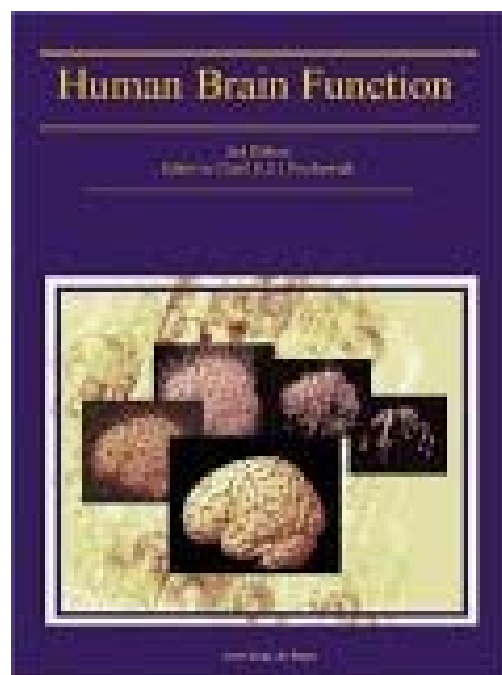


Reciprocal Links Between Emotion and Attention

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Reciprocal Links Between Emotion and Attention

INTRODUCTION

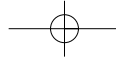
Emotion and attention represent fundamental human psychological processes that influence perception, action, and conscious experience. At any point in time, humans are confronted with a myriad of simultaneous competing environmental stimuli. Given a limited processing capacity, the brain must meet the challenge of detecting and representing only those stimuli most relevant for ongoing behaviour and survival. It is likely that attentional mechanisms evolved to enable the brain to regulate its sensory inputs so as to afford such selective perceptual processing and goal-oriented action.

A large body of work suggests that attention is necessary for an explicit representation of even basic stimulus properties in conscious awareness and to allow rapid and accurate discrimination among current sensory events (Posner and Petersen, 1990). Without selective attention, stimuli may escape conscious awareness or fail to enter working memory (Mack and Rock, 1998). However, there is evidence that a degree of stimulus processing can still take place independent of attention and awareness, and this pre-attentive processing may serve to preferentially guide attention to salient events (Merikle *et al.*, 2001). From an adaptive–evolutionary perspective, it can be assumed that emotion has a privileged role in biasing the allocation of attentional resources toward events with particular significance for an organism’s motivational state.

In this chapter, we review evidence from human functional neuroimaging investigation indicating that dedicated brain systems are specifically tuned to process emotional information. In particular, we address how emotional processing can interact with attentional systems, focusing on the neural mechanisms by which emotion can affect the allocation of attention, as well as the degree to which selective attention in turn influences emotional processing.

Converging data from human functional imaging in healthy subjects, neuropsychological studies of brain-damaged patients, and monkey neurophysiology indicate that selective attentional mechanisms rely on a complex neural network predominantly centred on parietal, frontal, and cingulate cortices that are in turn intimately connected with subcortical structures such as thalamus, basal ganglia, and basal forebrain nuclei (Mesulam, 1999; Posner and Petersen, 1990). This distributed attentional system can control conscious perception by regulating information processing in modality-specific areas (see Chapter X), thereby enhancing the neural representation of relevant stimuli and suppressing irrelevant representations. Brain systems implicated in emotional processing are anatomically distinct but nevertheless show important overlaps with classic attentional networks. For instance, the prefrontal cortex, anterior cingulate cortex, striatum, thalamus, and cholinergic basal forebrain nuclei are all implicated in both attentional and emotional processes, as are early sensory-specific pathways which offer a common input to

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both attentional and emotional control mechanisms. These overlapping sites provide a number of potential nodes for convergence between emotion and attention that might contribute either to the selection or suppression of salient environmental stimuli.

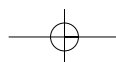
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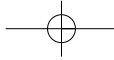
While evidence indicates considerable overlap between systems subserving attention and emotion, there remains the possibility that anatomically distinct routes might allow emotional information to be extracted with substantial independence from voluntary attention, and prior to access into conscious awareness. Thus, behavioural and neuroimaging evidence indicate that affectively significant events can be detected even without awareness of their occurrence (see Chapter X). Such unconscious or “pre-attentive” analysis of emotional value might enable an individual to respond to affectively relevant stimuli, regardless of ongoing cognitive processing and current allocation of attention. In keeping with this, we will outline a view suggesting that emotion and attention constitute two independent though highly interacting neural systems that exert dissociable regulatory influences at several different stages of cortical processing, from elaborating sensory inputs through to preparing response outputs.

BACKGROUND: BEHAVIOURAL AND NEUROPSYCHOLOGICAL FINDINGS

A variety of psychophysical studies have suggested that emotional signals can influence cognition, particularly attention. Only a brief overview will be given here (for extended reviews, see Öhman *et al.*, 2000; Robinson, 1998). Thus, many studies examining the cognitive consequences of emotion have adapted paradigms extensively used in the literature on attention, such as visual search (Eastwood *et al.*, 2001; White, 1995), exogenous orienting (Mogg *et al.*, 1994, 1997; Stormark *et al.*, 1999), inattention blindness (Anderson and Phelps, 2001; Mack and Rock, 1998), or Stroop interference (Mathews and Klug, 1993). In classic visual search tasks, the time to detect a specified target typically increases in direct proportion to the number of irrelevant distracters, indicating serial attentive processing of every stimuli in the display, unless the discrimination of targets from distracters occurs in early parallel processing stages that are independent of attention. In the latter case, attention is automatically drawn to the target (“pop-out”) and detection time can be independent of distracter number. Several search experiments have shown more rapid detection of emotional stimuli among neutral distracters than vice versa, with a relatively flat or much shallower search rate as a function of the number of distracters. Such attentional benefits in search experiments have been reported when targets were faces with positive or negative expressions (Eastwood *et al.*, 2001; Hansen and Hansen, 1988; Öhman *et al.*, 2001b; White, 1995), spiders (Kindt and Brosschot, 1997), or snakes (Öhman *et al.*, 2001a). These effects suggest that the emotional value of stimuli can be perceived by some rapid pre-attentive route that then facilitates focal attention to the location of an emotional target more efficiently than to a neutral target. The most consistent capture of attention by emotion is usually found with negatively valenced or fear-related stimuli (Öhman *et al.*, 2000), and search rate slopes seem shallower for schematic faces with a negative/angry than a positive/happy expression (Eastwood *et al.*, 2001). Moreover, the superiority of emotional targets is enhanced for fearful or angry faces in anxious individuals and for feared stimuli in phobic subjects (Öhman *et al.*, 2000). However, some studies in normal subjects do not find significant pop-out effects for emotional faces in visual searches (Nothdurft, 1993).

Another strategy has examined the effect of emotional versus neutral cues on spatial orienting of attention toward peripheral visual targets, following the classical paradigm developed by Posner *et al.* (1982). Orienting is typically faster to targets appearing on the same side as an emotional cue (*e.g.*, faces, spiders, threat words, conditioned shapes) and slower to those appearing on the opposite side (Armony and Dolan, 2002; Bradley *et al.*, 1999; Mogg *et al.*, 1994, 1997; Stormark *et al.*, 1999). In some cases, disengaging from invalid cues to reorient elsewhere appears to be especially slow when such invalid cues are emotional, suggesting that attention is not only captured but also tends to dwell longer on emotional stimuli (Fox, 2000). Similar effects can occur even when emotional cues are masked and not consciously perceived (Bradley *et al.*, 1997a). Again, these influences of emotion on attentional orienting are modulated by anxiety or phobic traits in the participants (Bradley *et al.*, 1999; Mogg *et al.*, 1994).





Enhanced detection of emotional faces has also been found in conditions where normal subjects must focus their attention to one location so that they will usually remain blind to stimuli presented at another unattended location (Mack and Rock, 1998). Similarly, the perception of words with aversive meaning is less disrupted relative to that of neutral words when attentional resources are limited, as during the attentional blink subsequent to discriminating successive targets in a rapid serial visual stream (Anderson and Phelps, 2001). Likewise, patients with unilateral spatial neglect and visual extinction after focal brain damage may suffer from an abnormal spatial bias in attention and fail to perceive a stimulus in their contralesional hemifield in the presence of a simultaneous stimulus on the ipsilesional side. However, this contralesional deficit is much less severe for faces with happy or angry versus neutral emotional expressions (Vuilleumier and Schwartz, 2001a) or for spiders versus flowers (Vuilleumier and Schwartz, 2001b). These findings suggest that processing of emotional stimuli occurs prior to selective attention and that this pre-attentive processing may serve to enhance stimulus detection. On the other hand, a recent study (Anderson and Phelps, 2001) has revealed that a resistance of aversive words to extinction from awareness during the attentional blink is not observed in patients with lesions in the amygdala, a structure critically implicated in emotion and fear processing (Armony and LeDoux, 2000), suggesting that a modulation of attention and awareness may arise from a specialised neural mechanism related to affective processing.

SEGREGATED AND INTEGRATED SYSTEMS FOR EMOTIONAL PROCESSING

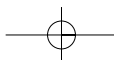
Before discussing reciprocal interactions between emotion and attention, we briefly review recent data concerning the neural basis of emotional processing (see also Chapter X). It seems reasonable to conjecture that different types of emotions, associated with distinct experiential qualities, are mediated, at least partly, by separate neural systems. Moreover, each type of emotion can be elicited by different cues in different sensory modalities. Accordingly, functional neuroimaging studies have used a wide variety of stimuli and procedures to investigate affective responses produced by external stimuli or internal states. Stimuli employed in these studies have included human faces with specific expressions (*e.g.*, fear, happiness, or disgust), words with emotional meaning (*e.g.*, sex or death), pictures with emotionally laden content (complex scenes or film clips with views of accidents, mutilation, spiders, etc.), or, more rarely, auditory words or voices with affective tones. Other studies have focused on somatosensory sensation using painful stimulation. This line of research has begun to delineate a number of brain areas engaged in emotional processing, although the precise function of individual regions is still unclear. Some regions may show an apparent selectivity for certain types of emotion or for certain classes of stimuli, whereas others may show more general responses to different types of emotion and different types of stimuli; however, a considerable heterogeneity across studies precludes definitive conclusions.

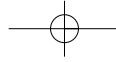
Many neuroimaging studies have examined differential brain activity in response to faces conveying distinct emotional expressions. Facial expressions provide a valuable tool to assess neural systems involved in affective processing because they constitute a crucial signal for social communication, and their recognition is universal and presumed to rely on hard-wired neuronal circuits (Ekman and Oster, 1979; Öhman *et al.*, 2000). The best identified emotion circuit is that mediating processing of fearful facial expressions and other non-facial, threat-related stimuli, where there is a high degree of convergence between human functional neuroimaging and neuropsychological investigations (Calder *et al.*, 2001). These data also accord with findings from animal physiology and computational modelling perspectives (Armony and LeDoux, 2000; LeDoux, 1996). Fear, a crucial emotion for adaptive and survival behaviour, is also likely to have privileged links with neural systems of attention governing perception and action (Armony and LeDoux, 2000).

A key structure implicated in fear processing is the amygdala, a heterogeneous collection of nuclei in anterior medial temporal lobe (Armony and LeDoux, 2000; LeDoux, 1996). Functional imaging studies such as those by Breiter *et al.* (1996), Morris *et al.* (1996), and Thomas *et al.* (2001) have consistently observed an activation of the amygdala when subjects are shown faces with a fearful expression, compared to neutral faces (see Chapter X), a finding consistent with

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deficits in recognising fearful expressions after amygdala damage (Calder *et al.*, 2001). The amygdala is also activated by fearful voices (Morris *et al.*, 1999; Phillips *et al.*, 1998b), pictures of threatening scenes (Irwin *et al.*, 1996; Lane *et al.*, 1997c, 1999), threat-related words (Isenberg *et al.*, 1999; Tabert *et al.*, 2001), and elementary visual or auditory stimuli with acquired aversive value due to Pavlovian conditioning (Buchel and Dolan, 2000; Buchel *et al.*, 1998, 1999; LaBar *et al.*, 1998). Fearful faces and other threat-related stimuli also activate anterior and posterior cingulate cortices (Maddock, 1999; Morris *et al.*, 1996, 1998a), inferior prefrontal cortices (Kesler-West *et al.*, 1999; Morris *et al.*, 1996, 1998a; Sprengelmeyer *et al.*, 1998; Whalen *et al.*, 1998b), and orbitofrontal cortices (Armony and Dolan, 2002; Sugase *et al.*, 1999; Vuilleumier *et al.*, 2001b); however, many of the latter areas are also activated by other categories of facial emotional expression suggesting that these may have a more general function in emotional behaviour rather than perceptual processing of signals representing fear *per se*.

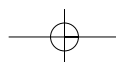
The amygdala has also been activated by faces with other negative expressions such as anger (Critchley *et al.*, 2000; Hariri *et al.*, 2000) or sadness (Blair *et al.*, 1999). Processing angry faces increases activity in anterior cingulate and lateral prefrontal cortices (Blair *et al.*, 1999; Kesler-West *et al.*, 1999; Sprengelmeyer *et al.*, 1998), as well as orbitofrontal cortices (Blair *et al.*, 1999). By contrast, sad faces activate anterior and medial temporal regions (Blair *et al.*, 1999; George *et al.*, 1995), although in other studies they do not produce significant effects compared to neutral faces (Kesler-West *et al.*, 2001). On the other hand, happy faces activate orbitofrontal (Kesler-West *et al.*, 2001; Morris *et al.*, 1996, 1998a), inferior prefrontal (Dolan *et al.*, 1996; Phillips *et al.*, 1998a), and anterior cingulate cortices (Dolan *et al.*, 1996; Phillips *et al.*, 1998a). In a few studies, a response in the amygdala to happy or highly arousing positive stimuli has been reported (Garavan *et al.*, 2001; Phillips *et al.*, 1998a). Thus, across studies, there is considerable variability in the reported activations for angry, sad, and happy emotion in faces.

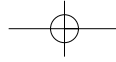
By contrast, facial expressions of disgust are associated with a more reliable pattern of activation, evoking consistent activity in insula and basal ganglia (caudate and putamen) in addition to inferior prefrontal and lateral temporal cortex (Phillips *et al.*, 1997, 1998b; Sprengelmeyer *et al.*, 1998). This role of insula and basal ganglia in mediating the perception of disgust is also in accord with the deficits reported following focal lesions in these regions (Calder *et al.*, 2001).

Functional neuroimaging studies have also revealed that some brain areas respond to emotional more than neutral stimuli, regardless of emotion or stimulus type. These include regions in temporal, orbitofrontal, prefrontal, and cingulate cortices, as well as ventral parts of basal ganglia, thalamus, or upper brainstem (Blair *et al.*, 1999; Critchley *et al.*, 2000; George *et al.*, 1995; Lane *et al.*, 1997c; Morris *et al.*, 1998a; Northoff *et al.*, 2000; Paradiso *et al.*, 1999; Phillips *et al.*, 1998b; Sprengelmeyer *et al.*, 1998; Thomas *et al.*, 2001; Vuilleumier *et al.*, 2001b). These areas might constitute final converging nodes for the processing of emotional stimuli in general (Sprengelmeyer *et al.*, 1998) or mediate nonspecific arousing effects. It is interesting to note that some of these same areas are also implicated in attentional and cognitive executive control processes. Thus, it has been suggested that prefrontal regions are in a position to enhance the representation of stimuli that are currently most relevant and inhibit those that are irrelevant, while cingulate regions may control the selection of appropriate motor action (Bush *et al.*, 2000; Posner and Petersen, 1990). A general response to a variety of emotional stimuli might therefore reflect neural mechanisms that have the capacity to influence ongoing processing and elicit appropriate behaviour based on affective cues or priorities. Also, nonspecific increases in activity are often found in visual cortical areas in response to visual emotional stimuli, suggesting enhanced sensory processing of affectively significant events (see below). Thus, at least some of the neural systems activated by emotion might not be necessary for the detection and evaluation of salient stimuli *per se*, but instead play a crucial role in adjusting the allocation of attentive and cognitive resources to the presence of such stimuli.

HOW ATTENTION INFLUENCES EMOTIONAL PROCESSING: AUTOMATIC VERSUS DELIBERATE PROCESSING OF EMOTIONAL STIMULI

A critical aspect of adaptive behaviour is the necessity to monitor the environment and detect potentially significant stimuli (*e.g.*, emotional) even when these are unexpected and hence not





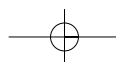
currently task relevant or are outside the focus of attention. Automatic emotional processing could provide the organism with a capacity to interrupt ongoing activities and redirect attentional resources toward unforeseen threats. In support of this idea, behavioural studies provide evidence that detection of emotional stimuli (particularly threat-related stimuli) occurs rapidly and automatically (Globisch *et al.*, 1999; Mogg *et al.*, 1997), even when stimuli are initially presented at unattended locations or outside awareness (Bradley *et al.*, 1997b; Mogg and Bradley, 1999; Stormark *et al.*, 1999), as reviewed above. Other behavioural findings in healthy subjects (Schweinberger and Soukup, 1998) and neuropsychological dissociations (Calder *et al.*, 2001) in relation to face processing also suggest that emotional expressions are analysed through specialised pathways, independent from those involved in the analysis of identity and other non-emotional facial features (*e.g.*, speech lip cues).

It is noteworthy that neuroimaging studies examining responses to emotional stimuli have employed experimental conditions where the emotional significance of stimuli had no bearing with the subjects' actual task. For example, faces with fearful expressions activate the amygdala and related brain structures, even when subjects were primarily asked to attend to the gender of the faces in order to make female/male judgments (Morris *et al.*, 1996, 1998a; Phillips *et al.*, 1997, 1998b; Sprengelmeyer *et al.*, 1998; Vuilleumier *et al.*, 2001b). This suggests that emotional features can be extracted from the stimuli even though these are not relevant to the gender decision task. Likewise, emotional effects produced by facial expressions of anger (Blair *et al.*, 1999; Sprengelmeyer *et al.*, 1998), sadness (Blair *et al.*, 1999), disgust (Phillips *et al.*, 1997, 1998b; Sprengelmeyer *et al.*, 1998), and happiness (Morris *et al.*, 1996, 1998a; Phillips *et al.*, 1998a) were also obtained when subjects made gender decision on the faces, without explicitly attending to the facial expressions *per se*. One study (Dolan *et al.*, 1996) also showed that during a delayed match-to sample memory task requiring subjects to hold a face identity in mind over a 45-second interval, neural activity was greater for happy than neutral faces in the fusiform and inferior frontal cortex, as well as anterior cingulate and thalamic regions. This again suggests that the emotional salience of faces was represented despite being irrelevant to the task.

Such effects, however, do not provide a direct demonstration that emotional expression is automatically processed without attention, because the differential emotional responses observed in these tasks could result from deliberate attentional and/or strategic factors. Several recent studies have addressed this issue by systematically comparing the effects of the same emotional stimuli across different task conditions. This approach has allowed a more direct assessment of whether some emotional effects may reflect mandatory responses, occurring independently of task or attention.

Task-Dependent Responses to Emotional Faces

Critchley *et al.* (2000) used fMRI to compare intentional ("explicit") and incidental ("implicit") processing of emotional faces. Subjects were presented with blocks of mixed angry and happy faces, alternating with blocks of neutral faces, while they judged either the gender (male versus female) or expression (neutral versus emotional) of each face. A main effect of emotion, independent of task (*i.e.*, evoked by the mixed angry and happy, compared to neutral faces during both judgment conditions) was found in visual areas including fusiform and peristriate cortex, middle temporal gyrus, and retrosplenial cortex, as well as in the vicinity of the posterior amygdala/superior hippocampal junction and pulvinar nucleus of the thalamus (all in left hemisphere). Activity in bilateral posterior amygdala/hippocampal regions was specifically increased during gender versus emotional judgements (*i.e.*, when emotional expressions were incidental to the task). A similar increase for incidental emotional stimuli was also found in left insula, left inferior prefrontal cortex, and bilateral anterior putamen. By contrast, intentional processing of emotion enhanced activity in left middle temporal gyrus, bilateral fusiform regions, and left posterior putamen. These findings suggest that explicit visual analysis of emotional traits may engage specific processes in middle temporal gyrus and fusiform cortex (see Fig. 21.1), consistent with the properties of neurons found in temporal lobe regions by neurophysiology studies in the monkey (Hasselmo *et al.*, 1989; Perrett *et al.*, 1992). On the other hand, fusiform cortex and limbic areas such as the reported amygdala/hippocampal regions and



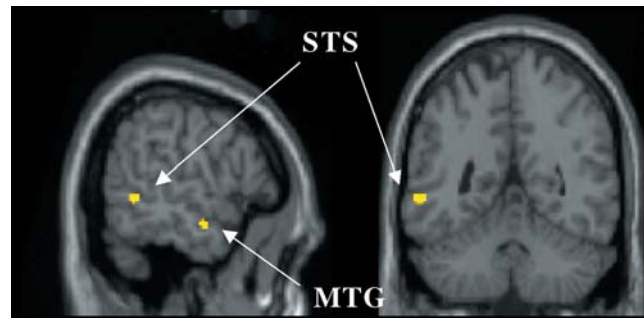


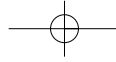
FIGURE 21.1

Explicit attention to faces with emotional expression (fearful versus neutral) may specifically increase activation in the superior temporal sulcus (STS), here in the left hemisphere ($-56, -50, -2$). A second peak is also seen in anterior middle temporal gyrus ($-54, -14, -16$). (Unpublished fMRI data.)

retrosplenial areas might be involved in incidental detection of emotional stimuli. However, limitations of this blocked study include not only a relatively imprecise anatomical localisation of the reported amygdala effects but also the failure to distinguish stimulus-driven responses from top-down modulations due to task set and the impossibility of differentiating effects of angry (aversive) and happy (positive) emotions. Furthermore, a true obligatory implicit processing of emotion should occur equally when subjects voluntarily attend to, or ignore, the expression in faces.

A similar approach was used in another blocked fMRI study by Naramuto *et al.* (2001). These authors compared the effect of matching pairs of faces based on emotional expression (happy, sad, or fearful) versus identity, and found that the intentional emotional task selectively increased activity in the right superior temporal sulcus. Matching the two faces' identity versus matching the shape of the faces' contour increased activity in bilateral fusiform regions. The right superior temporal region in this study (coordinates: $x = -49, y = -42, z = 4$) was relatively homologous to the temporal area on the left side ($-55, -52, 10$) previously reported in the Critchley *et al.* (2000) study. However, here again, any difference between distinct emotion types could not be assessed because the pairs of faces were presented in blocks mixing happy and sad expressions or mixing happy and fearful expressions. Notably no activation differences were found in a contrast between these blocks. Given that there were no blocks with neutral faces alone, Naramuto *et al.* (2001) could not assess effects due to obligatory processing of emotion, as this could have occurred for all three expressions when subjects were matching identity or when they were matching expression. Another limitation in this study was that analyses were restricted to a few regions of interest in fusiform and temporal cortex, previously defined by a preferential activation for all faces versus scrambled stimuli.

Gorno-Tempini *et al.* (2001) used functional magnetic resonance imaging (fMRI) in a paradigm similar to Critchley *et al.* (2000), in which single faces were shown each in turn. Processing of happy and disgust facial expressions were compared during either gender or emotional classification tasks. Faces were presented in blocks with a majority of happy faces, a majority of disgust faces or neutral faces alone. In contrast to previous findings (Morris *et al.*, 1996; Phillips *et al.*, 1997; Sprengelmeyer *et al.*, 1998), no brain region was found to exhibit a significant response to emotional expressions independent of task (for both happiness and disgust). However, the right caudate, right thalamus, and left amygdala were more activated by disgust versus happy faces during the emotion classification task (relative to the gender decision task). Conversely, bilateral orbitofrontal cortex showed activation to happy relative to disgust faces that was greater during the emotion classification task; however, the authors did not report whether emotional versus neutral expressions produced significant effects during the incidental (gender) conditions. While activity in the reported areas might be modulated by intentional attention to emotionality of the faces, other areas might possibly show distinct effects that are specific to such "incidental" conditions (see Critchley *et al.*, 2000).



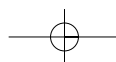
On the other hand, this study identified brain regions showing a main effect of intentional emotional processing. Activity in the right inferior and precentral frontal gyri, anterior insula, and right fusiform cortex was greater when subjects judged expression (irrespective of emotion type) as compared to gender. No effect was found in the superior temporal cortex, although bilateral increases in the latter regions were observed in a contrast of all faces (neutral or emotional) versus scrambled non-face stimuli ([56, -60, 8] and [-60, -60, 8]); however, the observed involvement of frontal areas converges with previous PET studies reporting similar results during deliberate processing of facial emotion. For example, selective increases have been observed in bilateral inferior frontal and right anterior cingulate cortex when subjects matched faces based on their expression versus identity (George *et al.*, 1993), while increases also occurred in inferior frontal gyrus when subjects judged emotional valence (positive or negative) of facial expression versus attractiveness (Nakamura *et al.*, 1999).

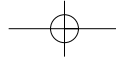
In a similar vein, Hariri *et al.* (2000) compared the effect of judging emotion from either faces or verbal labels in a blocked fMRI design. Subjects were shown a target face (with fearful or angry expression) and had to match the expression of this face either to one of two other simultaneously presented faces or to one of two simultaneously presented words (*afraid* or *angry*). Fearful and angry faces were always mixed. Compared to a simple shape-matching control task, the perceptual matching of emotional faces activated the right fusiform cortex, right thalamus, and bilateral amygdala; whereas, the linguistic matching of a verbal label with expression activated the right fusiform cortex and right inferior frontal cortex. The authors interpreted their results as indicating a suppression of the amygdala and thalamus response to emotional stimuli during the cognitive linguistic task, perhaps mediated by increased right frontal activity; however, there were at least two major confounds in this study. A decrease in amygdala responses might simply be due to the fact that only one emotional face per trial was presented in the linguistic condition versus a total of three faces per trial for the perceptual matching. Moreover, at least one fearful face was bound to appear on each trial in the perceptual matching, compared to only half of the trials in the linguistic condition, and these more frequent fearful expressions were likely to elicit the most effective responses in the amygdala.

A similar problem concerns a recent positron emission tomography (PET) study (Liberzon *et al.*, 2000) examining how cognitive task instructions could modulate the response to emotional non-face stimuli. The same pictures with aversive content (eliciting fear or disgust) or neutral content were shown first during an emotional rating phase, then a second time mixed with new face exemplars during a memory recognition phase. Right amygdala and thalamic increases for emotional compared to neutral pictures were found only during emotional rating, together with a left middle frontal response. However, because half of the pictures during the memory recognition task were repeated from the rating phase, these decreased emotional effects were potentially confounded with habituation versus novelty factors known to influence medial temporal lobe activity. In another PET study (Lane *et al.*, 1999), amygdala responses to arousing (both pleasant and unpleasant) stimuli were not modulated by attentional distraction during a dual task.

Alternatively, a modulation of amygdala responses to aversive stimuli by task demands might occur only for complex pictures in which the emotional content derives from a specific combination of elements in the context represented by the scene and not for fearful faces that constitute more special, biologically salient stimuli. Such a dissociation has indeed been suggested by a recent fMRI study (Keightley *et al.*, 2000) showing that intentional (explicit) versus incidental (implicit) emotional processing tasks increased amygdala activation for negative scenes but did not change the effect of negative faces. Moreover, the main effect of intentional versus incidental emotional tasks activated middle temporal gyri and orbitofrontal cortex bilaterally for faces alone but not for scenes (the latter elicited more activity in right superior prefrontal and occipital areas).

In sum, converging evidence suggests that selective attention to, and explicit categorisation of, emotional traits in faces can specifically activate middle or superior temporal cortical areas (Critchley *et al.*, 2000; Gorno-Tempini *et al.*, 2001; Keightley *et al.*, 2000; Narumoto *et al.*, 2001). This area (Fig. 21.1) might correspond to neurons in superior temporal sulcus that respond to facial expression in monkeys (Hasselmo *et al.*, 1989; Sugase *et al.*, 1999). Such regions might preferentially encode changeable aspects of faces such as expression, gaze, or



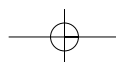


speech mouth cues (Haxby *et al.*, 2000), in contrast to ventral temporal regions in the fusiform cortex that are more concerned with invariant facial features related to identity. In addition, selective attention to emotionality in faces can also activate inferior dorsolateral frontal regions (George *et al.*, 1993; Gorno-Tempini *et al.*, 2001; Narumoto *et al.*, 2001), possibly implicated in more cognitive or attentional components of the task. It is unclear if the same frontal regions are also activated by emotional scenes (Keightley *et al.*, 2000). Alternatively, such frontal effects might reflect activation of premotor cortex controlling facial movements, possibly reflecting responses in “mirror” neurons involved in both motoric encoding of self facial expressions and perceptual recognition of others’ facial expressions (Dimberg *et al.*, 2000). In this regard, it would be of interest to investigate the overlap between activity elicited by perceptual discrimination of facial expressions in conspecifics and self-generated facial movements. Also, it remains to be established whether the superior temporal and inferior frontal cortices are similarly engaged by all types of facial emotion and whether different emotions produce specific hemispheric asymmetries, as suggested by the findings of Critchley *et al.* (2000) and Naramuto *et al.* (2001). On the other hand, the current neuroimaging studies do not provide clear evidence as to whether neural responses elicited by specific emotional stimuli are always obligatory, occurring regardless of task, or can be modulated by selective attention and task demands. Deliberate attention seems capable of influencing the response to some facial expressions—for instance, to happiness (*e.g.*, in orbitofrontal cortex) and disgust (*e.g.*, in basal ganglia)—but there is no convincing evidence that such an influence can also modulate the response to highly salient emotional expressions such as fearful faces (*e.g.*, in amygdala). Indeed, some facial expressions might constitute unique, biologically prepared cues that are more effective in eliciting obligatory emotional responses than complex scene pictures (Keightley *et al.*, 2000; Öhman *et al.*, 2000). Any modulation for other simple non-facial but strongly threat-related stimuli (*e.g.*, a fear-conditioned colour) is still open to inquiry. Indeed, an obligatory processing of fear-related cues (but not necessarily of any other emotional cues), independent of voluntary attention, would be consistent with a special status of fear processing pathways in the brain (Armony and LeDoux, 2000; LeDoux, 1996; Robinson, 1998) and previous findings that fear-conditioned stimuli can elicit both behavioural responses (Öhman *et al.*, 2000) and amygdala activation (Morris *et al.*, 1998b) without awareness of the eliciting event.

Effects of Spatial Attention on Emotional Face Processing

In an event-related fMRI study, Vuilleumier *et al.* (2001b) manipulated the effect of emotion and the effect of spatial attention in a systematic manner to examine how neural responses to fearful expression in faces were influenced by whether these faces were relevant for the task at hand and in the focus of attention, as opposed to task irrelevant and outside the focus of attention. On each trial, subjects were briefly shown two faces and two houses, arranged in a cross-format, with the pair of faces either horizontally or vertically aligned (and, consequently, the pair of houses either vertically or horizontally aligned, respectively; see Fig. 21.2A). The two faces had a fearful expression on half of the trials but a neutral expression on the other half. Subjects maintained eye fixation at the centre. During some blocks of trials, subjects were instructed to concentrate only on the two horizontal stimuli and judged whether they were the same or different pictures (*i.e.*, two same versus different faces, or two same versus different houses); during other blocks, they had to concentrate on the two vertical pictures and similarly judged whether these were the same or different. Thus, on any given trial, subjects could see two faces at task-relevant locations, with either a neutral or fearful expression, or equally often they could see two houses at task-relevant locations, with faces at ignored locations having either a neutral or fearful expression. In this way, the neural response to fearful emotional expression could be compared directly for faces in the focus of attention and faces outside the focus of attention. Importantly, the event order was fully randomised, so that subjects could neither predict the relevant stimulus category nor facial expression.

As expected, based on previous studies (Corbetta *et al.*, 1990; Wojciulik *et al.*, 1998), spatial attention strongly modulated extrastriate visual areas. Bilateral fusiform cortex (*i.e.*, the so-called fusiform face area) showed an increased activity when faces appeared at the relevant locations (Fig. 21.2B,C), whereas parahippocampal cortex (*i.e.*, the so-called place area) showed



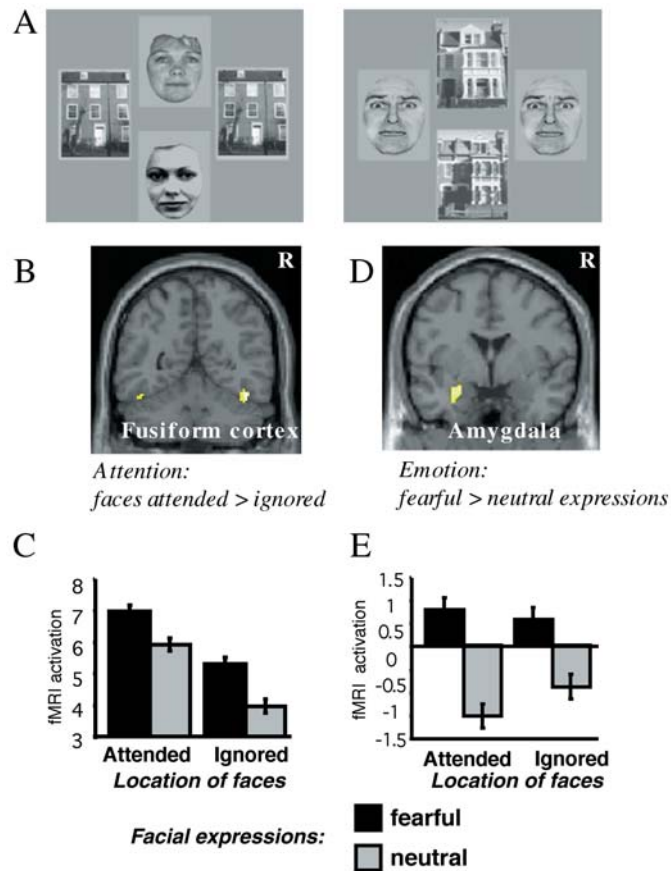
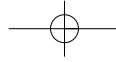
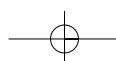


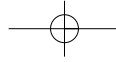
FIGURE 21.2

Distinct effects of emotion and attention on visual responses. (A) Examples of stimuli. On each trial, subjects were briefly shown two houses and two faces (with either fearful or neutral expression) but concentrated only on two prespecified locations (either horizontal or vertical) to make same/different judgments about the stimuli presented there. (B) Face-specific areas in fusiform cortex showed increased activity bilaterally when faces were presented at the attended locations (as opposed to houses). (C) Fusiform activity was also increased when fearful (as opposed to neutral) faces were presented, but this effect was independent from the effect of attention (*i.e.*, it occurred even when faces appeared at the ignored locations). (D) and (E) Left amygdala showed increased activity when fearful (versus neutral) faces were presented, regardless of whether faces were presented inside or outside the focus of attention. (fMRI data from Vuilleumier *et al.*, 2001b.)

an increased activity when houses appeared at the relevant locations, regardless of expression. Note that such increases were purely attributable to spatial attention, as the visual displays were in fact identical across all conditions. Critically, a left amygdala response to fearful compared to neutral faces occurred regardless of whether the faces were at the relevant/attended locations or at the irrelevant/unattended locations (Fig. 21.2D,E), demonstrating that fear processing in the amygdala was obligatory and unaffected by the same modulation of spatial attention that strongly influenced the fusiform response to faces. Note also that facial expression was never relevant to the task and thus was processed incidentally in all conditions.

Another remarkable finding in this study was that activity in the fusiform cortex was enhanced for fearful compared to neutral faces (Fig. 21.2C). This enhancement occurred both when the faces were at the relevant/attended locations or at the irrelevant/unattended locations. Moreover, this enhancement was specific to the face area in fusiform cortex but did not affect the place area in parahippocampal cortex. An explanation for this effect of emotional expression on fusiform activity is that it may reflect influences from amygdala feedback connections onto





extrastriate cortex, which exert modulatory influences enhancing the visual processing of emotionally relevant stimuli (Amaral *et al.*, 1992; Sugase *et al.*, 1999). A modulation of the fusiform gyrus as a function of fearful facial expression was similarly reported in a previous PET study (Morris *et al.*, 1998a). Importantly, the new findings from this event-related fMRI study (Vuilleumier *et al.*, 2001b) suggest that the effect of emotion on visual cortex is independent of, and additive to, the effect of spatial attention. We will return to this issue below.

Finally, the systematic 2×2 (attention × emotion) factorial design of this study also allowed a direct assessment of the effect of spatial attention on emotional processing (Fig. 21.3). Thus, some brain areas were found to respond to fearful versus neutral expressions specifically when the faces appeared at the relevant/attended locations. These areas included early visual areas in striate cortex, medial temporal pole, and caudal parts of the anterior cingulate cortex (all in the left hemisphere). Such effects might reflect increased alertness, arousal, or awareness of emotional cues (Bush *et al.*, 2000; Lane *et al.*, 1997a). Conversely, some brain areas responded to fearful more than neutral expressions, specifically when the faces appeared at the irrelevant/ignored locations. These latter regions included orbitofrontal cortex, ventral caudate nucleus, and caudal parts of the anterior cingulate (all in the right hemisphere). These effects might reflect mechanisms monitoring currently unattended sensory inputs and adjusting behavioural response according to task demands when emotionally salient information must be ignored (Robbins and Everitt, 1996; Rolls, 1996).

A further fMRI study (McKenna *et al.*, 2001) manipulated spatial attention toward or away from faces that had a fearful, happy, or neutral expression. In some blocks, subjects had to attend to centrally presented faces to judge their gender; in other blocks, they had to attend to two bar segments simultaneously presented in peripheral fields on each side of the central face and judge whether these bars had the same or different orientation. Fearful expressions activated the amygdala more than neutral or happy expressions, both when the face was selectively attended and when the bars were attended (*i.e.*, with faces now ignored). On the other hand, amygdala activity increased with attention to the face compared to the bars, but this occurred for all faces regardless of their emotional valence, although this effect was apparently greater for fearful than

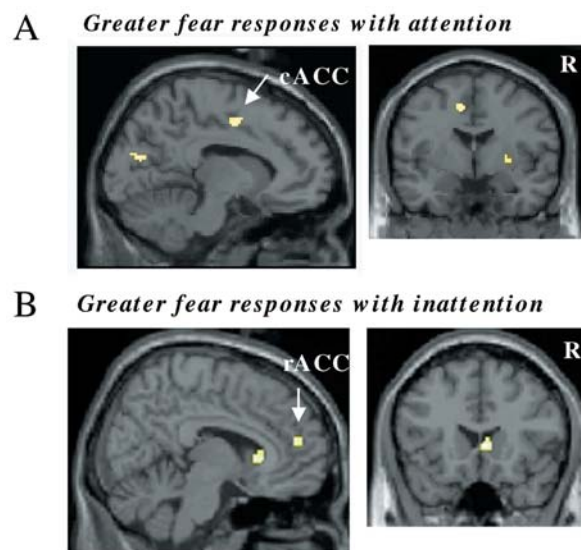
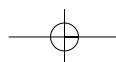
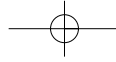


FIGURE 21.3

Effects of spatial attention on emotional responses. (A) The caudal region of left anterior cingulate cortex (cACC) (−10, −2, 48), as well as left primary visual cortex and right putamen, showed increased responses to fearful versus neutral faces specifically with attention to the faces (relative to attention to other locations occupied by houses). (B) Conversely, the rostral region of right anterior cingulate cortex (rACC) (8, 50, 16), as well as ventral caudate and orbitofrontal cortex (not shown), responded more to fearful versus neutral faces when attention was focused away from the faces (and directed to houses instead). (fMRI data from Vuilleumier *et al.*, 2001b.)





happy and neutral faces. The same pattern was also found in fusiform cortex. However, the attended stimulus category was fully predictable on each trial, and, given the general enhancement to all facial expressions, it is unclear from this study whether attention truly increased stimulus-driven responses to emotional cues or instead increased baseline activity in the amygdala through strategic top-down influences (Phelps *et al.*, 2001). Nevertheless, these results are consistent with an extraction of fear-related cues occurring for faces that are not selectively attended.

Direct support for emotional face processing occurring without attention also comes from a study in a right-parietal-damaged patient with left spatial neglect and visual extinction (Vuilleumier *et al.*, 2001a). This neurological disorder is characterised by a failure to direct attention to the side of space opposite the lesion (*i.e.*, to the left, in this case). In many instances, the patient remains unaware of a stimulus occurrence in the left visual field (LVF) when presented with a simultaneous competing stimulus stimuli in the right visual field (RVF), although the patient can detect the same left-sided stimulus when presented alone (Driver and Vuilleumier, 2001). Event-related fMRI was obtained in this left extinction patient (Fig. 21.4A), while pictures of fearful faces, neutral faces, or houses were briefly shown in the RVF, LVF, or both fields simultaneously (BS). On the critical BS trials, a face with either a fearful or neutral expression appeared in LVF, together with a house in RVF (Fig. 21.4B). The left-side faces were extinguished from the patient's awareness in 65% of BS trials. This design allowed a systematic 2×2 factorial analysis of critical BS trials, separately examining the effect of emotional expression (fearful versus neutral) and perception (conscious awareness versus extinction) of left-side faces, similar to the factorial design of our previous study in normal subjects (Vuilleumier *et al.*, 2001b). Results revealed that awareness relative to extinction of LVF faces increased bilateral fusiform activity (while extinguished faces in LVF produced covert activation in striate and extrastriate areas compared to trials with a house alone in RVF). However, fearful faces activated the left amygdala and bilateral orbitofrontal areas both when seen and when extinguished (Fig. 21.4C,D). Thus, amygdala responses to fearful faces did not significantly differ between conscious awareness and extinction, despite the strong increase in fusiform cortex activity associated with awareness. These findings parallel those in normal subjects (Vuilleumier *et al.*, 2001b) and converge with previous reports of an amygdala response to masked emotional stimuli in normals (Morris *et al.*, 1998b; Whalen *et al.*, 1998b).

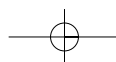
In addition, fusiform activity also showed an additional modulation by fearful expression independent of awareness or extinction (Fig. 21.4D), again consistent with our proposal of feedback influences from automatically elicited amygdala responses on visual cortical processing (Morris *et al.*, 1998a; Sugase *et al.*, 1999). This modulation might represent the neural substrate of an enhanced capture of attention by emotional stimuli as previously observed in behavioural studies of patients with neglect and extinction (Vuilleumier and Schwartz, 2001a,b). Consequently, this finding supports our results in normal subjects, suggesting that an emotional modulation of fusiform is independent of spatial attention mechanisms (presumably damaged in neglect and extinction).

It is of interest that unconscious processing of threatening faces has also been shown in patient GY with blindsight (see Chapter X). It remains a goal for future research to determine whether emotional processing can exhibit a similar independence from voluntary spatial attention for other categories of stimuli, including events with acquired aversive value due to past experience, such as occurs with fear conditioning, or facial expressions other than fear. One possibility is that that such pre-attentive emotional processing might occur only for threat-related information (Armony and LeDoux, 2000; Robinson, 1998).

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Effects of Attention on Non-Visual Emotional Processing

Much less is known about emotional responses to auditory stimuli and any effect of attention on such responses. While human-related sounds activate specific areas in lateral temporal cortex, compared to non-human sounds (Belin *et al.*, 2000), nonverbal affective relative to neutral vocalisations increase activity in left middle temporal gyrus, anterior insula, ventral prefrontal cortex, and right caudate nucleus (Morris *et al.*, 1999). Fearful voices evoke specific effects in amygdala compared to other (happy, sad, disgust, neutral) expressions (Dolan *et al.*, 2001;



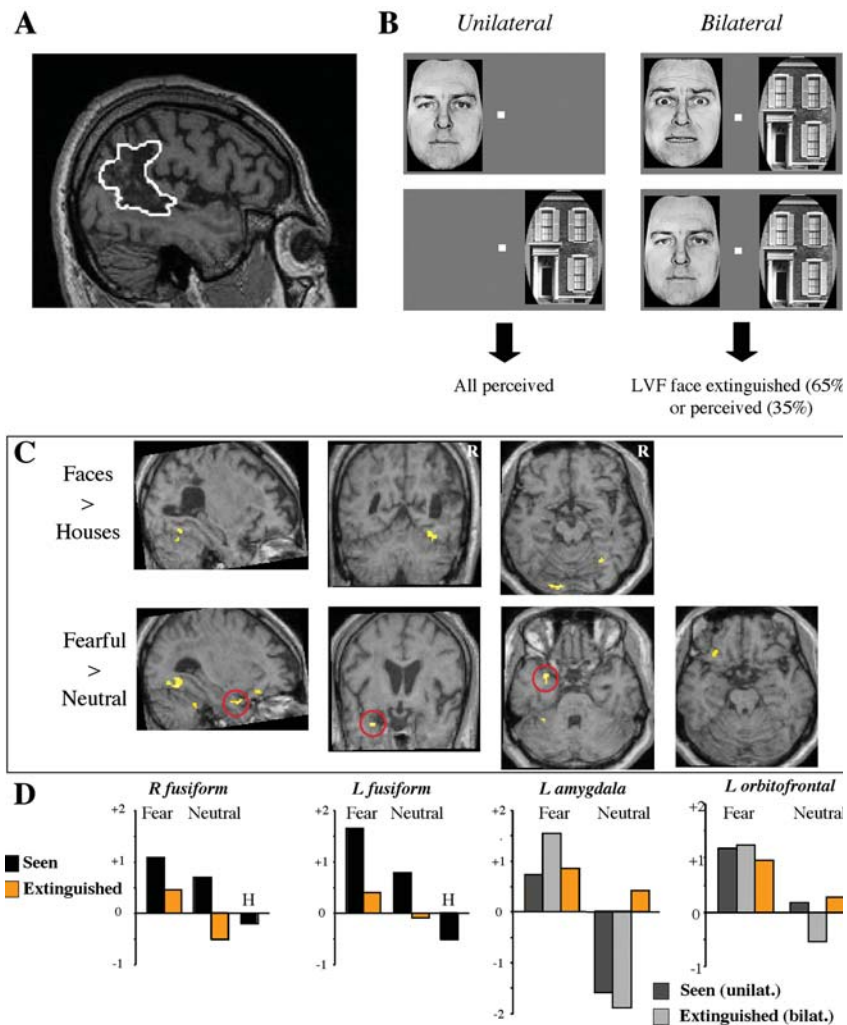
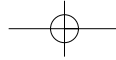
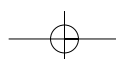


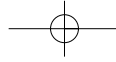
FIGURE 21.4

Fear processing with and without awareness in a patient with left spatial neglect and visual extinction. (A) Focal right parietal damage in the patient. (B) Example of stimuli. Faces or houses were presented unilaterally in either the right (RVF) or left (LVF) visual field. Faces had either a neutral or fearful expression. The critical stimuli were bilateral trials with a face in the LVF and house in RVF, in which the left-sided face was extinguished from the patient's awareness on many trials (65%) and consciously seen only on a few trials (35%). (C) Activation by seen faces, as opposed to seen houses, was observed in the right fusiform cortex (irrespective of emotional expression and field), and activation by fearful compared to neutral faces was observed in the left amygdala (red circle), as well as orbitofrontal and fusiform cortex. (D) Size of activation across stimulus conditions for the regions shown above. Fusiform activity increased when faces were consciously perceived, irrespective of expression, but also increased when faces were fearful, irrespective of awareness. Left amygdala and orbitofrontal cortex responded to fearful faces both when consciously perceived and extinguished. The left amygdala also showed a weak response to neutral faces when these were extinguished but no response to neutral faces when these were consciously seen. (fMRI data from Vuilleumier *et al.*, submitted.)

Morris *et al.*, 1999; Phillips *et al.*, 1998b). Both laughing and crying also activate bilateral amygdala and insula regions (Sander and Scheich, 2001).

In the fMRI study by Sander and Scheich (2001), amygdala responses to laughing and crying were independent of attention to emotion, occurring regardless of whether subjects had to passively listen to stimuli, monitor rare changes in sound pitch, or concentrate on affective meaning and self-generate the corresponding emotion. By contrast, insula responses to crying





were modulated by attention to self-generated emotion. Another PET study (Imaizumi *et al.*, 1997) also found task-dependent increases in insula, inferior frontal gyrus, and cerebellum when subjects classified emotional tones of words spoken by different actors, whereas activity increased in bilateral temporal poles and right superior frontal gyrus when subjects identified different actors' voices. This study did not include neutral tones and did not examine any possible differential effects between distinct emotion types (happy, angry, surprise, disgust).

Finally, an fMRI study (Jancke *et al.*, 2001) showed that responses to dichotic words with and without emotional content increase activity in contralateral auditory cortex with selective spatial attention to one ear, whereas a greater right-side response in superior temporal sulcus and inferior frontal gyrus, possibly attributed to emotion words, was not affected by spatial attention or by task demands (*i.e.*, involving discrimination of phonetic or affective cues in the words). However, this study did not directly compare emotional versus neutral words, and focused only on a few selected regions of interest.

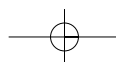
EFFECTS OF ATTENTION ON EMOTIONAL EXPERIENCE

Another kind of modulation is that exerted on emotional processes, in a top-down manner, when subjects direct attention to their internal affective states or feelings. It is beyond the scope of this chapter to review in detail the functional neuroimaging work related to this issue, but some results from this research provide interesting insights into neural mechanisms by which cognitive processes regulate emotional responses.

Selective attention to subjective emotional experience can be induced through different methods, with or without external stimulation. In several PET studies, subjects were presented with emotional faces (George *et al.*, 1995; Schneider *et al.*, 1995) or emotional film clips (Beauregard *et al.*, 1998; Lane *et al.*, 1997b, 1998; Reiman *et al.*, 1997) and asked to enter into the corresponding feeling states or to evaluate the degree of their own affective reactions to each stimulus. A consistent finding is that attention to self-experienced emotion increases activity in rostral anterior cingulate cortex (ACC) and adjacent medial frontal cortex (BA9). Other common areas of increased activity are found in bilateral insula, anterior temporal lobe, and subcortical structures such as thalamus and basal ganglia. A similar pattern (Fig. 21.5A) was found when making emotional versus spatial judgements on static emotional pictures (Lane *et al.*, 1997a) or when viewing pictures associated with emotionally evocative versus neutral captions (Teasdale *et al.*, 1999).

Other PET studies have examined the effect of evoking emotional representations without external stimuli—for instance, through intentional recall of personally experienced episodes (Damasio *et al.*, 2000; Lane *et al.*, 1997b; Pardo *et al.*, 1993; Reiman *et al.*, 1997), imagination of action plans in emotional versus neutral situations (Partiot *et al.*, 1995), or mental visualisation of aversive versus neutral pictures (Kosslyn *et al.*, 1996). Again, these various tasks produce consistent activation in medial prefrontal cortex and insula. Visualising aversive stimuli also enhanced cerebral blood in early visual cortex (BA17 and 18) relative to neutral stimuli (Kosslyn *et al.*, 1996). Differential effects associated with specific emotions (*e.g.*, sadness, happiness, or disgust) were found in orbitofrontal areas (Lane *et al.*, 1997b; Pardo *et al.*, 1993; Reiman *et al.*, 1997) and various subcortical regions (Damasio *et al.*, 2000). Altogether, these results suggest a general role of ACC and insula in volitional self-generation of emotion and conscious emotional experience.

A notable feature of many of these studies (Damasio *et al.*, 2000; Reiman *et al.*, 1997; Teasdale *et al.*, 1999) is an absence of significant modulation in the amygdala for purely mental evocations of affective states, including evocations of fear-related or aversive information; however, evocation of fear-related memories induces significant increases in regions such as the insula and midbrain (*e.g.*, Damasio *et al.*, 2000). This might reflect an amygdala involvement specifically in response to exteroceptive signals but not to purely endogenously driven cognitive or recall processes (Damasio *et al.*, 2000; Drevets and Raichle, 1998; Reiman *et al.*, 1997; Teasdale *et al.*, 1999). In other words, the functions of the amygdala may relate to perceptual processing of emotional stimuli and the generation of automatic and obligatory behavioural responses but have little to do with the elaboration of emotional experiences *per se*. This suggests



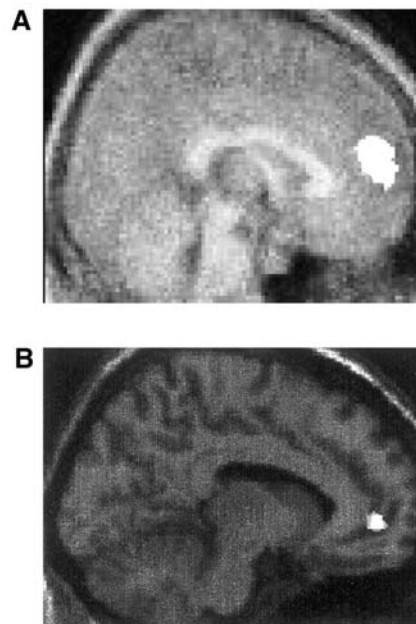


FIGURE 21.5

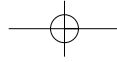
Regions in anterior cingulate cortex (ACC) that are modulated by attention to emotion. (A) Rostral regions in ACC and medial prefrontal cortex (peak: 0, 50, 16) show increased activity when subjects attentively judged their subjective feelings elicited by emotional pictures as compared to when they judged only spatial features of the pictures (indoor/outdoor). (PET data from Lane *et al.*, 1997.) (B) Subgenual region in ACC (peak: -6, 36, -3) showing increased activity in a Go/NoGo task when the targets (for Go responses) are words with emotional content, as compared to words with a neutral content. (fMRI data from Elliott *et al.*, 2000.)

a crucial distinction in neural systems mediating what has been termed *emotion generation* compared to those mediating the experience of feeling states (Damasio, 1999).

Nevertheless, both subjective feelings states and amygdala activation elicited by an external perceptual event can be modulated by cognitive factors and expectations that contribute to an aversive evaluation of incoming stimuli. For example, it has been demonstrated (Phelps *et al.*, 2001) that the occurrence of a cue that was expected to be paired with an electrical shock after verbal instructions (but actually never experienced with any shock) is sufficient to activate the amygdala, as well as the insula, ACC, and striatum. This result provide a demonstration that some forms of aversive reaction and learning in response to external events can be modulated by higher order cognitive representations and anticipatory attention.

HOW EMOTION INFLUENCES ATTENTION: ENHANCEMENT VERSUS INTERFERENCE EFFECTS ON COGNITIVE PERFORMANCE

An important role of basic emotions is to regulate an organism's state by influencing current sensory processing and preparing specific behavioural responses to meet environmental challenges. Thus, the consequences of elicitation of an emotion include a wide range of vegetative, sensorimotor, and cognitive mechanisms that can provoke a more detailed stimulus analysis, enhance the representation of relevant stimuli, suppress irrelevant information, increase speed of processing, or facilitate the resolution of conflict between competing alternatives (Armony and LeDoux, 1997; Armony *et al.*, 1997). From this perspective, it might be expected that emotional signals can affect the allocation of attentional resources in order either to facilitate



performance in a current task or to interrupt ongoing activity and redirect attention towards a more relevant event. Several imaging studies have specifically examined how emotional signals influence attentional, perceptual, and cognitive processes, even in conditions where emotion is not directly relevant to the task goals.

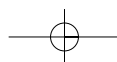
Modulation of Cortical Sensory Processing by Emotion

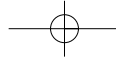
As already mentioned, a common finding in neuroimaging studies is an increased activation of sensory cortical areas in response to stimuli with emotional significance, as compared to neutral stimuli. Thus, emotional facial expressions enhance activity in inferior temporal and fusiform areas involved in visual analysis and identification of objects and faces. Such increases in fusiform cortex have most consistently been reported for fearful faces (Breiter *et al.*, 1996; Morris *et al.*, 1996, 1998a; Vuilleumier *et al.*, 2001b) and happy faces (Breiter *et al.*, 1996). Similarly, complex visual scenes with aversive compared to neutral contents increase activation of striate and extrastriate cortex, including medial and lateral occipital cortex (Lane *et al.*, 1997c, 1999; Lang *et al.*, 1998; Teasdale *et al.*, 1999), lingual and inferior temporal gyri (Fredrikson *et al.*, 1993; Taylor *et al.*, 2000; Teasdale *et al.*, 1999; Wik *et al.*, 1993), and occasionally more anterior (Lane *et al.*, 1999) or lateral (Kosslyn *et al.*, 1996; Taylor *et al.*, 2000) areas of temporal neocortex. Fewer studies have found such increases for pleasant pictures (Lane *et al.*, 1998, 1999; Simpson *et al.*, 2000).

Enhanced visual responses have also been observed for stimuli with acquired aversive value following Pavlovian fear conditioning (*e.g.*, previous exposure paired with an unpleasant loud noise or electric shock) (Armony and Dolan, 2002; Buchel *et al.*, 1998). In these studies, the same stimuli were counterbalanced across conditions so as to be either fear conditioned (CS+) or neutral (CS-) in different subjects. This suggests that the enhanced visual responses is unlikely to be simply due to differences in low-level visual features of the stimuli. Other studies have attempted to match featural and semantic complexities of neutral and emotional pictures (Lane *et al.*, 1999; Taylor *et al.*, 2000) or have kept facial features constant but changed their affective meaning by inverting them (Rotshtein *et al.*, 2001). These studies nonetheless report a selective modulation of visual cortex activity by emotional stimuli. Moreover, such effects cannot be explained by differential eye-movement scanning patterns (Lane *et al.*, 1999; Lang *et al.*, 1998; Vuilleumier *et al.*, 2001b). Altogether, these findings provide direct support for the idea that emotional significance augments the analysis of sensory inputs at early stages of cortical processing.

Emotion might have modulatory effects on sensory object processing in a number of ways. One possibility is that any enhancement reflects a direct interaction with mechanisms of attention, whereby the perceived affective or arousing value of stimuli can elicit more selective focusing and greater recruitment of cognitive resources through top-down influences mediated by, for example, frontoparietal and thalamic systems (Armony and LeDoux, 2000; Mesulam, 1999). A substantial body of evidence including neurophysiology in monkeys and functional imaging data in humans indicate that these attentional networks play a critical role in modulating sensory cortical areas at various stages of processing in order to enhance the representation of relevant objects, features, or locations, at the expense of irrelevant ones (Corbetta *et al.*, 1990; Posner and Petersen, 1990). Frontoparietal attentional systems might receive direct inputs from regions concerned with ascertaining the motivational significance of stimuli, such as, for example, through reciprocal connections with anterior and posterior cingulate cortices, basal forebrain nuclei (Maddock, 1999; Mesulam, 1999; Posner and Petersen, 1990), or orbitofrontal areas (Armony and Dolan, 2002; Rolls, 1996). Inputs from these regions might in turn serve to modulate the response to emotional stimuli.

Some evidence suggests, however, that a modulation of sensory cortices by emotion might be mediated by distinct processes, independent of other mechanisms of attention mediated by the classic frontoparietal networks. Thus, in the study by Vuilleumier *et al.* (2001) discussed above, activity in the fusiform cortex showed an enhanced activity for fearful compared to neutral faces regardless of whether these appeared at the relevant/attended locations or at the irrelevant/attended locations (Fig. 21.2C), suggesting that this modulation by emotion was independent of the modulation by voluntary spatial attention (and in fact strictly additive to it). A similar



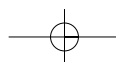


modulation of fusiform cortex by emotion was independent of awareness in the patient with spatial neglect in whom parietal cortical systems of attention are damaged (Fig. 21.4C,D). Therefore, top-down signals onto sensory cortices might involve direct feedback connections from regions that are primarily concerned with the detection and evaluation of affective stimuli, such as amygdala and orbitofrontal cortex. In particular, as already described, the amygdala sends re-entrant projections to all levels of the ventral visual processing stream, from early striate cortex to late higher order areas in extrastriate temporal cortex (Amaral *et al.*, 1992). These inputs might directly act to enhance sensory processing of stimuli once their emotional value is detected in the amygdala (Anderson and Phelps, 2001).

We have investigated a potential role for the amygdala in influencing visual cortical activity in an event-related fMRI study in patients with amygdala damage (Vuilleumier *et al.*, in preparation). This study used the same 2x2 factorial paradigm as the above experiment by Vuilleumier *et al.* (2001), in which fearful or neutral faces are presented at either task-relevant/attended locations or task-irrelevant/ignored locations (see Fig. 21.2A). Two groups of patients who had medial temporal lobe sclerosis and epilepsy were compared; one had both amygdala and hippocampal damage (H+A+), whereas the other had hippocampal damage only, without amygdala damage (H+A-), as determined from an abnormal T2 signal on structural MRI, using the fast-FLAIR (fluid-attenuated inversion recovery), dual-echo sequence (Woermann *et al.*, 2001). These patients were also compared to a group of healthy, age- and education-matched controls (H-A-). The critical results concerned areas showing a main effect of fearful versus neutral faces, regardless of attention. Consistent with the previous findings in young healthy subjects (Vuilleumier *et al.*, 2001b), such an effect of emotion was found in inferior temporal and fusiform cortex in normal controls and in patients with hippocampal damage only (H+A-); however, the patients with *amygdala* damage (H+A+) did not exhibit increased activity in response to fearful faces in their *intact* visual cortex (Fig. 21.6B). By contrast, the main effect of attention to faces versus houses showed a similar pattern of fusiform modulation in all three groups (Fig. 21.6A). This finding converges with results from a PET study (Morris *et al.*, 1998b) demonstrating that neural activity in extrastriate visual cortex shows condition-specific covariation with amygdala responses to facial expressions, suggesting significant functional connections between these areas. Similarly, recent single-cell recordings in the monkey visual cortex have revealed that face-selective neurons exhibit enhanced responses to emotional faces as compared to neutral ones, with a latency 50 ms longer than the initial discriminatory response to faces versus shapes, consistent with feedback modulation from other areas involved in emotional evaluation (Sugase *et al.*, 1999).

Subcortical neurotransmitter pathways might provide an alternative source of modulation to that provided by re-entrant amygdala-extrastriate connections. Cholinergic neurons in the basal forebrain receive prominent inputs from the amygdala and orbitomedial frontal cortex (Holland and Gallagher, 1999; Sarter and Bruno, 2000) and in turn project widely to the cortex, including posterior parietal areas involved in shifts of attention and early sensory cortical areas (Robbins, 1997; Sarter and Bruno, 2000). Animal studies have suggested that the basal forebrain cholinergic pathways may contribute to shifting attentional focus, enhancing signal to noise and prolonging neuronal responses to stimuli (Robbins, 1997). In fact, direct electrical stimulation of the amygdala evokes neocortical activation mediated by acetylcholine (Kapp *et al.*, 1994). The cholinergic system is thus well positioned to mediate both attentional and emotional modulation of cortical processing.

{AU}: update? → In an event-related fMRI study (Bentley *et al.*, in preparation), we have investigated this issue by again using the same factorial experiment (Vuilleumier *et al.*, 2001b) as described above (Fig. 21.2) to examine the effect produced by injection of a pro-cholinergic drug (physostigmine) versus placebo. Results from this study suggest that cholinergic modulation enhances the effect of attention on fusiform cortex, with greater responses to task-relevant faces after injection of drug than that observed after placebo. This would be consistent with an improved selectivity of attention and better filtering-out of irrelevant house distracters cortex (Furey *et al.*, 2000; Sarter and Bruno, 2000). A response to fearful faces was not affected by cholinergic stimulation in the amygdala itself but was associated with increased activity in left fusiform and inferior occipital cortex (though lessening over time). Increased effects of emotion were also found in bilateral prefrontal regions, particularly when fearful faces occurred at attended locations and



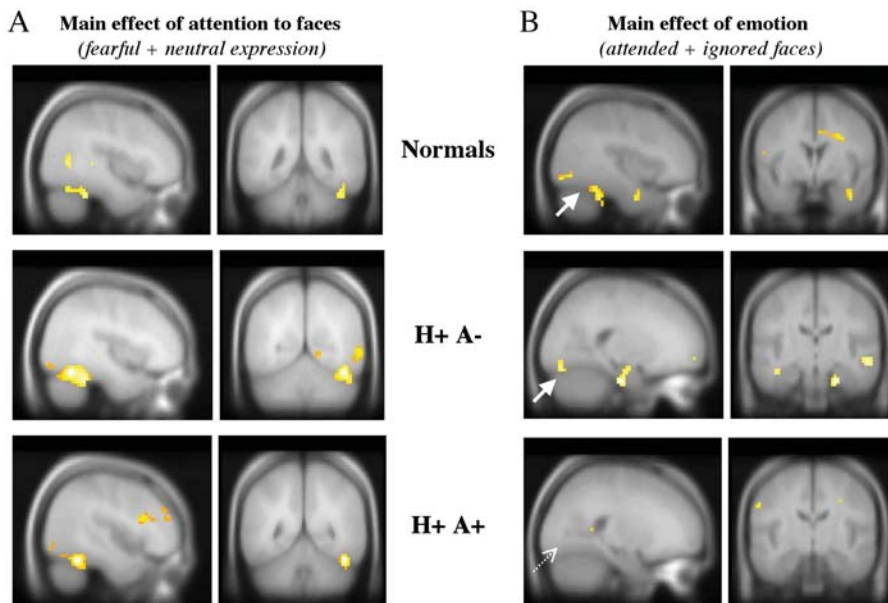
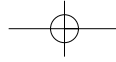
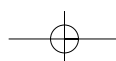


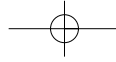
FIGURE 21.6

Remote effects of amygdala damage on visual cortical response to fearful faces; same experimental paradigm as in Vuilleumier *et al.* (2001b) (see Fig. 21.2A). Preliminary results in a group of patients with epilepsy and medial temporal lobe sclerosis (all left-sided) involving *only* the hippocampus and sparing the amygdala (H+A-, $n = 14$) or involving *both* the hippocampus *and* amygdala (H+A+, $n = 9$). Normal controls were a group of healthy relatives matched for age and education ($n = 10$). (A) Selective attention to faces versus houses increased fusiform activity in all three groups. (B) An increase produced by fearful versus neutral faces irrespective of attention was found in visual cortical areas (arrows) in healthy subjects as well as in patients with hippocampal damage only (H+A-) but not in patients with amygdala damage (H+A+). Note that visual cortex was similarly intact in all groups. (Unpublished fMRI data.)

in bilateral orbitofrontal cortex when fearful faces occurred at ignored locations. Such effects might reflect a greater distraction by emotional stimuli due to cholinergic modulation, requiring a subsequent engagement of frontal regions for monitoring potential response conflicts and adjusting ongoing goal-directed behaviour.

Finally, noradrenergic neurotransmitters might constitute another potential route through which emotional arousal influences cortical processing and redirection of attention. Arousal mechanisms implicate the locus coeruleus in the brain stem which receives substantial inputs from the amygdala and, in turn, sends extensive projections to the forebrain neocortex thought to regulate selective attention and attentional shifting (Aston-Jones *et al.*, 2000; Robbins, 1997). In keeping with this, a PET study by Lane *et al.* (1999) suggested that arousal can increase activation in visual cortex during exposure to emotional pictures, with the site of such effects overlapping with those due to selective attention and emotional valence. A $3 \times 2 \times 2$ factorial design was employed in which subjects were required to memorise different blocks of pleasant, unpleasant, or neutral scenes, each including either low- or high-arousal stimuli. Pictures were shown during either a low-load or high-load distracting auditory task. Extensive extrastriate visual areas showed a common effect for each of these three factors, with similar increases in right medial occipital cortex and anterior temporal cortex produced by emotional valence (unpleasant > pleasant > neutral), arousal (high > low), and selective attention (low > high distraction); however, a potential limitation of this study was that the different conditions were blocked, and common visual increases could potentially have resulted from changes in attentional set. Higher arousal also enhanced activity in right medial frontal regions, in the same way as greater selective attention did, suggesting an additional modulation of behavioural output and perhaps experiential stages of emotional processing. These frontal effects of arousal seem consistent with animal studies indicating that connections between locus coeruleus and anterior





cingulate cortex may be important in regulating attentional shifts and behavioural flexibility (Aston-Jones *et al.*, 2000).

Involuntary Orienting of Spatial Attention to Emotional Stimuli

Neuroimaging studies converge with behavioural studies in normal subjects (Mogg *et al.*, 1994; Öhman *et al.*, 2001b) and neglect patients (Vuilleumier and Schwartz, 2001a,b) to suggest not only that some emotional information can be “automatically” analysed even without attention but also that this may then serve to prioritise orienting of attention toward emotionally salient stimuli. Thus, spatial attention can be preferentially drawn to the location of emotional stimuli, with visual search (Eastwood *et al.*, 2001) or detection of a peripheral target (Stormark *et al.*, 1999) usually being faster when the target is preceded by an irrelevant emotional cue at the same spatial location, as compared to another location.

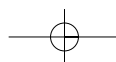
The mechanisms underlying such reflexive shifts of attention to emotional cues have been examined in an event-related fMRI experiment (Armony and Dolan, 2002) using a prototypical paradigm of spatial orienting (Gitelman *et al.*, 1999; Posner *et al.*, 1982). Subjects performed a simple task requiring them to detect, as quickly as possible, a small peripheral dot that could appear either in their right or left visual field. The dot was preceded by a very brief presentation (50 ms) of two angry faces at each location (Fig. 21.7A), with the faces being totally irrelevant to the task. Critically, only one of these faces (conditioned stimulus, CS+) was occasionally paired with an unpleasant, loud, white-noise burst noise (unconditioned stimulus, US). This procedure is known to induce a strong aversive affect toward the CS+ through classical Pavlovian fear conditioning, an effect known to involve enhanced amygdala activity as demonstrated in numerous animal studies (LeDoux, 1996) and neuroimaging studies (Buchel and Dolan, 2000). The critical experimental trials were those where the conditioned face (CS+) was presented on one side with the neutral face (CS−) on the other side (without the noise). Response times were found to be much slower when the target dot appeared on the side opposite the CS+ (incongruent trials) than when it coincided with the side of the CS+ (congruent trials), suggesting that spatial attention was indeed captured by the CS+ and had to be shifted contralaterally on incongruent trials. By contrast, attention was equally divided between the two hemifields on trials where the CS+ or CS− were presented on both sides.

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Bilateral activation in the amygdala and fusiform cortex was observed for trials with CS+ faces, as compared to trials with only CS− faces (Fig. 21.7D), demonstrating reliable fear conditioning. Importantly, in contrast to trials with bilaterally divided attention, those with a unilateral CS+ capturing attention activated an extensive network including intraparietal sulcus, frontal eye field, anterior cingulate/supplementary motor cortex, and lateral orbitofrontal cortex in both hemispheres (Fig. 21.7B). Moreover, trials in which the CS+ was presented in the left visual field produced a greater parietal activation in the right hemisphere, whereas right-field presentations of the CS+ activated both left and right parietal cortices. These findings reveal a striking overlap between activations evoked by a lateralised CS+ and frontoparietal systems known to play a key role in spatial orienting of attention (Gitelman *et al.*, 1999; Posner and Petersen, 1990), consistent with the idea that an enhanced saliency of emotional events can trigger shifts of attention toward their location within the environment.

Notably, the only difference between the emotional orienting effects found here and spatial orienting effects found in attentional studies was an additional bilateral activation in lateral orbitofrontal cortex (Fig. 21.7C). As lateral orbitofrontal cortex is reciprocally connected to posterior parietal areas and frontal eye fields, this region might provide a crucial interface between emotional and attentional processes, specifically those involved in the modulation of spatial orienting by the affective value of sensory stimuli (Armony and Dolan, 2002).

Similarly, an earlier PET study (Fredrikson *et al.*, 1995) found that pictures of snakes previously conditioned by pairing with electric shocks, compared to the same pictures before conditioning, evoked increased activity in the cortical attentional networks, including bilateral parietal, left prefrontal, and anterior and posterior cingulate cortex. In addition, subcortical activations were found in ventromedial thalamus, hypothalamus, and central grey of the midbrain. Altogether, such findings demonstrate that emotional fear responses involved distributed neural networks concerned with attentive and autonomic functions.



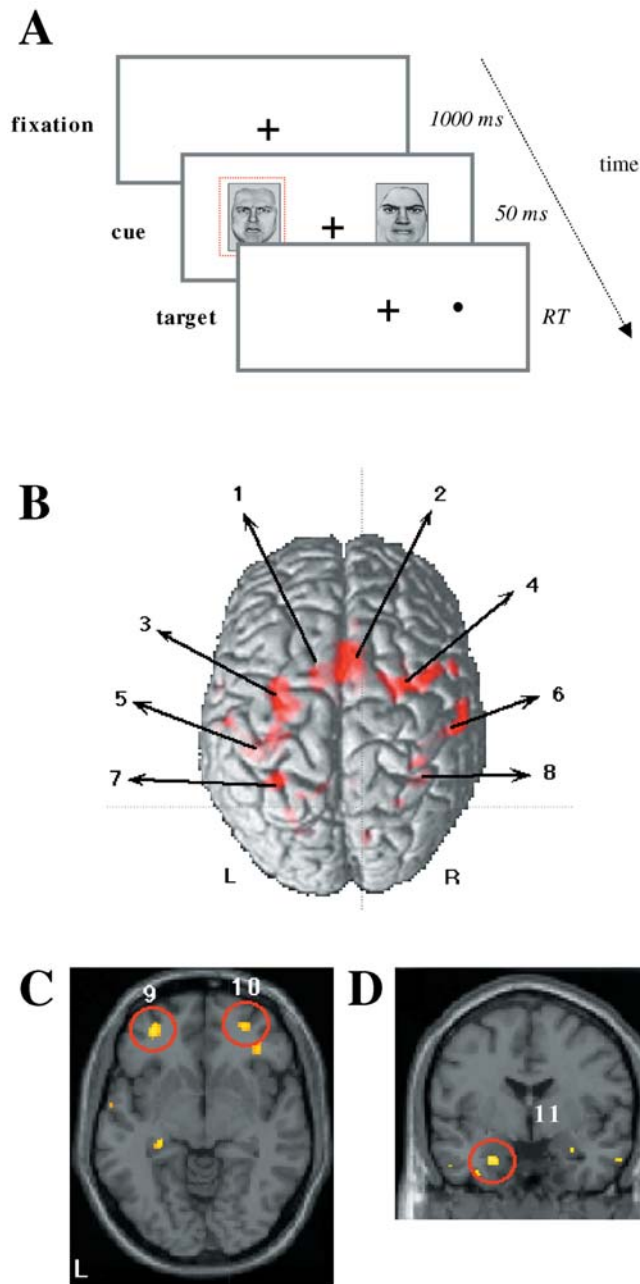
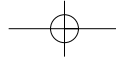
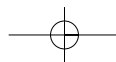
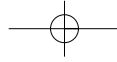


FIGURE 21.7

Effects of emotion on orienting of spatial attention. (A) Illustration of stimuli and task. On each trial, subjects had to detect a peripheral dot in the right or left visual field, preceded by a pair of angry faces. Only one face (CS+) is fear-conditioned by occasional pairing with a loud noise on trials where this face appears alone on both sides. On critical trials, the CS+ face (illustrated by dashed red lines) appears in one hemifield together with a CS- face in the other hemifield. Although task irrelevant, the CS+ faces produce a bias in spatial attention toward their location and slow the detection of target dots appearing on the opposite side. (B) and (C) Cortical regions showing increased activation on trials with a unilateral CS+ face capturing attention to one side, relative to trials with attention bilaterally divided to both sides (*i.e.*, two CS+ or two CS- faces). Nomenclature: 1, left SMA/anterior cingulate; 2, right SMA/anterior cingulate; 3, left frontal eye fields; 4, right frontal eye fields; 5, left anterior IPS/precentral sulcus; 6, right anterior IPS/precentral sulcus; 7, left intraparietal sulcus; 8, right intraparietal sulcus; 9, left orbitofrontal cortex; 10, right orbitofrontal cortex; 11, left amygdala. Note that the network of areas with such responses to a lateralised emotional cue is strikingly similar to the distributed neural system known to be implicated in spatial orienting of attention (B) but included additional activation in lateral orbitofrontal cortex (C). (D) The left amygdala was activated by all trials with CS+ faces versus CS- faces, indicating reliable fear conditioning. (fMRI data from Armony and Dolan, 2002.)





Modulation of Executive Control by Emotion

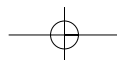
Emotional information can also affect the control of goal-directed action and its response preparation stages. Brain structures involved in basic emotional processing (such as the amygdala) have direct output projections toward motor systems that can mediate the expression of behavioural reactions, such as approach or avoidance. While simple and stereotyped reaction may be controlled by subcortical circuits (such as basal ganglia and central grey in brainstem), other flexible cognitive adjustments engage specific structures in prefrontal cortex.

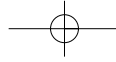
Elliott *et al.* (2000) used fMRI to investigate the effect of emotion on selective attention to action using a Go/NoGo paradigm. Subjects were shown series of words, briefly presented each in turn, and had to respond only to relevant target words in the series, based either on their orthographic form (plain or italic text) or their emotional meaning (sad or happy), while the emotional meanings of irrelevant distracter words were also varied (neutral or opposite emotion). Selective attention to word meaning versus orthographic form activated left inferior frontal gyrus and left dorsal ACC, irrespective of whether word meaning was emotional or neutral, consistent with a general role of these regions in semantic and executive control. By contrast, selective detection of emotionally valenced targets, compared to neutral targets, activated the right rostral subgenual ACC and the right insula, as well as the left hippocampal region, regardless of the emotional valence of the targets (sad or happy). These regions were considered to represent an interface between cognition and emotion, involved when behavioural responses must be guided by emotional cues. Indeed, it has been proposed that rostral ACC (Fig. 21.5B) might particularly be important for regulating response selection mechanisms in the presence of affective and motivational signals (Bush *et al.*, 2000). On the other hand, Elliott *et al.* (2000) found no differential effects due to the emotional valence of task-irrelevant distracters when subjects selectively responded only to neutral targets among the word stream. This suggests that the processing of sad and happy emotional meaning in the words did not occur automatically in such conditions, but rather depended on top-down control due to the task set. It remains a goal for future studies to see whether a more obligatory emotional response to distracters would be obtained in such a Go/NoGo task with negative words that have stronger aversive meaning or with biologically more relevant stimuli, such as emotional faces.

Other investigators (Whalen *et al.*, 1998a), using fMRI, have examined the interference effects of emotional word meaning on responses in the Stroop task, where different aspects of the stimulus compete to determine behaviour. In such emotional Stroop tasks, interference is typically elicited by irrelevant emotional versus neutral meaning of printed words for which the colour must be read aloud. In the emotional Stroop variant used by Whalen *et al.* (1998), subjects had to count the number of negative (or neutral) words presented on the screen. Blocks with negative words increased activity in the left rostral/pregenual ACC compared to blocks with neutral words, as well as in the left superior parietal cortex. This finding again suggests that a distracting effect due to irrelevant emotional content might specifically engage executive control mechanisms mediated by rostral ACC. Interestingly, in the same subjects, a non-emotional variant of this Stroop task (*i.e.*, the counting of number-words) activated more dorsal regions in ACC, suggesting a differential role in the control of interference based on more abstract cognitive representations (Bush *et al.*, 1998). However, all subjects had performed the cognitive

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Emotional processing may also reduce activity in some cortical areas that mediate higher level cognitive and attentional functions, not only compared to active performance of a cognitive task but also compared to passive resting state (Drevets and Raichle, 1998; Shulman *et al.*, 1997; Whalen *et al.*, 1998a). Such decreases have been reported in several PET studies for dorsal regions in ACC and dorsolateral prefrontal cortex (Drevets and Raichle, 1998), as well as inferior medial prefrontal cortex (Sheline *et al.*, 2000; Simpson *et al.*, 2001a). This has usually been interpreted as reflecting an interference caused by emotion on ongoing cognitive processes, which are transiently suppressed by concurrent affective states. Likewise, left prefrontal and ACC activation during a verbal fluency task is reduced by manipulations of mood states (*i.e.*, induced depression or elation) that concomitantly increase activity in orbitofrontal cortex (Baker





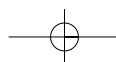
et al., 1997). In contrast, it has been proposed that during the performance of various cognitive or attentional tasks on neutral stimuli (*e.g.*, verbal fluency or visual discriminations), a similar reciprocal suppression of activity may occur in brain areas that are normally implicated in emotional processing, including the amygdala, rostral ACC, and orbitofrontal cortex (as well as in some other regions, such as the cuneus and posterior cingulate) (Drevets and Raichle, 1998; Shulman *et al.*, 1997; Whalen *et al.*, 1998a). Also, activity in inferior medial prefrontal cortex is reduced only when a task is well practiced and provokes no anxiety (Simpson *et al.*, 2001a,b). It has been hypothesised that such changes in emotion-related areas during cognitive tasks might reflect a reduction in spontaneous motivational and affective evaluation of environmental and bodily states during the performance of attentionally demanding cognitive processes (Drevets and Raichle, 1998), at least as long as these are carried out in a relatively neutral context or concern relatively neutral material. Such decreases may not be seen when similar cognitive tasks are performed on surface features of emotionally valenced pictures (Simpson *et al.*, 2000). Moreover, as we have described above, a number of behavioural (Anderson and Phelps, 2001; Mathews and Klug, 1993) and imaging (Armony and Dolan, 2002; Vuilleumier *et al.*, 2001b) results indicate that performing an attentionally demanding cognitive task in the presence of either relevant or irrelevant emotional stimuli (most typically threat-related) can still engage processes responsible for the evaluation of affective significance in stimuli (*e.g.*, in amygdala, rostral ACC, or orbitofrontal cortex). Overall, this would be consistent with a key role of these structures in monitoring incoming inputs for salient stimuli through attention-independent channels and then regulating the allocation of attentional resources to achieve priority goals, being turned down in a safe context but kicking in to interrupt higher order cognitive processes in the face of potential threat signals.

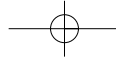
MODULATION OF MEMORY BY EMOTION

Attention not only governs the selection of information for conscious perception and goal-directed action but also enhances the formation of memory traces for later recall. Emotion again bears much resemblance to attention in this respect, as a large body of behavioural work has shown that stimuli with affective value, or stimuli presented in an emotional context, tend to be subsequently remembered much better than neutral stimuli. Several recent functional neuroimaging studies have begun to reveal the neural substrates of such emotional effects on memory (Cahill *et al.*, 1996; Hamann *et al.*, 1999; Maratos *et al.*, 2001), but it is beyond the scope of this chapter to review this emerging literature. Note that an emotional modulation of memory can occur both at encoding and retrieval stages (Dolan *et al.*, 2000; Taylor *et al.*, 1998) and might partly result from mechanisms reviewed above that intensify the sensory processing and enhance the allocation of attention toward emotionally relevant stimuli. In addition, there might be further mechanisms specifically related to memory consolidation that are directly modulated by brain areas involved in emotional and arousal processes, as has been proposed for the amygdala (Cahill *et al.*, 1996; Hamann *et al.*, 1999). As for the modulation of attention, the modulation of memory by emotion might thus implicate multiple, reciprocally interacting pathways between the amygdala or related structures, on the one hand, and distant areas in sensory cortices, prefrontal cortex, and hippocampus, on the other hand.

CONCLUSION

Attention and emotion share many reciprocal links. Thus, both attention and emotion involve distributed neural networks of highly interactive cortical and subcortical brain regions that are in a position to regulate processes related to perception, action, and memory. Likewise, both attention and emotion are intimately associated with conscious experience. Whereas attentional processes may control selective processing of sensory events that ultimately determine the content of conscious awareness, emotional processes may operate without attention or without awareness but can nonetheless influence the allocation of attention and hence readily permeate or intrude into awareness. It also remains possible that distinct stimuli and different kinds of





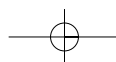
emotion might engage unique neural systems that in turn exert distinct effects on attentive and cognitive processes. Stimuli with intrinsic biological value (*e.g.*, faces) or special affective significance (*e.g.*, threat-related) might have a particular status in such interactions between emotion and attention. Thus, the fear system provides a dedicated neural system for mediating fast and automatic responses to signals of potential danger, with the amygdala being activated by fear-related stimuli regardless of whether attention is directed to other features or other locations in space. This in turn allows for a direct feedback modulation on visual cortices which can be preserved after damage to parietal systems of attention (as in neglect patients) but lost after damage to the amygdala itself (as in epileptic patients).

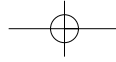
Moreover, reciprocal interactions between emotion, attention, and cognition have potentially important implications for understanding a number of psychiatric diseases. An abnormal modulation of attention by emotion, mood, or past affective experiences has now been observed by both behavioural and imaging studies in a variety of conditions, including anxiety, phobia, posttraumatic stress disorder, obsessive–compulsive disorder, depression, or schizophrenia. More generally, the study of such interactions between emotional and attentional–cognitive processes also raises the general question of individual differences and of their underlying neural substrates. This constitutes a new challenge for cognitive neuroscience, which can now be powerfully addressed by neuroimaging research.

Finally, new insights into the neural underpinnings of reciprocal interactions between emotion and attention emphasise a dynamic interplay between distinct areas, organised as extended system networks, that are engaged in reciprocal exchanges of information. Such a perspective on brain function clearly goes beyond views of a strictly modular specialisation of subcomponents and purely feedforward processing of information, as traditionally considered by cognitive neuroscience research.

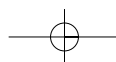
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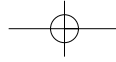
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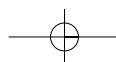


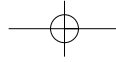
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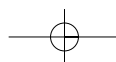


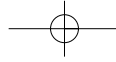
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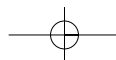
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Reciprocal Links Between Emotion and Attention

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