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Visual Attention and Emotional Perception

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Abstract

Over the past twenty-five years, a great deal has been learned about the neural mechanisms of visual attention. Converging evidence from single-cell recording studies in monkeys and neuroimaging and event-related potential studies in humans have shown that the processing of attended information is enhanced relative to the processing of unattended information. At the same time, there is increasing evidence that, in general, visual processing requires attention. In this chapter, we review several key issues at the interface between visual attention and emotional perception, namely, the perception of emotional-laden stimuli, such as a picture of a fearful face. We review findings that suggest that attention is also required for the processing of emotion-laden faces, a category of stimuli previously proposed to be processed “automatically”. We propose that, when attentional resources have not been exhausted, emotional stimuli can bias competition for processing resources. A likely source of biasing signals for emotional stimuli is the amygdala, a key structure involved in the processing of valence.

I. Introduction

Because the processing capacity of the visual system is limited, selective attention to one part of the visual field comes at the cost of neglecting other parts. Thus, several investigators have proposed that there is *competition* for neural resources. One instance of this proposal is the *biased competition model* of attention (Desimone and Duncan, 1995). According to this model, the competition among stimuli for neural representation, which occurs within visual cortex itself, can be biased in several ways. One way is by bottom-up sensory-driven mechanisms, such as stimulus salience. For example, stimuli that are colorful or of high contrast will be at a competitive advantage. But, another way is by attentional top-down feedback, which is generated in areas outside the visual cortex. For example, directed attention to a particular location in space facilitates processing of stimuli presented at that location. Stimuli surviving the competition for neural representation will have further access to memory systems for mnemonic encoding and retrieval and to motor systems for guiding action and behavior. At the neural level, an important consequence of attention is to enhance the influence of behaviorally relevant stimuli at the expense of irrelevant ones, providing a mechanism for the filtering of distracting information in cluttered visual scenes (Kastner and Ungerleider, 2000).

II. Attention is needed to process visual stimuli

An implicit prediction of the biased competition model is that only items that survive the competition for neural representation in visual processing areas will impact on subsequent memory and motor systems. A related, but stronger, proposal has been advanced by Lavie, who has suggested that the extent to which unattended objects are processed depends on the available capacity of the visual system. If, for example, the processing load of a target task exhausts available capacity, then stimuli irrelevant to that task would not be processed at all. Hence, perceptually such stimuli may not even reach awareness.

Consistent with this idea, psychophysical studies in the past decade have demonstrated that processing outside the focus of attention is attenuated and may be eliminated under some conditions. Rock and colleagues showed that even the simplest visual tasks are compromised when attention is taken up elsewhere (Rock et al., 1992), a phenomenon they termed “inattention blindness.” Further, in a striking demonstration, Joseph and colleagues showed that so-called “preattentive” tasks, such as orientation pop-out, require attention to be successfully performed (Joseph et al., 1997). The necessity of attention for perception is perhaps most compellingly illustrated by “change blindness” studies, in which subjects may miss even very

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large changes in complex scenes, provided the changes are not associated with stimulus transients that capture attention.

But what is the fate of unattended stimuli? In extrastriate areas V2 and V4, single-cell studies in monkeys have shown that when an effective and ineffective stimulus are placed within a neuron's receptive field, spatially directed attention to the effective stimulus results in a response similar to the one elicited by the effective stimulus presented alone (Reynolds et al., 1999). Remarkably, spatially directed attention to the ineffective stimulus results in a response similar to the one elicited by the ineffective stimulus when presented alone. In essence, it is as if the unattended stimulus, be it the effective or ineffective one, were not in the receptive field. These findings suggest that, at the neural level, responses evoked by unattended items may be eliminated.

Such an interpretation is consistent with fMRI studies demonstrating that the stimulus-evoked fMRI response is essentially abolished when subjects are engaged in a competing task with high attentional load. In one study, Rees and colleagues showed that moving stimuli did not elicit fMRI activation in area MT when subjects performed a concurrent, highly demanding linguistic task (Rees et al., 1997). In a related study, Rees and colleagues showed that activations associated with words were not elicited when subjects performed a concurrent, highly demanding object working memory task (Rees et al., 1999). Thus, like the processing of visual motion, even word processing seems to require attention, contrary to claims for full automaticity.

III. Is attention necessary for the processing of emotion-laden faces?

A major exception to the critical role of attention may be in the neural processing of emotion-laden stimuli, which are reported to be processed automatically, namely, without attention (Vuilleumier et al., 2001; Ohman, 2002). For example, subjects exhibit fast, involuntary autonomic responses to emotional stimuli, such as aversive pictures or faces with fearful expressions. Other behavioral studies suggest that such autonomic responses to facial expressions occur not only "automatically" but may even take place without conscious awareness (Ohman, 2002). This conclusion is also supported by imaging studies of the neural processing of emotional stimuli in the amygdala, a structure that is known to be important in emotion, particularly the processing of fear (Aggleton, 2000). Such studies report that the amygdala is activated not only when normal subjects view fearful faces, but even when these stimuli are masked and subjects appear to be unaware of their occurrence. Using the backward masking paradigms developed by Ohman and colleagues, Whalen and colleagues showed that fMRI signals in the amygdala were significantly larger during viewing of masked, fearful faces than during the viewing of masked, happy faces (Whalen et al., 1998). In another study, Morris and colleagues combined backward masking with classical conditioning to investigate responses to perceived and non-perceived angry faces (Morris et al., 1998). Although the participants never reported seeing the masked, angry stimuli, the contrast of conditioned and non-conditioned masked, angry faces activated the right amygdala.

The view has thus emerged that the amygdala is specialized for the fast detection of emotionally relevant stimuli in the environment, and that this can occur without attention and even without conscious awareness. If this were indeed the case, amygdala activity would reflect an obligatory response independent of the locus of spatial attention. Vuilleumier and colleagues tested this prediction in an fMRI study in which subjects fixated a central cue and matched either two faces or two houses presented eccentrically (Vuilleumier et al., 2001). Both fearful and neutral faces were utilized. As in earlier studies, activity in the fusiform gyrus, which is known to respond strongly to faces, was modulated by attention. At the same time, Vuilleumier and colleagues failed to see evidence that attention modulated responses in the amygdala, regardless

of stimulus valence. Not surprisingly, these results were interpreted as further evidence for obligatory activation of the amygdala by negative stimuli.

IV. A strong test of automatic amygdala activation

In a recent study, we tested the alternative possibility, namely, that the neural processing of stimuli with emotional content is not automatic and instead requires some degree of attention, similar to the processing neutral stimuli (Pessoa et al., 2002). We hypothesized that the failure to modulate the processing of emotional stimuli by attention in previous studies was due to a failure to fully engage attention by a competing task. In other words, activation in the amygdala by emotional stimuli should resemble activation in MT to moving stimuli; if the competing task is of high load, activation should be reduced or absent. We therefore employed fMRI and measured activations in the amygdala and other brain regions that responded differentially to faces with emotional expressions compared to neutral faces and then examined how those responses were modulated by attention.

We measured fMRI responses evoked by pictures of faces with fearful, happy, or neutral expressions when attention was focused on them (attended condition), and compared the responses evoked by the same stimuli when attention was directed to oriented bars (unattended condition). In designing our bar orientation task, we chose one that was sufficiently demanding to exhaust all attentional resources on that task and leave little or none available to focus on the faces, even though they were viewed foveally during the bar orientation task. We found that attended compared to unattended faces evoked significantly greater activations bilaterally in the amygdala for all facial expressions (Fig. 1A). Importantly, there was a significant interaction between stimulus valence and attention. That is, the differential response to stimulus valence was observed *only* in the attended condition (Fig. 1B). Moreover, for the unattended condition, responses to all stimulus types were equivalent and not significantly different from zero. Thus, amygdala responses to emotional stimuli are not automatic and instead require attention.

Figure 1

Our findings are in direct contrast to those by Vuilleumier and colleagues who failed to see evidence that attention modulated responses in the amygdala, regardless of stimulus valence (Vuilleumier et al., 2001). What is the explanation for their negative findings? The most likely explanation is that the attentional manipulation in the Vuilleumier et al. study was not as effective as ours. For example, behavioral performance for the bar orientation task in our study and house matching in the Vuilleumier et al. study was 64% and 86% correct, respectively, indicating that our competing task was a more demanding one (see Pessoa et al., 2002 for further discussion).

To summarize, contrary to the prevailing view, we found that the amygdala responded differentially to faces with emotional content only when sufficient attentional resources were available to process those faces. Indeed, when all attentional resources were consumed by another task, responses to faces were eliminated, consistent with Lavie's proposal that if the processing load of a target task exhausts available capacity, stimuli irrelevant to that task will not be processed. Indeed, we also found that other brain regions responding differentially to faces with emotional content, including the superior temporal sulcus, the orbitofrontal cortex, the fusiform gyrus, and even the cortex within and around the calcarine fissure, showed a similar dependency on attentional resources. It therefore does not appear that faces with emotional expressions are a "privileged" category of objects immune to the effects of attention. Like neutral stimuli, faces with emotional expressions must also compete for neural representation. This is illustrated within the context of the biased competition model of attention in Figure 2.

Figure 2

A recent study by Holmes, Eimer, and colleagues has also obtained evidence that the processing of emotional expression requires attention (Holmes et al., 2003). In a paradigm very similar to the one employed by Vuilleumier et al. (2001), Holmes et al. investigated event-related potentials (ERPs) when subjects determined whether two faces were the same or not (“attended condition”), and when subjects determined whether two houses were the same or not (“unattended condition”). In the latter case, the faces, which could be either fearful or neutral, were unattended. During the attended condition, several ERP components were modulated by facial expression, including very early (~120 ms post-stimulus) and “late” components (between 300-500 ms post-stimulus). However, early as well as later differential responses were completely eliminated on trials in which the faces were presented at unattended locations. In another study (Eimer et al., 2003) these results were confirmed and extended by showing that differential ERP signals elicited by the six “basic” emotions (anger, disgust, fear, happiness, sadness, and surprise) were eliminated when attention was away from the faces (Fig. 3). As in our study, subjects performed a demanding competing task involving a difficult comparison of the length of two small bars close to fixation. The above results corroborate our findings that attention modulates the processing of emotional faces and further reveal that even the earliest emotional modulations appear to be gated by attention.

Figure 3

V. Emotional stimuli can bias competition for processing resources

Although our results indicate that attentional resources are required for processing stimulus valence, they do not imply that humans are unable to respond to potential threats outside the focus of attention or that the amygdala only responds to attended stimuli. Indeed, if attentional resources are not exhausted, then even ignored items of *neutral* valence can attract attention and interfere with on-going processing. Moreover, numerous studies have demonstrated that negative stimuli are a more effective source of involuntary interference to on-going tasks than neutral and positive ones, and more readily recruit attention.

It therefore appears that emotional (especially negative) stimuli can bias the competition for processing resources, such that they are at a competitive advantage compared to neutral stimuli. If so, then just as attention enhances activity within visual cortex to items at attended locations, so too should emotional pictures evoke stronger responses in visual cortex than neutral ones. This is indeed the case. We and others have found that both posterior visual processing areas, such as the occipital gyrus, and more anterior, ventral temporal regions, such as the fusiform gyrus, exhibit differential activation when emotional and neutral pictures are contrasted (Moll et al., 2002; Mourão-Miranda et al., 2003). Remarkably, we also obtained evidence for valence-dependent responses in and around the calcarine fissure (V1/V2) (Pessoa et al., 2002). It therefore appears that, like attentional modulation of activity in visual cortex, emotional modulation can provide a top-down influence on very early processing areas.

In sum, just as attention can favor the processing of attended items, so too do stimuli with emotional valence. Thus, we hypothesize that the increased activation produced by emotional stimuli in visual cortex reflects *emotional modulation* by which the processing of this stimulus category is favored as compared to that of neutral stimuli.

VI. What is the source of the biasing signal for emotional stimuli?

In the past decade or so, the amygdala has been shown to be a critical node in a circuit mediating the processing of stimulus valence, notably fear. Because of its widespread projections to cortical sensory processing areas (Amaral et al., 1992), it has been suggested that the amygdala may be

the source of modulation of activity evoked by emotional stimuli. Consistent with this proposal, Morris and colleagues found that amygdala signals covary with signals from visual areas in a condition-dependent manner (Morris et al., 1999). Such changes in “functional connectivity” highlight changes in the *coupling* between brain regions. In their study, the correlation between amygdala and visual cortical activity increased when subjects viewed fearful faces compared to happy ones. In our study (Pessoa et al., 2002), we also observed increased coupling during attended compared to unattended trials between the amygdala and visual areas, including the superior temporal sulcus, the middle occipital and the fusiform gyri. Interestingly, we found increased amygdala coupling with the calcarine fissure, which is consistent with projections from the amygdala to very early visual areas, including V1 and V2 (Amaral et al., 1992). Increased coupling was not restricted to visual processing regions, however, but also included the orbitofrontal and parietal cortex.

While the results from our study and others are consistent with a modulatory role for the amygdala, the type of analysis employed (based on activity covariation) cannot determine the direction of the interaction. More direct evidence that the amygdala is a source of emotional modulation comes from a recent study by Anderson and Phelps, who showed that patients with bilateral amygdala lesions did not show an advantage at detecting word stimuli with aversive content compared to neutral content, in stark contrast to the behavior of normal subjects (Anderson and Phelps, 2001).

Emotional modulation can potentially be implemented in one of two ways. First, it could rely on the direct feedback projections from the amygdala to visual processing areas (Amaral et al., 1992). Alternatively, the amygdala could modulate activity within these processing areas via its projections to frontal sites that control the allocation of attentional resources, including dorsolateral prefrontal and anterior cingulate cortex (Amaral et al., 1992). Of course, these two possibilities are not mutually exclusive. Finally, although we have emphasized the role of the amygdala in the attribution of stimulus valence, several brain regions, including the orbitofrontal and ventromedial prefrontal cortices, might act in concert with the amygdala in determining the behavioral and social significance of incoming stimuli.

VII. Attention and awareness

We have proposed that attention is required for the expression of stimulus valence. How does one reconcile this view with the finding that amygdala responses are evoked by masked faces of which subjects are presumably unaware (Morris et al., 1998; Whalen et al., 1998)? In such instances, it is possible that attentional resources to the masked stimuli were not sufficiently reduced by a competing task. Typically, in masking paradigms, subjects are required to direct attention to the location of the stimulus in the absence of any competing task, suggesting that attentional resources are available to allow for subliminal responses to the emotional stimuli. Thus, while attention appears to be necessary for the processing of faces with emotional expressions, it may not ensure that they reach awareness.

We hypothesize that the lack of awareness may be associated with weak neural signals. When sufficient attention is devoted to a stimulus, its neural representation will be favored, leading to stronger neural signals. Strong neural signals may be essential for visual awareness. For example, imaging studies of visuospatial neglect show that signals evoked by unseen faces are weak compared to those evoked by seen faces. Moreover, activity in the fusiform gyrus correlates with the confidence with which a subject reports recognizing an object. Thus, it appears that some threshold in visual cortex must be reached before visual awareness is possible. It should be stressed, however, that other factors are likely to be important in determining whether or not a stimulus reaches awareness, including the activation of fronto-parietal regions and temporal

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synchrony of neuronal firing. Interestingly, these factors may also contribute to the generation of robust, strong neural representations.

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Figure Captions

Figure 1. Attention is required for the processing of stimulus valence. Left: Attended faces compared to unattended faces evoked significantly greater activations for all facial expressions. Circles indicate the region of the amygdala. Right: Estimated responses for the right amygdala region of interest as a function of attention and valence.

Figure 2. Biased competition model of visual attention and the processing of emotion-laden stimuli. Facial expressions must compete for neural representation, just as neutral stimuli do. Emotional stimuli may be at a competitive advantage (see heavier arrows) because they are suggested to receive biasing signals from the amygdala, which assesses whether stimuli have emotional valence or not.

Figure 3. Effect of attention on event-related potential (ERP) waveforms. Top: Average ERP response to neutral and emotional faces for trials in which the subjects were instructed to report whether the faces were neutral or emotional. Bottom: Average ERP response to neutral and emotional faces for trials in which the subjects were instructed to report whether two small lines near fixation were of the same length or not. The differential responses observed in the top plot were completely eliminated. Results adapted from Eimer et al. (2003).

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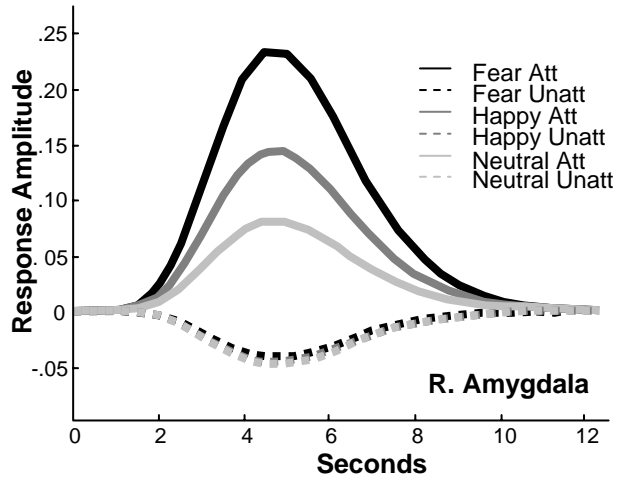
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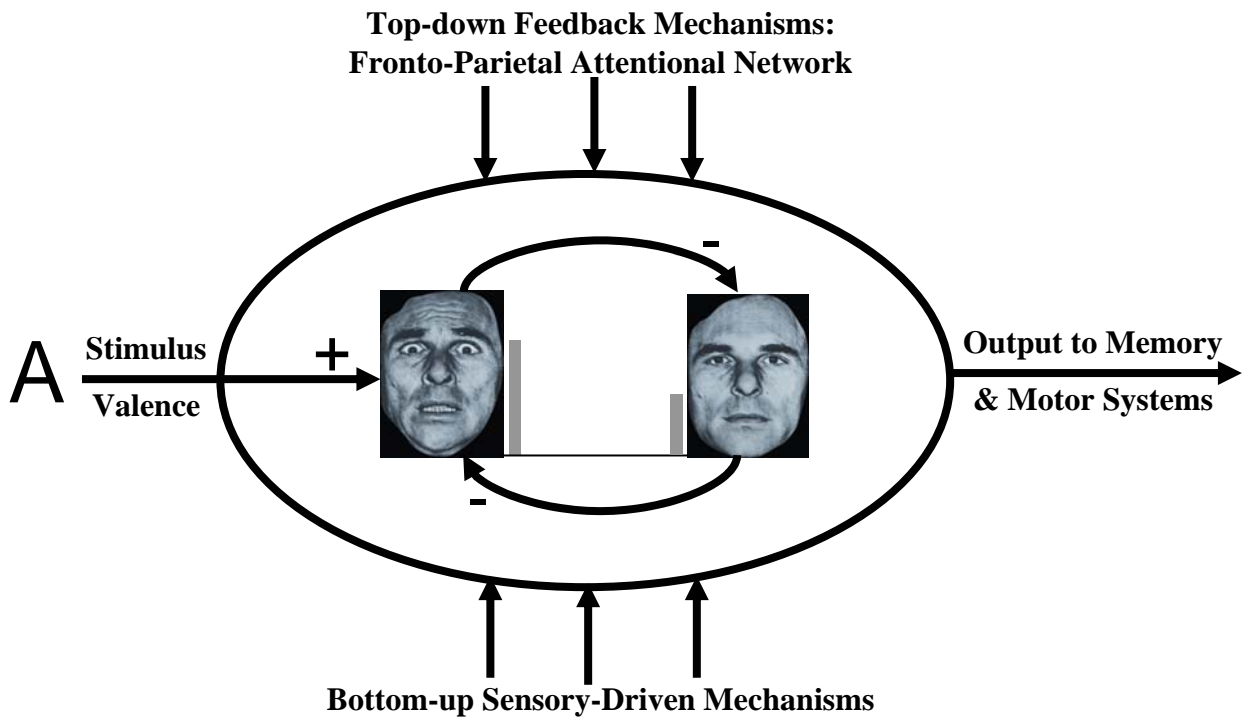
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Fearful

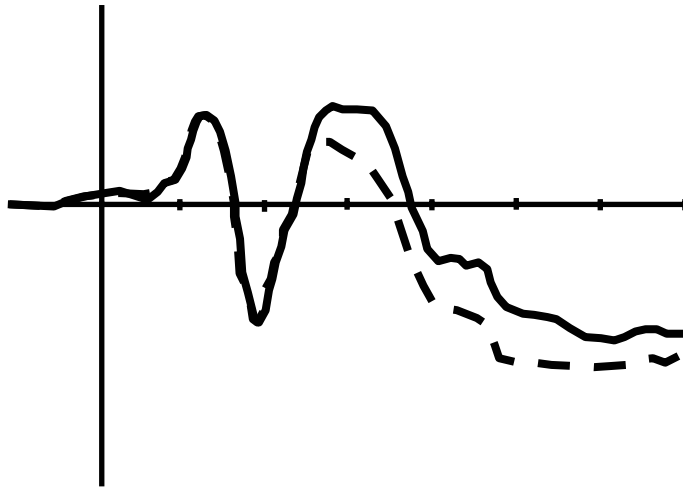


Attended > Unattended

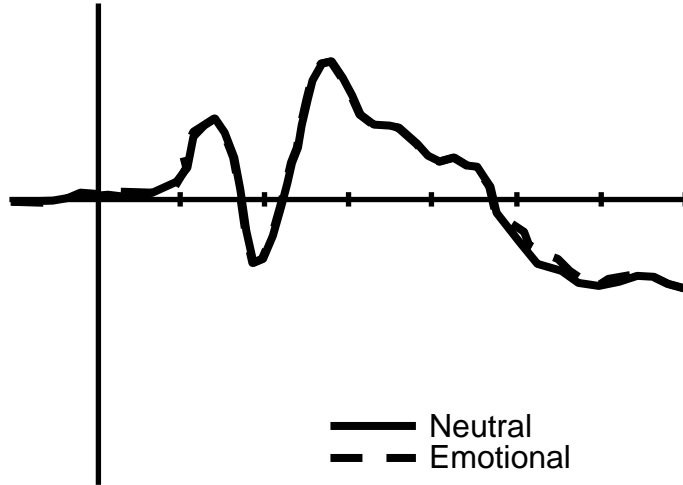




Emotion Task



Line Task



— Neutral
- - Emotional