A.A., Ferber, S., Pratt, J., 2011. Electrophysiological evidence for biased competition in V1 for fear expressions. J. Cogn. Neurosci. 23, 3410–3418.

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 (5704), 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. J. Neurosci. 18 (1), 411–418.

Wiens, S., Sand, A., Olofsson, J.K., 2010. Nonemotional features suppress early and enhance late emotional electrocortical responses to negative pictures. Biol. Psychol. 86 (1), 83–89.

Wieser, M.J., McTeague, L.M., Keil, A., 2010. Sustained preferential processing of social threat cues: bias without competition? J. Cogn. Neurosci. 23 (8), 1973–1986.

Williams, L., 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. Hum. Brain Mapp. 21 (2), 64–74.

Williams, M., Mattingley, J.B., 2004. Unconscious perception of non-threatening facial emotion in parietal extinction. Exp. Brain Res. 154 (4), 403–406.

Williams, M., McGlone, F., Abbott, D.F., Mattingley, J.B., 2005a. Differential amygdala responses to happy and fearful facial expressions depend on selective attention. NeuroImage 24 (2), 417–425.

Williams, M.A., Moss, S.A., Bradshaw, J.L., Mattingley, J.B., 2005b. Look at me, I'm smiling: visual search for threatening and nonthreatening facial expressions. Vis. Cogn. 12 (1), 29–50.

Winston, J.S., Vuilleumier, P., Dolan, R.J., 2003. Effects of low-spatial frequency components of fearful faces on fusiform cortex activity. Curr. Biol. 13 (20), 1824–1829.

Woldorff, M.G., Hazlett, C.J., Fichtenholtz, H.M., Weissman, D.H., Dale, A.M., Song, A.W., 2004. Functional parcellation of attentional control regions of the brain. J. Cogn. Neurosci. 16 (1), 149–165.

Wolfe, J.M., Horowitz, T.S., 2004. What attributes guide the deployment of visual attention and how do they do it? Nat. Rev. Neurosci. 5 (6), 495–501.

Xu, Y., 2010. The neural fate of task-irrelevant features in object-based processing. J. Neurosci. 30 (42), 14020–14028.

Yantis, S., Serences, J.T., 2003. Cortical mechanisms of space-based and object-based attentional control. Curr. Opin. Neurobiol. 13 (2), 187–193.

Yukie, M., 2002. Connections between the amygdala and auditory cortical areas in the macaque monkey. Neurosci. Res. 42 (3), 219–229.

Zajonc, R.B., 1984. On the primacy of affect. Am. J. Psychol. 39, 117–123.

Zeelenberg, R., Bocanegra, B.R., 2010. Auditory emotional cues enhance visual perception. Cognition 115 (1), 202–206.