Brain mechanisms for emotional influences on perception and attention:

what is magic and what is not

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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.

Keywords: emotion; attention; perception; amygdala; gain control

On the varieties of attention mechanisms

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).

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, Snyder, & Davidson, 1980; Marois & 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 & Ungerleider, 2000; Driver & 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 & 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 & Rainer, 2003; Wolfe & 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, Remington, & Johnston, 1992), while other simultaneous but irrelevant events will fail to be noticed (as exemplified by the change blindness phenomena; see Simons & Levin, 1997; Pourtois, De

Pretto, Hauert, & Vuilleumier, 2006). 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 & West, 2006), it can be modulated by top-down factors related to expectations and task demands (Folk, et al., 1992; Hopfinger & Ries, 2005). Moreover, even subliminal (and hence unseen) exogenous cues can capture spatial attention (Mulckhuyse & Theeuwes, 2010), but such effects may nevertheless be contingent on current task goals and readiness to respond to particular stimulus features (Ansorge, Kiss, & Eimer, 2009). Similarly, endogenous attention is usually associated with voluntary and effortful control (Posner, et al., 1980; Kastner & Ungerleider, 2000), and yet it can also be influenced by automatic and unconscious activation of goals (Moskowitz, 2002; Dijksterhuis & Aarts, 2010). At the neuroanatomical 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 & Dehaene, 1994), but also show substantial overlap and functional interactions (e.g. Corbetta & Shulman, 2002; Chica, Bartolomeo, & Valero-Cabre, 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, Davis, Russell, Turatto, & Freeman, 2001; Yantis & 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, Baylis, & Rafal, 1992; Downing, Liu, & Kanwisher, 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, Riddoch, Forti, & Ackroyd, 2004; Vuilleumier, Valenza, & Landis, 2001; McMains & 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; Vuilleumier, 2009; Shackman, Maxwell, McMenamin, Greischar, & Davidson, 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 Figures 1 and 4) that does not share all its functional and anatomical components with classical attention mechanisms (Lucas & Vuilleumier, 2008; Brosch, Pourtois, Sander, & Vuilleumier, 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 & 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, De Raedt, Goeleven, Franck, & Crombez, 2005; Bishop, 2007; Rossi & 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, Kastner, & Ungerleider, 2002), 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 (Armony & Dolan, 2002; Pourtois, Thut, Grave de Peralta, Michel, & Vuilleumier, 2005; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2006). 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, Bradley, & Cuthbert, 1992; Holland & 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.

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, Wager, Kober, Bliss-Moreau, & Feldman Barrett, in press). This boosting is reminiscent of the typical gain control mechanism associated with endogenous or exogenous attention (Hillyard, Vogel, & Luck, 1998), 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, Henaff, Vighetto, Bertrand, & Mauguiere, 2004; Luo, Holroyd, Jones, Hendler, & Blair, 2007; Luo, et al., 2010; Pourtois, Spinelli, Seeck, & Vuilleumier, 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, Behniea, & Kelly, 2003; Krolak-Salmon, Fischer, Vighetto, & Mauguiere, 2001; Vuilleumier & Pourtois, 2007; Pourtois, Spinelli, et al., 2010b; Pourtois, Spinelli, Seeck, & Vuilleumier, 2010a; Rossi & 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 & Duncan, 1995; Carrasco, Loula, & Ho, 2006). 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 & Dehaene, 1994; Corbetta & 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 & Duncan, 1995; Chelazzi, Miller, Duncan, & Desimone, 1993; Hillyard, Vogel, et al., 1998; Luck, Woodman, & Vogel, 2000; Kastner & Ungerleider, 2000; Vuilleumier & 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, Armony, Driver, & Dolan, 2001; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Surguladze, et al., 2003; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005). These effects may take place in the primary visual cortex (Lang, et al., 1998; Halgren, Raij, Marinkovic, Jousmaki, & Hari, 2000; Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Stolarova, Keil, & Moratti, 2006; Padmala and Pessoa, 2008) or involve category-selective regions of the infero-temporal cortex, including the fusiform face area (Morris, et al., 1998; Vuilleumier, Armony, et al., 2001; Sabatinelli, et al., 2005; Pourtois, Spinelli, et al., 2010a) or the extrastriate body area (Peelen, Atkinson, Andersson, & Vuilleumier, 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 & Pessoa, 2008; Damaraju, Huang, Barrett, & Pessoa, 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, Wager, Taylor, & Liberzon, 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, Armony, et al., 2001), 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; Sabatinelli, Lang, Keil, & Bradley, 2007; Sabatinelli, et al., 2010). Similar results have been obtained in voiceselective areas of the lateral temporal cortex for emotionally-salient auditory stimuli, such as angry or happy voices (Grandjean, et al., 2005; Ethofer, et al., 2011; Ethofer, Van De Ville, Scherer, & Vuilleumier, 2009) as well as affective vocalizations or screams (Fecteau, Belin, Joanette, & Armony, 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; Vuilleumier, 2005), which may beneficially enhance attention towards them (Dennis & Chen, 2007; Bocanegra & Zeelenberg, 2009; Vuilleumier, 2009) and/or alter attention towards other concomitant stimuli in the same or different modalities (e.g. Zeelenberg & Bocanegra, 2010; Dominguez-Borras, Garcia-Garcia, & Escera, 2008). Accordingly, greater responses to emotional faces correlate with better detection across different visual tasks (Vuilleumier, et al., 2002; Lim, Padmala, & Pessoa, 2009; Kouider, Eger, Dolan, & Henson, 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 & Cabeza, 2006; Buchanan, 2007).

Insert box 2 about here

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, Ling, & Carrasco, 2006; Bocanegra & Zeelenberg, 2009,

2011; Brosch, Pourtois, & Sander, 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 sensitivity for the orientation of a subsequently presented low-spatial frequency stimulus (such as a Gabor patch; Phelps, et al., 2006; Bocanegra & 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 & Zeelenberg, 2009). Visual search (Eastwood, Smilek, & Merikle, 2001; Öhman, Lundqvist, & Esteves, 2001), attentional blink (Keil & Ihssen, 2004; Anderson, 2005), and spatial orienting tasks (Armony & 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, Grandjean, Sander, & Scherer, 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 & Meck, 2007). Such effects might result from a stronger and quicker engagement of attention towards emotional stimuli (Shimojo, Miyauchi, & Hikosaka, 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.

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, Flaisch, Stockburger, & Junghöfer, 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, Nordin, Sequeira, & Polich, 2008; Wiens, Sand, & Olofsson, 2010; Hajcak, Macnamara, Foti, Ferri, & Keil, in press).

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 & Axford, 1972; Clark, Fan, & Hillyard, 1995; Rossi & Pourtois, in press; see Rauss, Schwartz, & Pourtois, 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, Anderson, Ferber, & Pratt, 2011), fear-conditioned gratings (Stolarova, et al., 2006) or affective states (Rossi & 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 & Anllo-Vento, 1998; but see Kelly, Gomez-Ramirez, & Foxe, 2008; Rauss, Pourtois, Vuilleumier, & Schwartz, 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; Pourtois, Thut, et al., 2005).

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, Luck, Mangun, & Hillyard, 1990; Vogel & Luck, 2000), which reflect activity in extrastriate visual areas (Hillyard, Teder-Salejarvi, & Munte, 1998; Di Russo, Martinez, & Hillyard, 2003; Martinez, et al., 2001). Several studies have found that the extrastriate P1 response is also influenced by emotion (Batty & Taylor, 2003; Pourtois, et al., 2004; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; 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 & Anllo-Vento, 1998; Heinze, et al., 1990; Pourtois, et al., 2004). Similarly, larger amplitudes are evoked for negative/threatrelated stimuli relative to neutral stimuli, including fearful faces, even when the attentional demands are balanced between conditions (see Batty & Taylor, 2003; Pourtois, Dan, et al., 2005). 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; Pourtois, Thut, et al., 2005). 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 & Duncan, 1995; Hillyard, Vogel, et al., 1998; Kastner & 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, Pourtois, Schwartz, & Vuilleumier, 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, Schupp, Renner, & Junghöfer, 2009 for emotional gestures; Kissler, Herbert, Peyk, & Junghöfer, 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, Palazova, Sommer, & Schacht, 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., in press). 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, Iglesias, Garcia, & Ballesteros, 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, Moratti, Sabatinelli, Bradley, & Lang, 2005; Müller, Andersen, & Keil, 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, Teder-Sälejärvi, & Hillyard, 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, McTeague, & Keil, 2010). Likewise, SSVEP evoked by non-emotional targets may be reduced when presented together with emotionally engaging, task-irrelevant distractors (Muller, 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, Armony, et al., 2001) 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, McKenna, et al., 2002), 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 separate top-down signals, even when converging on the same sensory pathways.

Neural mechanisms for emotional attention

As we (Vuilleumier, 2005; Vuilleumier & Driver, 2007; Pourtois & Vuilleumier, 2006) and others (Lang & 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, Jones, Donato, & Ffytche, 2003; Gschwind, Pourtois, Schwartz, Van de Ville, & Vuilleumier, 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, Armony, et al., 2001; 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, McKenna, et al., 2002) and extrastriate areas in occipital cortex (Lane, et al., 1997; Sabatinelli, et al., 2005; Sabatinelli, et al., 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 & Shulman, 2002; Pourtois, Thut, et al., 2005).

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, Richardson, Armony, Driver, & Dolan, 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 mesiotemporal 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 intrahemispheric 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, Allison, Puce, Perez, & McCarthy, 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 & Duncan, 1995; Kastner & Ungerleider, 2000; Corbetta & 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 & Vuilleumier, 2001). Both exogenous and endogenous mechanisms of spatial attention are usually impaired, particularly in the acute stage (Bartolomeo, Thiebaut de Schotten, & Doricchi, 2007; Corbetta & 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 & Schwartz, 2001a; Fox, 2002; Lucas & Vuilleumier, 2008; Grandjean, Sander, Lucas, Scherer, & Vuilleumier, 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 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 & 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, Vuilleumier, Thiel, Driver, & Dolan, 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; Vuilleumier, 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, Wik, Fischer, & Andersson, 1995; Armony & Dolan, 2002; Pourtois, Schwartz, et al., 2006) 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, Thut, et al., 2005) 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, Schwartz, & Vuilleumier, 2011) levels. In addition, brain systems involved in other facets of affect and motivation might possibly also have distinct influences (Cardinal, Parkinson, Hall, & Everitt, 2002). However, much remains to be discovered about the exact role and interaction between these different pathways (Vuilleumier, 2005; Vuilleumier, 2009).

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 & 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. 2-3), for which a cortical frontoparietal network is predominantly implicated (Kastner & Ungerleider, 2000; Vuilleumier & 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 & Schwartz, 2001a; Vuilleumier, et al., 2002; Williams & Mattingley, 2004; Fox, 2002; Tamietto & de Gelder, 2010), as well as fMRI (Morris, Öhman, & Dolan, 1999; Whalen, et al., 1998), ERP (Williams, et al., 2004; Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004; Carretie, Hinojosa, Mercado, & Tapia, 2005) and MEG studies (Bayle, Henaff, & Krolak-Salmon, 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, McKenna, et al., 2002 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, Changeux, Naccache, Sackur, & Sergent, 2006; Kouider & Dehaene, 2007; Vuilleumier & 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 & 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 & Whalen, 2001; Sander, Grafman, & Zalla, 2003; Armony, Servan-Schreiber, Cohen, & Ledoux, 1997). This does not preclude that different task demands or voluntary emotion regulation strategies can alter (increase or decrease) this readiness to respond (Ochsner & Gross, 2005; Vrticka, Sander, & Vuilleumier, 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 of focus of attention (Vuilleumier, Armony, et al., 2001; Vuilleumier, et al., 2004; Bentley, et al., 2003; Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Williams, McGlone, Abbott, & Mattingley, 2005). 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 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, Kastner, et al., 2002; Pessoa, McKenna, et al., 2002) 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, Kastner, et al., 2002; Pessoa, McKenna, et al., 2002). 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 & 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 & Phelps, 2001; Vuilleumier, Armony, et al., 2001; Pessoa, McKenna, et al., 2002), 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, Spinelli, et al., 2010). 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 & Shulman, 2002; McMains & 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, Armony, et al., 2001), 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, McKenna, et al., 2002) 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, Finoia, Raffone, Belardinelli, & Spence, 2008) and object-based attention (Xu, 2010; McMains & 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, Vocat, et al., 2010) 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, Duncan, & Lawrence, 2004b; Rossi & 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, McGlone, et al., 2005; 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.

Insert Figure 2 about here

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. 3AB; Pourtois, Spinelli, et al., 2010b; see also Seeck, et al., 1997; Halgren, Baudena, Heit, Clarke, Marinkovic, & Clarke, 1994; Holmes, Vuilleumier, & Eimer, 2003). In this study, intracranial ERPs were obtained from the structurally intact left lateral amygdala of a patient with refractory/pharmaco-resistant epilepsy (Pourtois, Spinelli, 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, Armony, et al., 2001; Vuilleumier, et al., 2004). Early following stimulus onset (140-290 ms), fearful faces elicited a differential response in the amygdala relative to neutral faces (Fig. 3AB), 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. 3AB). 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 & Anllo-Vento, 1998; Pourtois & 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. 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.2AB).

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, Armony, et al., 2001; Vuilleumier, et al., 2004; Sabatinelli, et al., 2005), including the fusiform face area for emotional faces (Kanwisher, McDermott, & Chun, 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. 3CD; Pourtois, Spinelli, 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. 3CD), peaking around 150 ms after onset, in agreement with previous neurophysiological results (i.e. N200 component; see Allison, Puce, Spencer, & McCarthy, 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. 3CD; Pourtois, Spinelli, et al., 2010). This pattern is consistent with a feedback modulation arising from the amygdala (Matsumoto, Okada, Sugase-Miyamoto, Yamane, & Kawano, 2005; Sugase, Yamane, Ueno, & Kawano, 1999; Vuilleumier, et al., 2004; Vuilleumier, 2005) and beginning just after the differential emotional activity in this region (Pourtois, Spinelli, 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; Luo, et al., 2007) or outside the current focus of attention (Pourtois, Spinelli, 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, Armony, et al., 2001; Pourtois, Spinelli, et al., 2010a), via both direct and indirect pathways projecting back to the cortex (Amaral, et al., 2003; Vuilleumier, 2009; Vuilleumier, 2005; Sabatinelli, Lang, Bradley, Costa, & Keil, 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. 3CD).

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 & Davis, 2001) and observations in human patients with blindsight after damage of area V1 (Morris, DeGelder, Weiskrantz, & Dolan, 2001; Anders, et al., 2004; Pegna, Khateb, Lazeyras, & Seghier, 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 & 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, Mayes, & Schultz, 2004; Liddell, et al., 2005). Furthermore, damage to human pulvinar may impair detection and spatial orienting to threat (Ward, Calder, Parker, & Arend, 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, Hyona, & Calvo, 2006, 2009; Devue, Belopolsky, & Theeuwes, 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, Wei, Chomsung, Petry, & Bickford, 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 & Adolphs, 2010). For instance, in monkeys, the superior colliculus projects to V2 (Shipp, 2003) and visual pulvinar projects directly to V4 and V5 (Shipp & Zeki, 1995); whereas direct connections between pulvinar and

fusiform cortex have also been found in humans in post-mortem studies (Clarke, Riahi-Arya, Tardif, Eskenasy, & Probst, 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 & 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 & 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 & 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, Fize, & Marlot, 1996), that is, before the typical latency associated with voluntary attention control (Hillyard & Anllo-Vento, 1998; Hillyard, Teder-Salejarvi, et al., 1998). 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, Spinelli, 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 & Adolphs, 2010), just like evidence for subliminal perception of words or numbers (Dehaene, et al., 1998; Dehaene, et al., 2001; Kouider & Dehaene, 2007) or unconscious priming of motor processes (Eimer & 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 the higher level of processing hierarchy, including 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 occipitotemporal 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, Vroomen, Pourtois, & Weiskrantz, 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, Loeys, Delplanque, & Pourtois, 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, Armony, Driver, & Dolan, 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, Vuilleumier, & Dolan, 2003) and EEG studies (Pourtois, Dan, et al., 2005; Alorda, Serrano-Pedraza, Campos-Bueno, Sierra-Vazquez, & Montoya, 2007; Carretie, Hinojosa, Lopez-Martin, & Tapia, 2007; Vlamings, Goffaux, & Kemner, 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 lowspatial 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, Vuilleumier, Winston, Driver, & Dolan, 2007). In agreement with this view, detection and orienting to threatrelated stimuli can be facilitated when these are presented in low rather than high spatial frequencies (Holmes, Green, & Vuilleumier, 2005; Mermillod, Droit-Volet, Devaux, Schaefer, & Vermeulen, 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 & 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 & Zeelenberg, 2009; Bocanegra & Zeelenberg, 2011).

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 (Vuilleumier & Dominguez-Borras, in press). Such effects are manifested by faster RTs and/or enhanced accuracy in various tasks, including visual search (Eastwood, Smilek, & Merikle, 2003; Fox, et al., 2000; Williams, Moss, Bradshaw, & Mattingley, 2005), attentional blink (Anderson & Phelps, 2001; Anderson, 2005), or spatial

orienting (dot probe task; e.g. Brosch, et al., 2011; Pourtois, et al., 2004; Fox, Russo, Bowles, & Dutton, 2001; for review, see Frischen, Eastwood, & Smilek, 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, Tranel, Damasio, & Damasio, 1994; Adolphs, Tranel, Damasio, & Damasio, 1995; Adolphs, 1999; LaBar, LeDoux, Spencer, & Phelps, 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 & 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 & 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 & 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 & 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 & 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, Moradi, Felsen, Yamazaki, & Adolphs, 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, Talmi, Hurlemann, Patin, & Dolan, 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, Reddy, & Koch, 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 lowlevel features that contribute to discriminate faces with fearful expressions (e.g. big eyes) from other emotions (see Purcell, Stewart, & Skov, 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 & Schwartz, 2001a, 2001b; 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 & 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 topdown biases on visual selective attention (Lucas & 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, Lucas, Mayer, & Vuilleumier, 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 & 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, Zikopoulos, & Timbie, 2010).

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 emotionallyrelevant stimuli in the environment and extract relevant information about their nature and location (Vuilleumier, 2005; Vuilleumier & 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 topdown 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 & Duncan, 1995; Kastner & Ungerleider, 2000; Posner & Dehaene, 1994; Corbetta & 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, Armony, et al., 2001; Keil, et al., 2005; Brosch, et al., 2011; Rossi & 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 adapted behavior, but based on their affective value rather than sensory or spatial attributes (Vuilleumier, 2005; Vuilleumier & Huang, 2009; Lang, Bradley, & Cuthbert, 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 & 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, Valenza, et al., 2001; McMains & Kastner, 2011), which act to increase the competitive strength of relevant information in the selection for attention (Driver, et al., 1992; Baylis & Driver, 1993).

Furthermore, like object-based and exogenous mechanisms of attention, emotional influences on perception and attention appear to be "reflexive" (Hodsoll, Viding, & Lavie, 2011) in the sense that these effects are usually tacit, arising irrespective of the task demands, and triggered involuntarily or without conscious monitoring (Moors & 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, De Houwer, & Crombez, 2010; Vogt, De Houwer, Moors, Van Damme, & Crombez, 2010), as well as modulations by perceptual load and expectations (Pessoa, McKenna, et al., 2002; Hahn & 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, Hermans, Qin, & Fernandez, 2009; Rossi & 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 & 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, Vocat, et al., 2010), and perhaps also contribute to diminish threatselectivity of activations in this structure in some conditions (Williams, McGlone, et al., 2005; 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 (threatrelated) biases in attention and perception across various tasks (Fox, 2002; Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van Ijzendoorn, 2007; Bradley, et al., 1997; Mogg & Bradley, 1998), and the circuitry reviewed here provides plausible mechanisms to account for these effects (see Fig. 4).

Insert box 3 about here

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, Kastner, et al., 2002; 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 & Huang, 2009). Modulations by 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, preattentive 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 & 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, Dan, et al., 2005). 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 & Driver, 2007; McMains & 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 & 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. 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 higherorder regions in medial prefrontal/anterior cingulate/orbitofrontal regions involved in emotion regulation processes (see Fig. 4; Drevets & Raichle, 1998; Ochsner & Gross, 2005; Etkin, Egner, & Kalisch, 2010), 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, Prater, Hoeft, Menon, & Schatzberg, 2010) might increase vulnerability to and maintenance of anxiety and negative affect (Bishop, 2007; Bishop, Duncan, & Lawrence, 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 & 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 & LeDoux, 2005) and the direct implications for psychopathology (Öhman & 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, Belova, Morrison, & Salzman, 2006; Baxter & 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, Sander, Pourtois, & Scherer, 2008). Moreover, reward learning can enhance perception and attention (Hickey, Chelazzi, & Theeuwes, 2010), and also modulate the activity of parietal neurons that are usually related to attention (Maunsell, 2004; Platt & 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).

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; Mobbs, et al., 2007; see also Vuilleumier & Dominguez-Borras, 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 & 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.

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Figure legends

Figure 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 potentials). (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 kind of biasing signals.

Figure 2. Examples of different patterns of voluntary attention effects on the processing of emotional faces. (A) Data from Vuilleumier et al. (2001). 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. (2002). Participants either made gender judgments on a central face (fearful, happy, or neutral) or 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 increased activation for the ignored neutral faces while activation to ignored 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.

Figure 3. Temporal dynamics of emotion and attention effects in amygdala and fusiform cortex. Data from Poutois et al. (Pourtois, Spinelli, et al., 2010b; Pourtois, Spinelli, et al., 2010a) 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**).

Figure 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.

Box contents

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, Armony, et al., 2001; Anderson, et al., 2003; Keil, et al., 2005) or perceptual load (Pessoa, McKenna, et al., 2002). 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 & 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 & 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 & 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, Spinelli, et al., 2010b; Luo, et al., 2010; Brosch, et al., 2011; Ciesielski, Armstrong, Zald, & Olatunji,). Altogether, these results converge to support a multiple systems architecture responsible for attention control (Corbetta & 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.

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 & de Gelder, 2010). However, most of these findings were obtained using BOLD-fMRI (see Vuilleumier, Armony, et al., 2001; Vuilleumier, et al., 2004; Bentley, et al., 2003; Bishop, et al., 2004a, 2004b), 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 sec (Pourtois, Spinelli, 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; Pourtois, Thut, et al., 2005; 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, Thut, et al., 2005). 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, Baudena, Heit, Clarke, & Marinkovic, 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Chauvel, 1994; Allison, et al., 1999). Recent work in such patients (see Kawasaki, et al., 2001; Pourtois, Spinelli, et al., 2010b; Pourtois, Spinelli, et al., 2010a) 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, Spinelli, 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, Quirk, & LeDoux, 1998; Gothard, Battaglia, Erickson, Spitler, & Amaral, 2007; Mosher, Zimmerman, & Gothard, 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.

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 & Gross, 2005; Etkin, Egner, et al., 2010; Cornwell, et al., 2011; Pezawas, et al., 2005; Hariri, et al., 2002; Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 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, Vuilleumier, 2009) provides a plausible neuro-anatomical 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, McKenna, et al., 2002), 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, Padmala, & Pessoa, 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, Derakshan, Santos, & Calvo, 2007; Derryberry & 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 baso-lateral 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 & 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 & 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.

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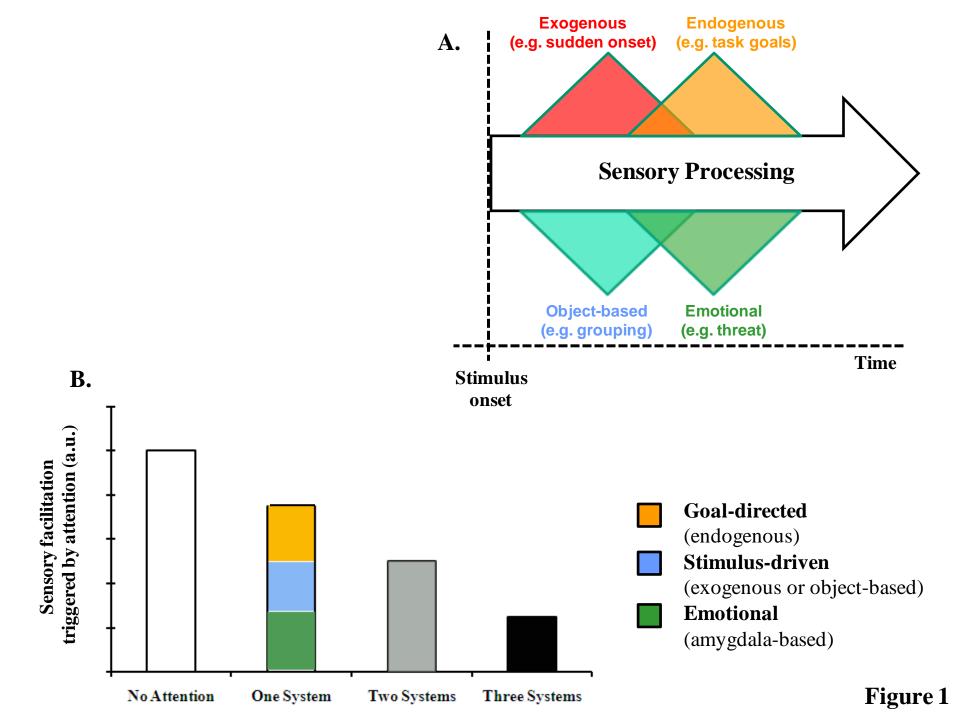
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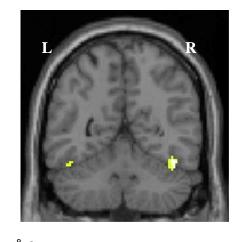






- Attention focused on faces
- Attention focused on houses

Fusiform « face » area



Fearful Neutral Fearful Neutral Faces Faces

Amygdala



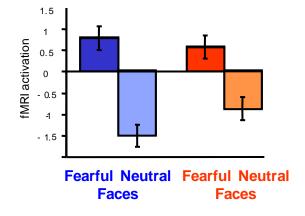


Figure 2A

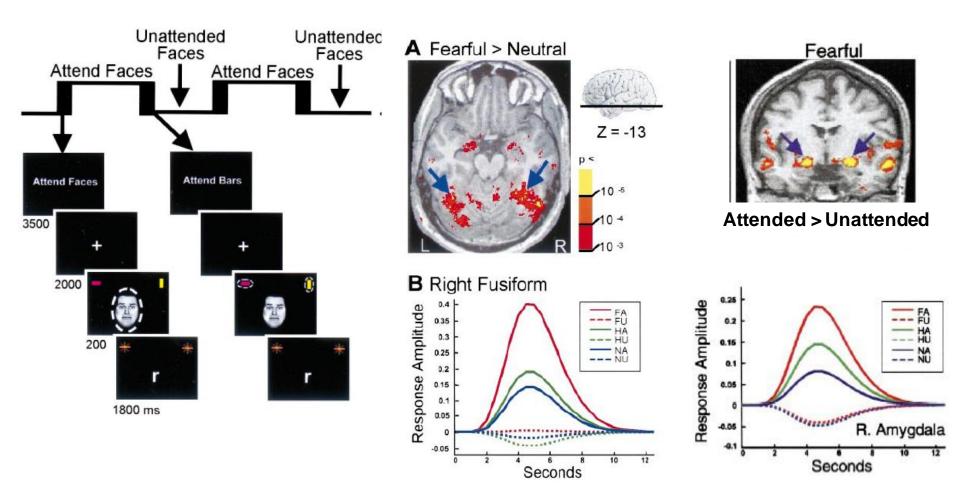
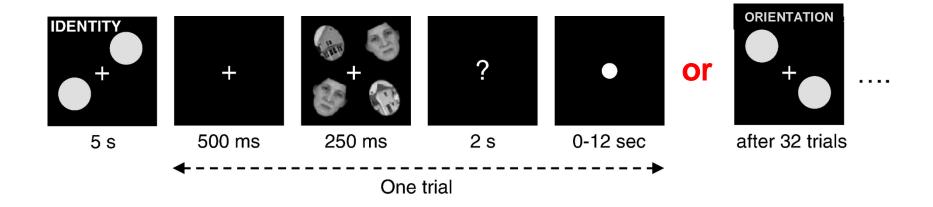


Figure 2B



Right amygdala [26 -4 -18]

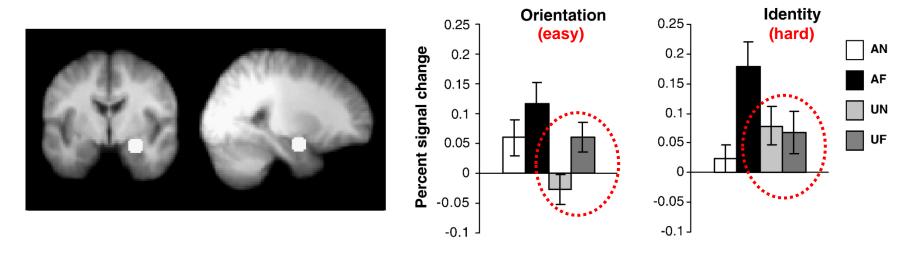


Figure 2C

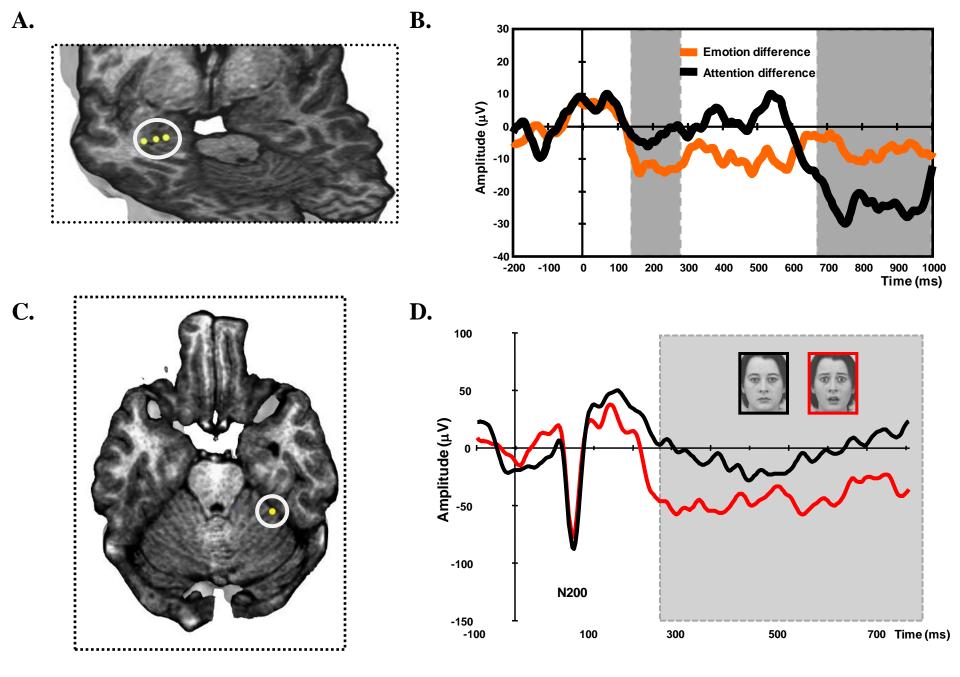


Figure 3

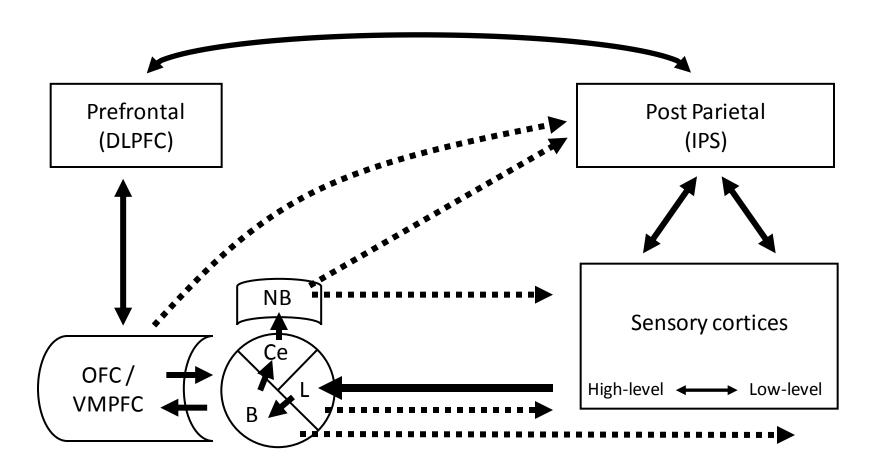


Figure 4