

How brains beware: neural mechanisms of emotional attention

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Emotional processes not only serve to record the value of sensory events, but also to elicit adaptive responses and modify perception. Recent research using functional brain imaging in human subjects has begun to reveal neural substrates by which sensory processing and attention can be modulated by the affective significance of stimuli. The amygdala plays a crucial role in providing both direct and indirect top-down signals on sensory pathways, which can influence the representation of emotional events, especially when related to threat. These modulatory effects implement specialized mechanisms of 'emotional attention' that might supplement but also compete with other sources of top-down control on perception. This work should help to elucidate the neural processes and temporal dynamics governing the integration of cognitive and affective influences in attention and behaviour.

Introduction

A major constraint on sensory systems is their limited capacity of processing, and the need to detect vital information in a multifarious world. Our brains possess different mechanisms to cope with these limitations and to adjust flexibly to the environment, including mechanisms to guide sensory processing and resolve between competing choices. Such abilities are generally imputed to selective attention and executive functions, which allow the brain to deal with a subset of information in the environment based on its current relevance or salience [1,2]. But how does the brain evaluate what is relevant or salient?

Several findings suggest that different mechanisms of selection exist and operate simultaneously during perceptual processing [1]. The aim of this review is to highlight how some aspects of selective attention might be influenced by the affective significance of sensory events, and how such influences implicate specific neural systems that might act (at least partly) independent of other mechanisms associated with more voluntary components of attentional control. In recent years, abundant research has investigated the neural substrates of emotion processing, now allowing us to pinpoint brain circuits implementing specialized mechanisms for 'emotional attention'. Our understanding of emotional influences on perception

can now also be integrated with recent advances concerning the neural effects of selective attention on sensory systems [3]. These data raise new questions on the possible influences of emotion on other aspects of behaviour and higher-level representations, beyond perception, including memories, thoughts, or actions. Here I will focus on neural mechanisms of emotional biases acting on the representation of sensory events, but similar biases might operate in other domains of executive control [2] and still need to be more fully explored.

Emotional salience modulates attention

Many behavioural observations indicate that people more readily pay attention to emotional than neutral stimuli. These effects often arise in a reflexive or involuntary manner. In variants of the Stroop task, naming the colour of a word or picture is slowed when the stimulus has an emotional meaning (e.g. [4,5]), even though emotion is irrelevant to the task (and in fact counterproductive for optimal naming speed). This interference suggests that people are not only very sensitive to emotional meaning, but unable to fully ignore such meaning under these conditions. Similarly, in visual search tasks where a unique target must be found among distractors, detection times are faster when the target has some emotional value, such as an angry or happy face among neutral faces (e.g. [6,7]), or a snake or spider among flowers (e.g. [8]). Although these results were sometimes interpreted as a 'pop-out' effect to suggest that emotional stimuli might be processed in 'parallel', rather than serially inspected as neutral stimuli, the advantage of emotional targets is clearly different from true 'pop-out' produced when targets are distinguished by basic visual features such as colour, size, or orientation. Search is *facilitated* by emotion but is still essentially serial, showing a reduced cost of increasing the number of distractors [6], rather than a lack of cost irrespective of distractor number. These effects are not caused by differences in basic visual features (e.g. luminance or contrast) because they do not occur when emotional faces are inverted or made of the same features arranged in a different configuration [6].

A similar facilitation by emotion arises when multiple stimuli are shown in rapid succession, rather than simultaneously as in search displays. In 'attentional blink' paradigms, a visual target is often missed when presented shortly after another target within a continuous stream of stimuli, but such failures are reduced when

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the second target is emotionally arousing [9], as compared with when it is neutral. These effects are independent of visual properties and familiarity of stimuli [9]. Likewise, in exogenous cueing paradigms, drawing attention to the location of an invalid cue has a higher cost on target detection when the cue is emotional (e.g. [7,10,11]), even when cues are non-predictive and their emotional meaning is task-irrelevant. It is unclear, however, whether these effects reflect faster orienting [7,10] or prolonged holding of attention [12,13], or both. Remarkably, visual detection threshold for low-contrast stimuli is improved following valid emotional cues, suggesting a transient capture of spatial attention and enhancement of early processing stages for information at the affectively cued location [14]. On the other hand, emotional effects on spatial attention are exacerbated by higher degrees of anxiety as a result of slower re-orienting from invalid cues, rather than quicker orienting to valid cues [12]. It is possible that different attentional processes might be differentially modulated in different conditions.

These findings suggest that under conditions where the deployment of attentional resources is limited, in space or in time, emotional information is prioritized and receives privileged access to attention and awareness (see also [7,15]). However, this 'emotional salience' does not imply that emotional stimuli should remain insensitive to any other regulatory influences, including suppressive effects due to sensory competition or high attentional load [16]. Instead, their representation in the visual system can exhibit a greater resistance or persistence relative to neutral stimuli under the same conditions of limited resources. This advantage is produced by various emotional signals, including faces, words, complex scenes, or aversively conditioned stimuli, as well as feared objects in people with specific phobias (e.g. snakes, spiders), but no investigation has systematically compared distinct classes of stimuli as a function of precisely defined degrees of affective values. Emotional biases are probably stronger with 'biologically prepared' stimuli (e.g. faces), and with negative or threat-related emotions (e.g. fear or anger) [17], although pleasant and arousing stimuli can sometimes have similar effects, suggesting that arousal value rather than just valence (negative vs positive) plays a crucial role [9]. However, threat and arousal are usually highly correlated.

Individual differences in personality or anxiety level can also modulate the magnitude or nature of emotional biases in attention [4,7,10,12,13], even in non-clinical populations. Although some studies found faster orienting to threat stimuli in highly anxious people only [10], others emphasized slower disengagement [12] or reduced 'avoidance' relative to non-anxious people [13], suggesting that distinct attentional components might be involved and/or that differences in habituation or emotional regulation [18] might further contribute to overt behaviour. A greater salience of emotional information impacting on the allocation of attention is likely to reflect some intrinsic property of the brain operating across different tasks in all individuals [19], but with variations resulting from context, personality, or past experience [20]. We still need to understand more about the role of these distinct factors and relate them to specific neural substrates.

Sensory processing is enhanced by emotion

Many neuroscience studies show that selective attention in perception is mediated by amplified processing within sensory pathways. Neuroimaging and neurophysiology results demonstrate a relative boosting of the neural representation of task-relevant (i.e. attended) information, at the expense of competing and irrelevant (i.e. unattended) stimuli [1,3]. Thus, neural activity produced by visual stimuli will be either enhanced or suppressed depending on whether the stimulus is attended or not, at both early (e.g. V1) and later stages of processing (e.g. temporal cortex).

Likewise, neuroimaging studies using PET (e.g. [21,22]) or fMRI (e.g. [23,24]) have shown enhanced responses to emotional stimuli relative to neutral stimuli – including angry or fearful faces, threat words, aversive pictures, and fear-conditioned stimuli (for review, see [25]). Enhanced responses to emotional visual stimuli can arise in category-selective areas, such as the fusiform face area (FFA) for emotional faces [23,24], and in posterior occipital and parietal regions [21,26,27]. Similar increases are seen in auditory cortex for emotional sounds or voices [28–30]. EEG and MEG studies also show amplified responses to emotional visual events, involving early sensory components (e.g. P1 and N1 at 120–150 ms; [31–34]), as well as later cognitive components (e.g. after 300–400 ms; [35,36]). These increased sensory responses often arise even when people are not required to pay attention to the emotional meaning of stimuli. Tasks requiring more explicit evaluation of affect can produce stronger or additional activations, particularly in higher-level brain regions such as superior temporal sulcus or ventromedial prefrontal cortex [25,35,37], but these effects are probably related to more complex appraisal processes [18,37] rather than perceptual processing *per se*.

Enhanced sensory responses to emotional stimuli provide a plausible substrate for their greater salience in attracting attention, as observed behaviourally. Stronger neuronal activation can render emotional stimuli more resistant to the suppressive interference caused by distractors. Consistent with models of attention based on biased competition (Box 1), this boosting of responses can generate a more robust and sustained representation of emotional stimuli within the sensory pathways, yielding a stronger weight in the competition for attentional resources and prioritized access to awareness, relative to the weaker signals generated by any competing neutral stimuli. To the extent that the result of such boosting is equivalent to the typical effect of attention on sensory processing [1,3], this might account for the fact that emotional events are more swiftly discerned, or more difficult to ignore, than ordinary neutral events. A crucial issue, then, is whether such effects of attention and emotion reflect different modulatory signals.

Different sources of top-down control can influence perception

Enhanced perceptual processing by selective attention is thought to result from top-down modulation of sensory cortex by higher-level regions in parietal and frontal cortex [3]. This control can be driven by endogenous factors related to current goals, or by exogenous factors

Box 1. Both attention and emotion can bias neuronal responses

Research on the neural substrates of selective attention reveals that neurons in visual cortex show markedly reduced responses to an optimal stimulus when distracters are also present in the scene, indicating competitive suppression between the representations of simultaneous stimuli [3,45]. Directing attention to the optimal stimulus can counteract such interference, by enhancing information processing at this location and restoring an optimal response, similar to the same stimulus presented alone (see Figure 1a). Thus, selective attention provides a mechanism to bias neuronal activity to represent behaviourally relevant stimuli in cluttered scenes, irrelevant information being filtered out. This attentional modulation is not present during the initial phase of response but starts ~150–200 ms after stimulus onset (see Figure 1a) [45], presumably resulting from top-down influences from fronto-parietal regions [3].

A similar modulation can arise from emotion signals. Recordings of face-selective neurons in monkeys have found enhanced responses for emotional relative to neutral expressions (see Figure 1b), with such enhancement occurring 50–100 ms after the initial face-selective activity. Other neurons show similar increases in the later part of their response for faces of particular individuals [43]. In both cases, such modulations were attributed to re-entrant influences from distant brain regions such as the amygdala and/or other limbic areas, which might convey affective or familiarity information contributing to a fine-grain representation of faces at later latencies. Such influences might provide a mechanism strikingly analogous to attentional modulation to bias sensory representations in favor of affectively significant events, in parallel or before attention itself.

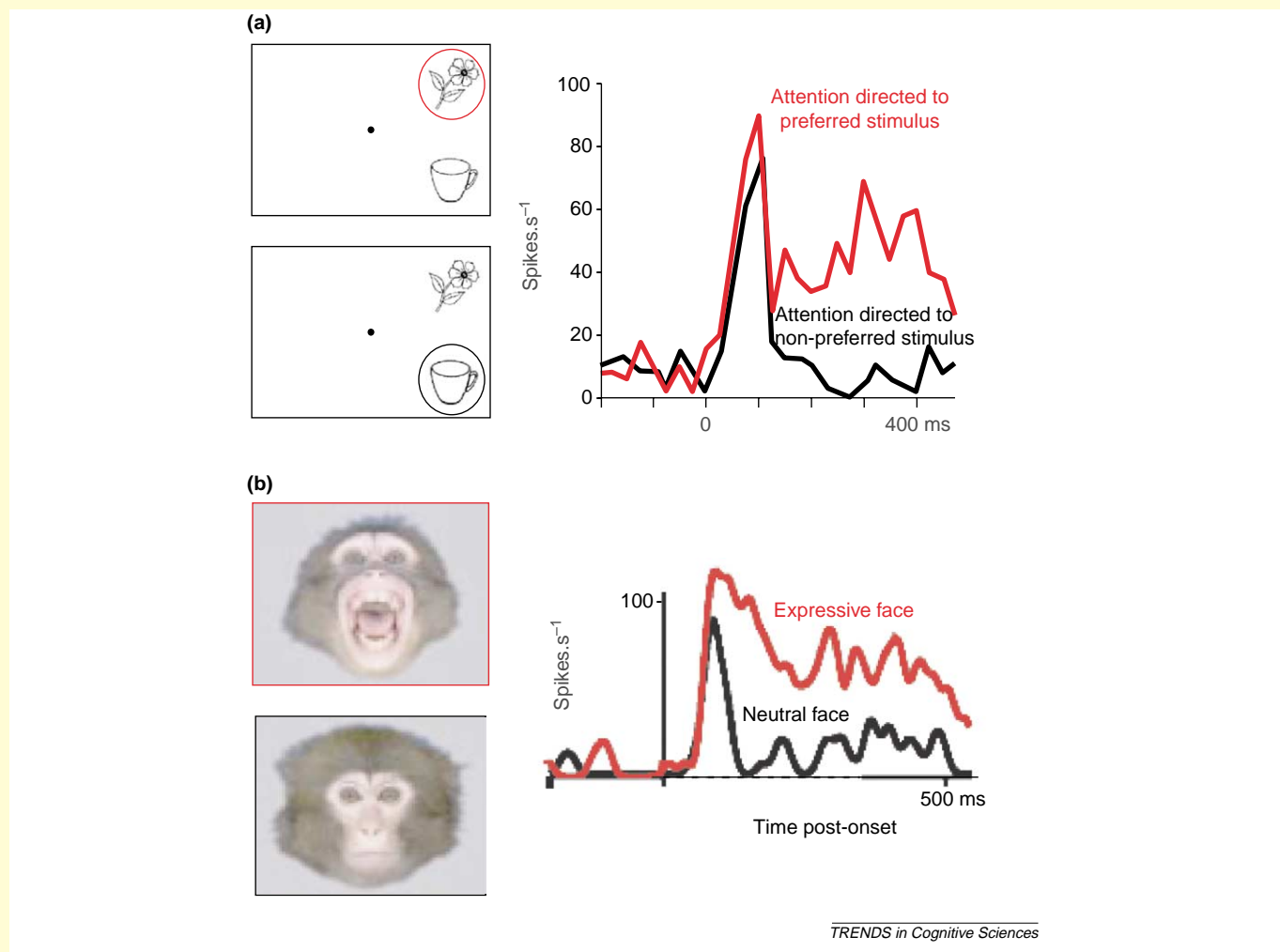


Figure 1. (a) Directing attention to a preferred stimulus (e.g. the flower) can counteract the interference of a distractor stimulus (the cup), restoring the neuronal response (right). Response to the preferred stimulus alone would be similar to the attended case (red curve), whereas the distractor stimulus alone would produce no response. Adapted from [45]. (b) Recordings of face-selective neurons in monkeys revealed a similar delayed enhancement of responses to emotional relative to neutral expressions. Adapted from [43].

such as abrupt changes and sensory salience of external inputs (e.g. loudness, brightness, pop-out, etc.). However, although this form of selective attention clearly plays a key role in the control of perception and behaviour, it could also be deleterious if significant events occurring outside the current focus of voluntary attention were totally ignored. It would be advantageous if unexpected events, especially those with a particular emotional value (e.g.

threat), could be monitored and detected at least to some extent independently of the current attentional goals. Such monitoring process should then also act to redirect processing resources and promote shifts of attention to a new focus of interest.

Several results suggest that distinct neural circuits might be responsible for enhancing the perception of emotional events, operating through direct top-down

signals that are separate from those generated in parietal and frontal cortex. In particular, powerful influences of emotion on perception seem exerted by the amygdala – an almond-shaped nucleus in the anterior medial temporal lobe with widespread connections to many other brain regions [38]. The amygdala is known to be crucial for fear processing and fear learning, but presumably also important for a wider range of functions related to affective pertinence [39] and reflexive emotional reactions [38]. It is well positioned to modulate perceptual processing because not only does it receive rich sensory inputs from all modalities, but also sends projections to many cortical and subcortical regions, potentially capable of influencing perception and behaviour in multiple ways [40,41]. Direct monosynaptic projections from amygdala neurons reach all cortical stages along the ventral visual system in a topographically-organized manner, including primary visual cortex [40] (Figure 1a).

Amygdala activity can influence visual processing

Several neuroimaging studies show that amygdala activity correlates with enhanced responses to emotional stimuli in visual cortex [22,24,26]. Connectivity analyses also reveal a greater ‘coupling’ of amygdala with fusiform [22] and primary visual cortex [26] when seeing fearful vs neutral faces. More direct evidence for a modulatory role comes from recent fMRI results [42] showing that amygdala lesions can abolish the enhanced visual activation for fearful faces relative to neutral faces, despite visual areas remaining structurally and functionally intact. Patients with hippocampus damage but intact amygdala show normal increases for fearful faces in visual cortex, whereas patients with amygdala damage show no such increase (Figure 1b). The severity of amygdala lesions is inversely correlated with fusiform enhancement in the same hemisphere, consistent with a role of ipsilateral connections between amygdala and cortex [40]. Lesions in medial temporal lobe extending to the amygdala can also abolish the detection advantage for

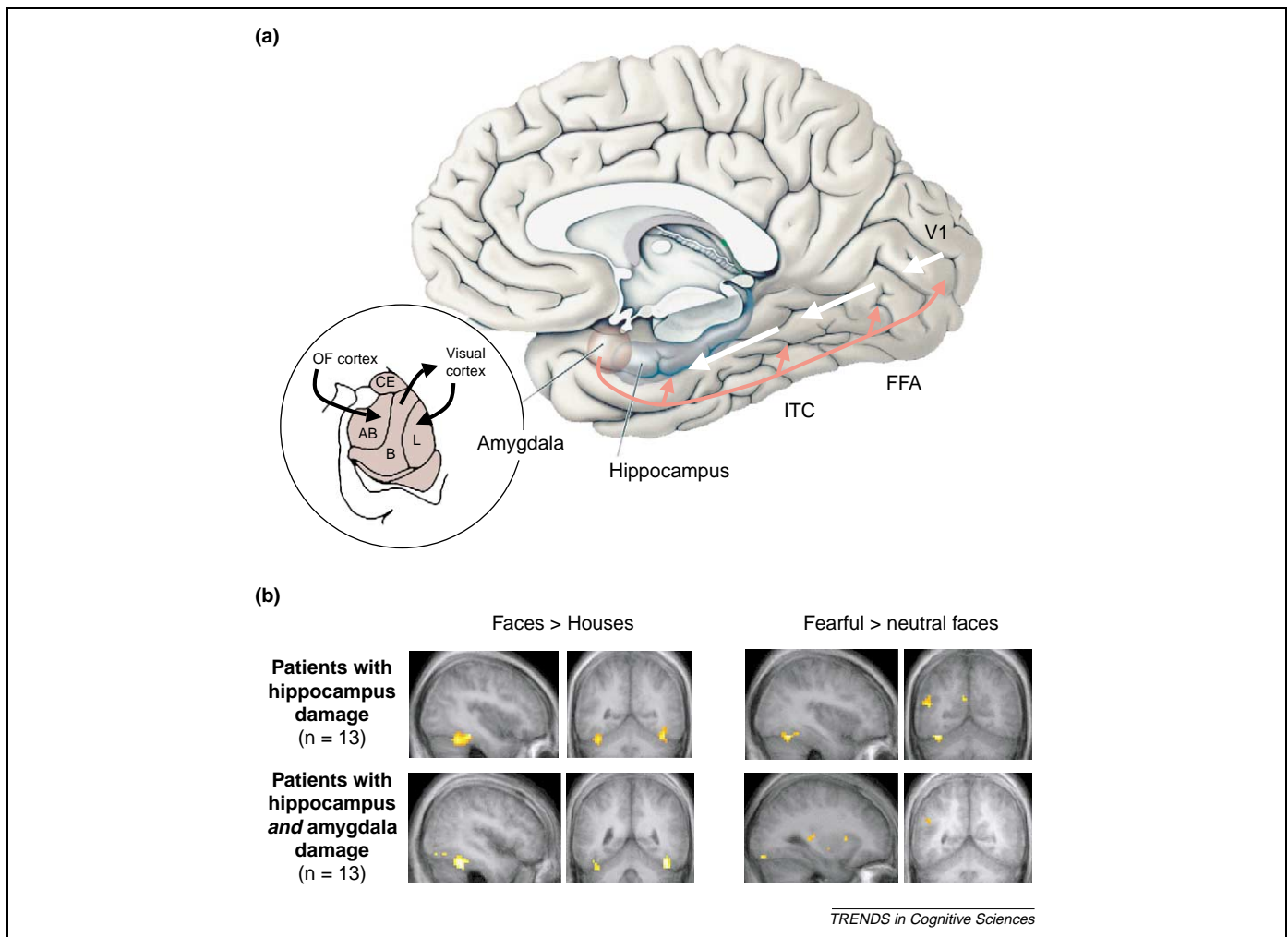


Figure 1. Feedback connections between amygdala and visual cortex. **(a)** Anatomical tracing studies in the monkey show that the amygdala not only receives inputs from ventral visual cortical pathways (in its lateral nucleus), but also sends connections (from its basal nucleus) back to virtually all processing stages along the ventral visual system, including primary visual cortex (area V1). These connections project to layers I/II and V/VI, consistent with a feedback role. (AB, accessory basal nuclei; B, basal nuclei; CE, central nuclei (of the amygdala); FFA, fusiform gyrus face area; ITC, inferior temporal cortex; L, lateral nuclei; OF, orbitofrontal). Adapted from [40]. **(b)** Functional brain imaging results in humans support a role of the amygdala in modulating visual responses to emotional stimuli. Patients with medial temporal lobe sclerosis who have lesions involving the hippocampus alone (upper row) show normal activation of the fusiform cortex when contrasting fearful vs neutral faces (right), as do healthy subjects (not shown). Patients with additional lesions involving the amygdala (lower row) show no effect of fear expression in visual cortex. However, fusiform cortex is still normally activated in both patient groups when they perform a task on faces relative to houses (left). These results suggest that amygdala damage can have distant functional consequences on the activity of visual cortex, selectively affecting the emotional modulation. Adapted from [42].

emotionally salient stimuli in ‘attentional blink’ experiments [9].

Increased perceptual processing of emotional (especially threat) stimuli might therefore result from direct ‘feedback’ signals imposed by amygdala on cortical pathways, potentially additive or competing with other top-down influences imposed by attentional systems in frontal and parietal cortex. Interestingly, a modulation of face-selective neurons by expression occurs with some delay (~50 ms) after response onset [43], consistent with re-entrant influences (Box 1). In auditory cortex, only late

neuronal responses to aversive tones depend on amygdala inputs; early responses (<50 ms) do not [44]. Similarly, attentional signals from fronto-parietal regions probably feed back to lower sensory areas after an initial sweep of feedforward inputs (~150–200 ms post-onset [45,46]). Thus, the representation of a stimulus in sensory cortices might be biased by several concurrent re-entrant signals originating from different sources but converging on a common perceptual pathway.

The relative timing of these signals and the mechanisms governing their integration remain largely unknown.

Box 2. Two pathways vs. two stages for emotional control of perception

The amygdala is known to be sensitive to coarse visual information, such as wide-open eyes in fearful faces [58] or blurry low-spatial frequency (LSF) images [47]. Enhanced responses to fearful faces in visual cortex also depend on LSF cues [32,55]. Reliance on crude inputs could allow rapid and preserved amygdala activation when cortical processing is reduced by diverting attention [23,57,60] or masking [58, 59,61], or when unexpected stimuli occur in visual periphery with poor acuity [11]. The amygdala might, however, fail to respond when emotional signals are too brief or too weak [48], and when processing resources are fully depleted by another demanding task [16,26].

Different routes might potentially convey crude sensory information to the amygdala when cortical processing is reduced, but this remains controversial [48]. A two-pathway hypothesis suggests a role for subcortical inputs, perhaps through the superior colliculus and pulvinar (Figure 11a). Thus, amygdala responses to emotional stimuli persist in patients who are blind after destruction of visual cortex [70, 71]. The superior colliculus and pulvinar are activated by unseen faces in these patients [70], as well as by masked [59] or blurred visual stimuli [47]; and both receive LSF inputs from magnocellular visual pathways. Some neurons in superior colliculus preferentially respond to complex

visual patterns [76]. Pulvinar inputs might reach the amygdala either directly [77] or indirectly via projections to extrastriate areas [78].

Alternatively, a two-stage hypothesis suggests that coarse magnocellular inputs might reach the amygdala through an initial feedforward sweep within the visual system [49], affording rapid amygdala activation and subsequent feedback signals before complete processing in cortex (Figure 11b). Rapid magnocellular inputs to parietal and frontal areas also plays an important role in guiding visual attention [49] and object recognition [50,79]. Thus, an initial appraisal of emotional significance might take place in the amygdala based on a limited amount of information, or after just a few first spikes [79], such that some aspects of emotional categorization would require less sensory evidence and proceed quicker than the more elaborate and prolonged cortical processing associated with conscious awareness. This could explain why ERPs to fearful expressions in faces already arise ~120 ms post-onset [31–33,80], before a fine-grain encoding of faces is completed in visual cortex (at ~170–200 ms [32,33]), and before any attentional modulation of these cortical responses (from ~170 to 300 ms) [31].

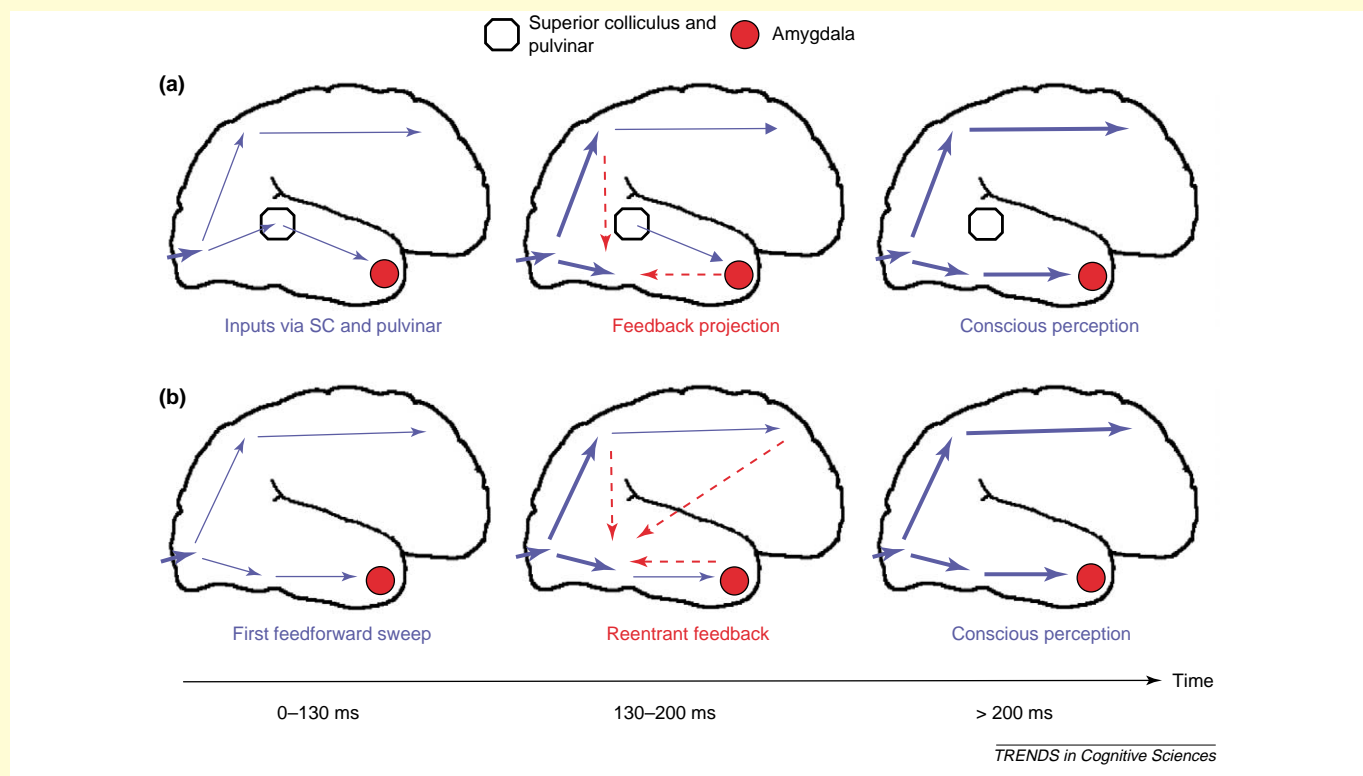


Figure 11. (a) Two-pathway hypothesis for emotional processing of perceptual input by the amygdala. (SC, superior colliculus. Note that the SC and amygdala are subcortical structures, seen here through the cortical surface.) (b) Two-stage hypothesis suggests instead an initial feedforward sweep through the visual system before complete processing. (See text for details.)

These are important issues to investigate in greater detail in the future. Furthermore, the ability of emotional cues to reach the amygdala before they are accessed by conscious awareness may be important in affording such feedback influences. This is possibly related to the extraction of coarse sensory cues that can propagate rapidly in perceptual pathways [47], but the exact nature and origin of these inputs remain controversial [48] (Box 2). Frontal and parietal areas involved in attention also respond rapidly to coarse features [49] that can then be 'retro-injected' into sensory areas to guide ongoing processing

[50]. Thus, similar principles seem to be exploited by the brain to regulate selective sensory processing through different subcortical and cortical systems for emotion and attention, respectively.

Additivity of emotional and non-emotional top-down control

The idea that modulation of visual processing by emotion and voluntary attention might reflect distinct influences was specifically tested by event-related fMRI [23] using faces in a task where both factors were manipulated

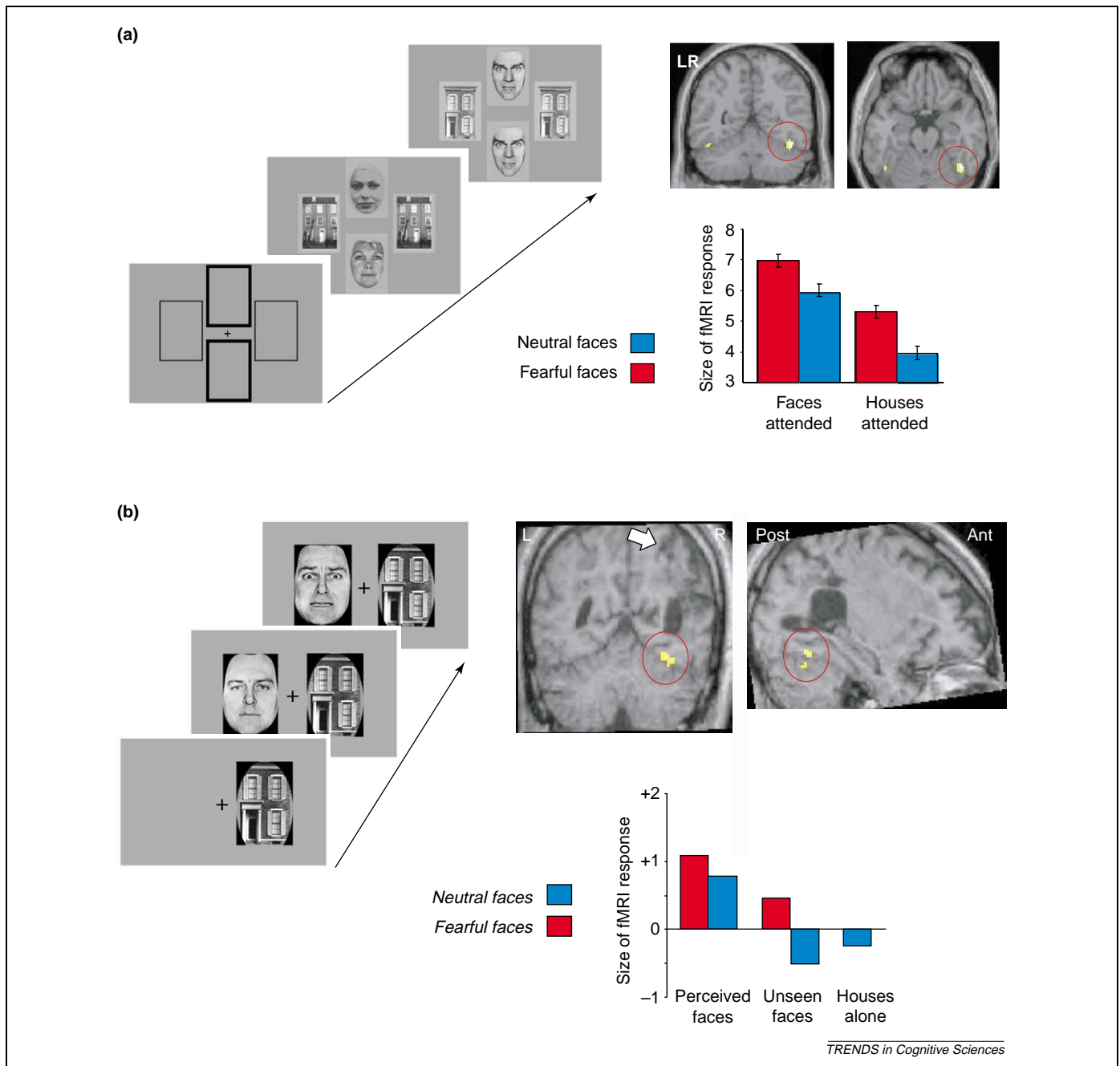


Figure 2. Additivity of emotional and attentional modulations. **(a)** fMRI results in a task where two faces (fearful or neutral) and two houses appeared on each trial (200 ms). Subjects were scanned while attending only to the vertical or horizontal pair of images. Activity in the face-sensitive fusiform cortex is plotted for each trial type (faces either attended or ignored; expressions either fearful or neutral), showing independent modulations by attention and emotional expression. Adapted from [23]. **(b)** fMRI results in a patient with right parietal damage (white arrow) and left spatial neglect. Pictures of houses were briefly shown in the intact right visual field, either alone or with a fearful or a neutral face in the left affected visual field (400 ms). Fusiform activation showed additive effects of fearful expression and awareness for faces in the affected left visual field, consistent with some influence still arising from the amygdala despite parietal damage and inattention to the left side. Adapted from [75].

separately (Figure 2a). The 'fusiform face area' was more activated when faces were shown at task-relevant locations, rather than at other locations; but more crucially, it was always more activated by fearful than neutral faces, even when faces were task-irrelevant and produced a reduced activation overall. This strongly suggests that amygdala feedback could influence visual cortex additively, over and above the concomitant modulation by voluntary attention, because the amygdala also responded to fearful expression regardless of increases or decreases owing to attention or inattention in this situation (although this might not always arise in different task conditions [26]). When using the same fMRI paradigm in patients with amygdala lesions [42], fusiform cortex was still modulated by attention but not by emotion.

Likewise, an earlier PET study [21] found that emotional pictures (i.e. pleasant or unpleasant) and attention to pictures (i.e. during low vs high auditory distraction) both produced similar increases in occipital cortex. Additive effects of emotional content and selective attention were also found in ERP evoked by visual scenes over contralateral parieto-occipital regions [51].

Similar increases arise in auditory cortex for affectively significant sounds, such as screams or laughs [28,29]. Angry prosody enhances activity in a voice-sensitive region of the posterior superior temporal sulcus (STS) [30], equally so when angry voices are heard in the task-relevant or task-irrelevant ear during dichotic listening (Figure 3). At the same time, selective attention produces further increases in STS, regardless of prosody. This

additive pattern of emotion and attention for voices in STS replicates the effect found for faces in fusiform [23].

However, emotion and attention do not produce additive effects only, but sometimes act in an interactive manner, depending on the brain areas [23,52] or task demands [26]. When attention is directed to faces, greater activation by fearful compared with neutral expression can arise in primary visual cortex [23,26], as well as in temporal pole, anterior cingulate, and orbitofrontal cortex [23,53–55]. Such effects might reflect the integration of exogenous emotional processes with other cognitive operations related to endogenous attention and current goals [52,53]. Moreover, the amygdala might fail to influence the cortex when emotional signals are too weak [48] or suppressed by high perceptual competition [16,26,56]. But importantly, amygdala responses can persist in some conditions where cortical responses are reduced [23,57–61] and thus contribute to amplify cortical processing when sensory inputs are otherwise insufficient.

Direct and indirect influences of amygdala

Besides direct feedback to sensory cortices, several other mechanisms might allow the amygdala to influence perceptual processing. Emotional signals could modulate parietal and frontal regions involved in attention control, indirectly affecting perception by common top-down signals. Both fMRI [27] and ERPs [11,51] show parietal activation by negative visual events. In monkeys, parietal neurons are also modulated by the motivational value of targets, although this is better established for reward than threat [62].

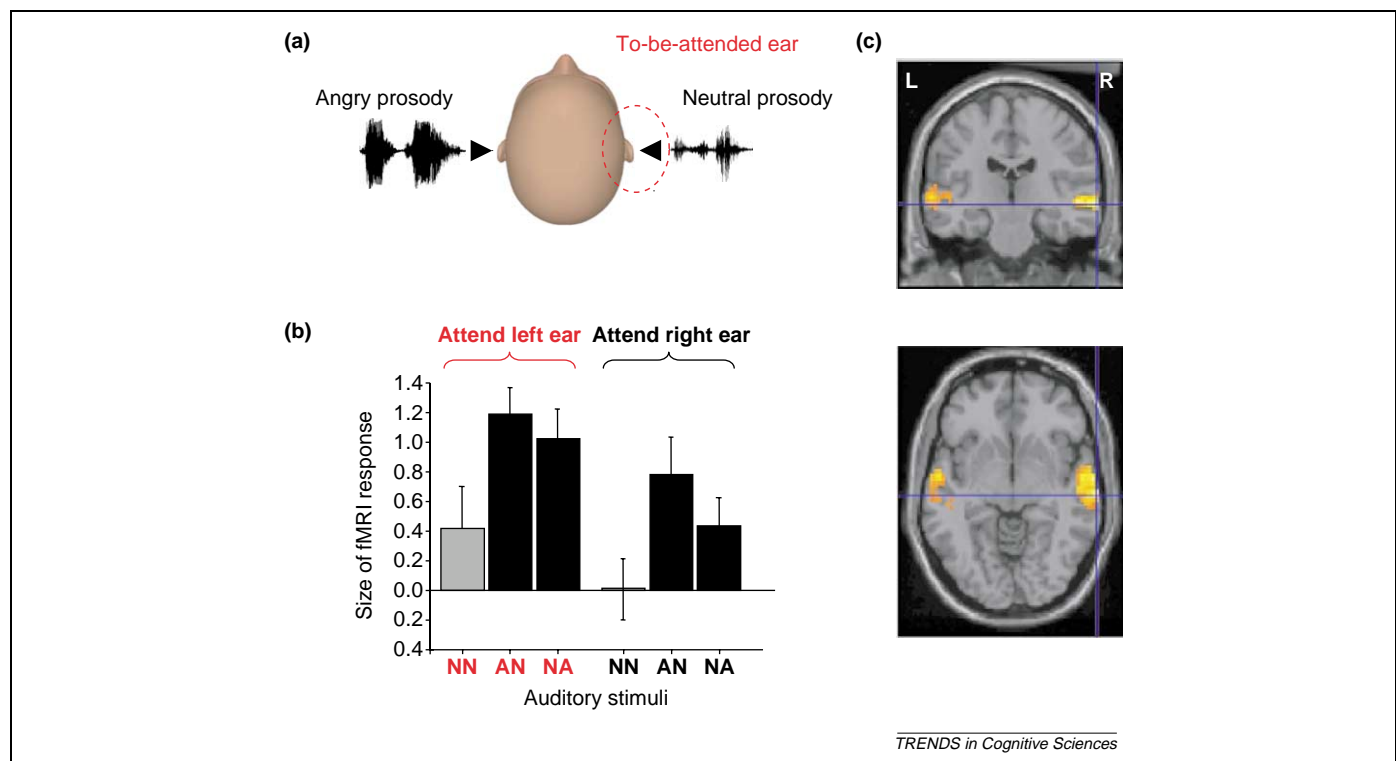


Figure 3. Additive modulation by emotion and attention in auditory cortex in a dichotic listening task (a) where participants selectively attended to either the right- or left-sided voice of a pair of voices (NN, neutral on both sides; AN, angry on the left and neutral on the right; NA, vice versa). Activity is plotted (b) for a voice-selective area of the right superior temporal cortex (c). All conditions produced a concomitant activation of the amygdala. Adapted from [30].

However, emotional enhancement can still operate when spatial attention is impaired as a result of parietal damage. These patients might show spatial neglect but detect emotional stimuli better than neutral stimuli in the affected hemifield [7,15]. Furthermore, fMRI results in such patients (Fig. 2b) indicate that fusiform activity is greater for fearful compared with neutral faces even when faces are neglected [63], and conscious perception of faces produce further increases, similar to the additive pattern of attention and emotion in healthy people [23].

The amygdala might also influence widespread brain regions through its projections to cholinergic nuclei in basal forebrain, which in turn innervate most of the neocortex [41]. In animals, stimulation of the amygdala increases cortical arousal through acetylcholine release [64]. However, fMRI results in humans indicate that emotional enhancement in visual cortex is not amplified by a drug (physostigmine) stimulating acetylcholine release [65]. By contrast, cholinergic stimulation can modulate parietal and orbitofrontal responses to emotional distracters [65], suggesting some effect on attentional control rather than on sensory processing *per se*. Activation of the noradrenergic system by amygdala projections to the locus coeruleus can also modulate attention [66], but the role of this pathway is still unresolved.

Finally, orbitofrontal cortex provides another route by which emotion might influence attentional systems, as it has bidirectional connections with the amygdala (Fig. 1a) and projects to parietal and lateral prefrontal areas [67]. Mutual interactions between dorsolateral and ventral regions in prefrontal cortex have been hypothesized, dorsal regions being activated by task-relevant targets but deactivated by emotional distractors, whereas ventral regions are activated by emotional distractors but deactivated by task-relevant neutral targets [53,54]. These reciprocal relationships might underlie functional interactions between emotional and cognitive factors that regulate the allocation of processing resources and determine goals in behaviour. Whereas most data reviewed here primarily concern emotional biases on the selection of sensory inputs, similar influences might operate on the selection of higher-level representations beyond perception, including memories, thoughts and actions, possibly by imposing affective biases on the activity of prefrontal regions that represent internal goals and implement 'executive' control functions [2]. These in turn could influence the flow of sensory processing and response selection by modulating the current configuration of various functional pathways. Future research should clarify how conflicts between emotional and cognitive sources of bias are monitored and resolved, but it is likely that some regions in prefrontal and anterior cingulate cortex are crucially involved in these regulatory processes [18,52,68].

Conclusions and future directions

Converging evidence has accumulated to show that direct amygdala projections to sensory cortices provide an effective mechanism to enhance processing of emotional events. This direct access to perceptual pathways might

allow emotional influences to operate in parallel with influences from fronto-parietal systems, suggesting that multiple sources of control can guide sensory processing simultaneously. This adds to recent views that attentional mechanisms involve more than a single neural system, but a range of different processes that together select and organize sensory inputs for access to awareness [1]. These might not only encompass traditional concepts of spatial attention (e.g. related to covert oculomotor plans or intentions) and object-based attention (e.g. related to surface segmentation or grouping), but also emotional and motivational processes (e.g. related to the predictive value of events and actions).

Although this neural circuitry is now well established for threat stimuli [17], it remains to be determined whether similar effects exist for positive or reward-related cues, and what brain pathways would then be implicated (see Box 3). Mechanisms of 'emotional attention' could also prove crucial for emotional influences on memory [69]. However, we still need to elucidate the crucial sensory events [39,47,58] and extent of cortical processing [23,48,57,59,70,71] necessary to activate the amygdala.

Box 3. Questions for future research

- Much of the past research on emotional attention has concentrated on fear and threat-related stimuli. What are the effects on attention produced by positive or rewarding events? Are they common to the effects produced by arousing negative stimuli, or do they act through different neural systems, with different time courses, and controlled by different modes of learning? The differential role of arousal and valence also needs further clarification.
- Much debate has concerned the precedence of attention over emotion processing, or vice versa. To what extent are these influences separate and to what extent additive? What is the relative contribution and relative timing of the feedback modulations exerted by emotional and attentional signals on perceptual processing? Can voluntary attention fully override emotional effects, and vice versa? Does such attentional control on emotion responses act on sensory inputs only, or on the amygdala and other emotion-related systems?
- How do anxiety states and personality factors modulate the effects of emotional attention? What are the effects of transient or more sustained changes in mood? Are they caused by intrinsic changes in amygdala circuits, or by higher-order influences on the amygdala that can be mediated by other brain regions, for example, in orbital and medial prefrontal cortices?
- What is the role of different subnuclei in the amygdala in triggering emotional effects on attention, and in modulating these emotional responses as a function of attention, goals or context? Future imaging studies in humans should better take into account the functional complexity of amygdala subregions.
- How do cognitive and emotional sources of attentional biases interact in higher-level brain areas such as prefrontal cortex? Can these interactions determine a differential engagement of both controlled voluntary processes and more reflexive emotional processes? How are these factors modulated by anxiety traits or states? Can emotional biases in perceptual processing become exaggerated when focal lesions or deactivations by TMS involve frontal or parietal regions mediating 'executive' or 'controlled' biases in attention?
- Emotion has long been known to modulate learning, causing both enhancements and costs for different aspects of subsequent memory. To what extent might some memory effects reflect indirect consequences of increased processing of emotional information and reduced processing of concurrent neutral information? Hippocampal circuits involved in memory are clearly modulated by amygdala inputs, but a modulation of sensory cortical areas might also contribute to effects on subsequent memory for emotional events.

Further work should also refine current controversies and dichotomous views on reflexive and controlled processes in emotion responses [20,72]. Complex relationships might determine the relative strength of emotional and attentional biases in different tasks or different individuals, perhaps through contextual or goal-related settings mediated by prefrontal representations [2] that not only influence voluntary control, but might also differentially 'prime' emotional computations and outputs in the amygdala [73], even when these take place outside attention or awareness [74]. New insights on how individual people differ in amygdala activation [60,61] or control functions [18,52,72] should also yield a better understanding of psychopathological disorders characterized by heightened sensitivity to affective events, such as anxiety, phobias or depression.

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