

Automaticity in Cortical Processing of Emotion

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Abstract

Over the course of evolution, humans have likely developed special ways for detecting emotionally significant stimuli in the environment. There are two sources of evidence that the brain places special status on emotionally significant events: 1) biologically prepared stimuli (i.e., fearful facial expressions) are represented in specialized neural structures such as the amygdala, an evolutionarily older, subcortical structure, and 2) unlike the majority of neocortical functions that require attention for processing, amygdala processing is largely independent of attention. In this study, we investigated whether cortical processing of stimuli with acquired emotional value may also be independent of attention. Subjects' attention was manipulated, as they focused either on a face (judging it to be male or female) or an emotional or neutral word (judging it to be a word or a nonword). Face and word stimuli were superimposed on each other in a single display. When subjects were attending to words, the cortical response revealed enhanced activation to emotional versus neutral verbal stimuli in traditional word regions associated with semantic processing -- bilateral middle temporal (LMTG, RMTG) and superior temporal (LSTG, RSTG) gyri and the left inferior prefrontal cortex (LIPFC) -- as well as in emotion processing regions -- the medial prefrontal cortex (MPFC), anterior and posterior cingulate cortex. Even during cases of inattention, when the subjects were only attending to faces, enhanced processing of emotionally arousing words remained in the LMTG, LIPFC and left MPFC. These results suggest that automaticity in processing of emotional stimuli is not restricted to innate biologically prepared stimuli processing by the amygdala, but extends to learned, linguistic stimuli processing in the cortex.

Introduction

Imagine that you and a friend are standing on the corner of a busy street, engaging in conversation. You are discussing the weekend plans and coordinating your schedules. You are so engrossed in dialogue that you are completely unaware of the other passersby, the barking dogs and police siren in the background. However, when a car loses control and veers onto the sidewalk directly at you, you instantly jump out of the way. This is a classic example of selective attention – unknowingly, we simply attend to a minority of the incoming sensory stimuli from our environment at every moment of consciousness, yet emotionally relevant stimuli seem to trump the benign, and we shift our attention accordingly. What is the mechanism for this attention modulation in the brain and what role does emotion play?

Amygdala and Automaticity

Most studies of emotion processing have focused on “biologically prepared” stimuli, for example, facial expressions signaling threat and fear. From an evolutionary standpoint, such emotionally significant events represent important cues to relevant environmental threat (Öhman & Mineka, 2001) and, not surprisingly, are treated differentially by the brain on two accounts: emotionally significant stimuli are represented in specialized neural structures in the brain and the representation and processing of such stimuli operate automatically in these neural structures, independently of attention.

The amygdala, an evolutionarily older, subcortical structure, has repeatedly been shown to play an essential role in the evaluation of emotionally significant stimuli (Anderson & Phelps, 2001; Morris et al., 2001). Neuroimaging studies have implicated

the amygdala in the processing of fearful and angry facial expressions (Breiter et al., 1996; Morris et al., 1996; Whalen et al., 1998) and threatening scenes (Hariri et al., 2002). Each study has shown significantly greater activation in the amygdala to emotionally evocative stimuli than to neutral stimuli. Even during conditions of impaired awareness, several studies have suggested that amygdala processing persists. Such “automaticity,” indexed by a lack of reduction in activation with reduced attention, has been demonstrated in both fMRI and behavioral experiments. Functional imaging studies suggest automaticity in amygdala response in the processing of fearful faces during cases of decreased attention (Vuilleumier et al., 2001; Vuilleumier et al., 2002) and awareness under conditions of subliminal presentations (Whalen et al., 1998). There have been similar findings in patients with visual neglect (Vuilleumier et al., 2002) and cortical blindness (Morris et al., 2001). Visual neglect and cortical blindness are conditions where patients have lesions in visual processing areas of the cortex and fail to “see” items presented to a portion of their visual field. Vuilleumier et al. (2002) and Morris et al. (2001) have demonstrated that subcortical processing in the amygdala of threat faces, however, remains robust in such lesion patients. This confirms that amygdala processing of biologically prepared events operates automatically, independent of attention and consciousness.

Attention and Cortical Processing

Is the principle of automaticity unique to the amygdala processing of fear and emotion, or do cortical systems exhibit this property, as well? Several attention manipulation studies have suggested that processing in the cortex is highly dependent on attention. Corbetta et al. (1990) presented subjects with stimuli that had several salient

properties: shape, color and motion. When subjects were attending to motion attributes of the stimulus, for example, brain areas selective for motion processing were most active, and areas selective for shape and color processing were much less active. When subjects switched attention to one of the other attributes and ignored the motion properties of the stimulus, activations in brain regions selective for motion were dramatically reduced, and activations in regions selective for color or shape processing were increased. This finding of attentional modulation of cortical processing has been shown to be even more pronounced in higher-order regions specialized for complex object processing. Studies have shown that the degree of activation in face processing regions is dependent on the degree of attention towards face stimuli (Haxby et al., 1994; Clark et al., 1997; Wojciulik et al., 1998; O'Craven et al., 1999). For instance, Wojciulik et al. (1998) manipulated attention in subjects presented with face and house stimuli simultaneously. When subjects performed a face related task with the stimuli, activity in the fusiform face area (FFA) in the ventral occipitotemporal region increased. However, when performing a house related task, activation in the FFA was substantially reduced, and activation in an area related to place processing (the parahippocampal place area) increased. Thus, the need for attention appears to be a fundamental prerequisite for information processing in the cortex. The present study challenges this notion.

Linguistic Processing

Although nature may have equipped the brain with some instinctive emotional responses, the majority of emotional associations are learned. For instance, humans communicate emotional significance through both verbal and nonverbal means. Unlike fearful facial expressions (showing the whites of the eyes, mouth agape), words are not

“biologically prepared,” -- they are learned over the course of an individual’s lifetime, and do not depend on evolutionarily derived templates. We cannot predict the emotional quality of a word from its appearance alone, since the same linguistic units will comprise words of emotional and neutral quality. Finally, linguistic processing occurs primarily in the cortex, with limited subcortical contributions.

Due to the acquired nature of words, corresponding cortical characterizations are likely to be distributed across several regions, rather than residing in a single neural structure alone. Traditionally, the primary language zones include the area surrounding the Sylvian fissure in the left hemisphere of right-handed individuals, nearby Broca’s area (the inferior frontal gyrus) and Wernicke’s area (the middle and superior temporal gyri) (Ni et al., 2000).

Studies have repeatedly outlined and distinguished between orthographic (lower level), phonological (mid-level) and semantic (higher level) word processing. In reading, this multi-level language network begins when words are processed at the sublexical, orthographic level, at the level of letters that compose it, in the word form area (WFA) located in the inferior temporal lobe (Pugh et al., 1996; Polk et al., 2002). Activations in the dorsal aspect of the left inferior prefrontal cortex (LIPFC) and anterior cingulate have been cited during mid-level phonological (phoneme access) processing of words (Rumsey et al., 1997; Poldrak et al., 1999). At the highest level, words are processed by meaning and semantics, in the middle temporal gyrus (MTG) and the posterior superior temporal gyrus (PSTG) (Wernicke’s area) (Pugh et al., 1997; Kiehl et al., 1999). Representing yet another level of differentiation of word processing in the cortex, the LIPFC has also been recognized as working on the semantic level in search and retrieval

from lexical memory (Pugh et al., 1997; Kiehl et al., 1999; Poldrak et al., 1999; Fiebach et al., 2002). Furthermore, consistent with the modality independence of semantic processing, these areas have been activated in visually as well as orally presented word processing studies (Chee et al., 1999; Newman & Twieg, 2001; Binder et al., 2003). The complex human language network not only couples multiple levels of linguistic processing, it extends across sensory modalities.

Words and Attention

Word processing in the cortex, like face and place processing, has been shown to be attentionally dependent. Rees et al. (1999) presented subjects with a stimulus display of superimposed pictures and letter strings, and instructed them to attend only to the pictures or only to the letter strings. When subjects were attending to pictures, and ignoring the lexical stimulus content, activation in word processing regions did not differentiate between meaningful words and random letters. If word processing were fully automatic, words and non-word strings would activate different brain regions, i.e., those involved in semantic analysis, when the stimuli were unattended. However, there was no evidence for differential processing of such unattended stimuli, suggesting semantic information is simply not processed during inattention.

Studies of the automatic nature of emotion processing have primarily focused on the amygdala. In the present study, we examined the effect of attention on emotional stimuli processing in the cortex. Will emotional word stimuli elicit attention dependent patterns, consistent with prior studies of attentional influences on the cortex, or will they evoke attention independent patterns, consistent with prior studies of automaticity in the

amygdala? If automatic processing of affectively significant events extends beyond amygdala processing, then cortical processing of emotionally significant words will be accomplished independently of attention. This would suggest attentional dependence is not a fundamental property of all cortical processing. If emotion does not influence the processing of words, related cortical areas will reflect the modulatory effect. Further, the present study examines the level on which emotion will affect cortical representations of linguistic processing, from low-level orthographies to higher-level semantic analysis.

To address these issues, we used event-related fMRI to investigate the effect of attention on cortical representations of emotional word stimuli. The design allowed for manipulations of visual attention to test for the effect of emotion during decreased awareness. If cortical activations are attentionally modulated, emotional word processing will not persist during conditions of inattention. If activation to emotional words remains when attention is reduced, these brain regions will suggest at least some automaticity.

Methods

Participants

Seventeen subjects (seven males, ten females), without significant psychiatric or medical history between the ages of 19 and 26 (mean age 22.5), were recruited from the local Stanford University community. All subjects were native English speakers and right-handed as judged by the Edinburgh handedness survey. Subjects were paid \$25 for each hour of participation and gave informed consent in accordance with guidelines set by the Stanford University Panel on Human Subjects in Medical Research.

Stimuli

Each stimulus comprised a photograph of a neutral face superimposed with a word or non-word. Eighteen face stimuli (9 males, 9 females) were taken from the Ekman and Friesen facial affect set and were centered on a black background. Faces were placed in an oval aperture, where hair and facial shape were removed or disguised, so that gender could not be inferred directly from these features. All face stimuli were 200 x 250 pixels in size (at 72 dpi).

Word stimuli were chosen from an original list of 100 emotionally arousing words. Six volunteers rated each of the words for valence and arousal, and the 36 “strongest” (most emotionally evocative) were chosen for the experiment, according to the rater’s average arousal ratings. Correlations between raters were calculated, and average correlation across all raters was 0.71. Emotional words were then matched with neutral counterparts by word length, number of syllables, and Kucera-Francis word frequency (in the English language). We generated non-word matches for each of the emotional words by substituting the vowels for consonants, so that the letter string was unpronounceable and contained no meaning. For example, the emotional word “cancer” was matched with neutral and non-word counterparts, “aboard” and “cgnchr,” respectively. In total, we used a set of 108 items.

All face and word stimuli were then standardized for luminosity, contrast and transparency, and were rendered semi-transparent before they were superimposed. All stimuli were presented in the scanner using a magnet-compatible back-projector (Resonance Technology, Inc., Van Nuys, CA). A tilted mirror was mounted on the head coil in the magnet core so subjects could see the projected images without generating any

additional head or eye movement. Psyscope was used to generate the order of stimuli and to collect behavioral responses.

Design

The fMRI design was an intermixed trial, event-related model. Stimuli were presented in a fixed randomized order that counterbalanced for trial type history, to control for overlapping hemodynamic responses from distinct trial types. On each trial, a fixation crosshair was first displayed in the center of the screen (1 s). Then a color-coded prompt appeared for 750 ms to specify a gender judgment task (subject should attend to the face) or a lexical decision task (subject should attend to the word), followed by a 250 ms lag before the superimposed face/word stimulus was presented for 350 ms. This short stimulus duration ensured that subjects were only able to attend to one item of the display presented. Subjects were asked to indicate with a button box as quickly and as accurately as possible, either the lexical value of the word, if it was a real word or a non-word (the *attention* condition), or the gender of the face (the *inattention* condition). For “word” and “male” judgment responses, participants were to press the button under the index finger of their right hand; for “non-word” and “female” judgment responses, they were to press the button under the middle finger of their right hand. Responses and response times were recorded by the Psyscope program, calculated from stimulus onset to the button press response.

The experimental task included four sessions. Within a session, stimuli were presented to subjects every eight seconds; each session lasted approximately ten minutes.

Image Acquisition

Participants were scanned with a 3-Tesla Signa (General Electric, Milwaukee, WI) scanner with a prototype head coil. Foam padding was placed around the head to minimize movement. T1-weighted spin-echo structural images were acquired in 16 4 mm slices from the body of the corpus callosum to the ventral surface of the anterior temporal lobe, as well as a T1-weighted whole brain anatomy for normalization of functional data into common stereotaxic space. Functional images were then taken at these same slice locations using a T2*-weighted spiral pulse sequence (in plane resolution=3.755 ms; TR=1000 ms; TE=30ms; 60° flip angle, 24cm field of view, 64x64 matrix acquisition). The intertrial interval was eight seconds. 648 frames were collected across the four sessions, with 36 repetitions for each of the six trial types (*attention condition* (attend to word): emotional word, neutral word, nonword; *inattention condition* (attend to the faces): emotional word, neutral word, nonword). The first two trials at the beginning of each session were added to allow for equilibration of the scanner and were later discarded from the data set.

Analysis

The data were preprocessed and analyzed using SPM99. The functional images were reconstructed and realigned to correct for motion, and then slice time correction, coregistration, normalization and spatial smoothing (FWHM=8mm) were performed. Structural images for each subject were segmented and spatially normalized to a MNI gray matter template (provided in SPM99). Contrast images from individual subjects were submitted to a group level random effects analysis ($p < 0.005$, uncorrected) allowing population wide inferences.

Results

There are two states of interest to us: the *attention* and *inattention* conditions. In the attention condition, subjects focused (and performed a task) on the word stimulus, and ignored the face. In the inattention condition, subjects focused (and performed a task) on the face stimulus and ignored the word. We are primarily interested in brain activation patterns when subjects attended to emotional versus neutral words, compared to when subjects attended to faces with simultaneous presentation of emotional versus neutral words in the “background.”

Behavioral Performance

We assessed subject’s behavioral performance during the scans to ensure that they were following instructions on each trial. For all behavioral conditions, we set the alpha value at 0.05. Subjects were equally accurate in judging faces and words ($81.3 \pm 8.3\%$ vs. $83.2 \pm 14.8\%$; $F_{1,16} < 1$). Subjects’ responses were also equally accurate for all word types ($F_{2,32} = 2.06$; $p > 0.14$). We were particularly concerned that the inattention condition was not influenced by word type, but the interaction of attention and word type effects was non-significant ($F_{1,32} = 2.84$; $p > 0.10$). Specifically, subjects’ average accuracy for gender judgments (inattention condition) when emotional words were present versus neutral words was non-significant ($78.1 \pm 9.4\%$ vs. $82.2 \pm 8.6\%$; $F_{1,32} = 2.84$; $p > 0.10$).

Further, average response times did not differ between trial types and conditions. Average response times were statistically equivalent for faces and words (904.0 ± 237.0 ms vs. 920.1 ± 223.7 ms; $F_{1,16} = 1.195$; $p > 0.29$). Collapsing across conditions, response latency was not influenced by word type ($F_{1,16} = 2.03$; $p > 0.14$), nor did word type influence response latency for gender judgments ($F_{1,32} = 0.228$; $p > 0.79$). Subjects’

average response time for gender judgments when emotional words were simultaneously presented versus neutral words was non-significant (910.6 ± 236.7 ms vs. 902.6 ± 231.6 ms; $F_{1,32}=0.15$; $p>0.70$). This suggests that attentional manipulations were successful because subjects were devoting appropriate attentional resources to the attended stimulus, not to the to-be-ignored background stimulus.

Attention Condition

When words were attended, there was no evidence of greater regional blood oxygenation level-dependent (BOLD) activity to neutral than emotional words. Thus, no parts of the brain were more involved in processing neutral words than emotional words. However, emotional words elicited much greater activation than neutral words in the attention condition. We find increased activation in areas specific to word processing as well as to emotion processing for attended emotional words.

While attending to emotional versus neutral words, activation in regions specific to word processing included the middle temporal gyrus (MTG) (Brodmann's areas (BA) 21) and superior temporal gyrus (STG) (BA 22/39) approaching Wernicke's area (Fig. 1). Activations are seen bilaterally, but remain slightly more robust in the left middle and superior temporal gyrus (961 voxels) than the right (862 voxels) (Table 1). There was also activation in the left inferior prefrontal cortex (LIPFC) (BA 44/45) ($T_{1,16}=4.60$, $P<0.0002$), and a smaller activation in the right insula/inferior prefrontal cortex region ($T_{1,16}=3.15$, $P<0.004$) (Fig. 2). These data indicate that emotional words generated increased semantic processing compared to neutral words.

Activations in regions specific to emotion processing include a large contiguous area in the medial prefrontal cortex (BA 9,10,11) extending from a more ventral site

($T_{1,16}=5.61$; $P<0.0001$) to a more dorsal site ($T_{1,16}=5.03$; $P<0.0001$), including the superior frontal region ($T_{1,16}=4.04$; $P<0.0005$) (Fig. 3). Increased activity in the posterior cingulate (BA 23) ($T_{1,16}=4.02$; $P<0.0005$) and anterior cingulate (BA 24) ($T_{1,16}=3.81$; $P<0.0008$) was seen, as well (Fig. 3).

Inattention Condition

When words were unattended (subjects attended to faces), critical regions remained active in emotion versus neutral word presentation trials, including the left anterior MTG ($T_{1,16}=5.10$; $P<0.0001$) and the LIPFC ($T_{1,16}=4.46$; $P<0.0002$) (Fig. 4). Furthermore, an emotion processing region in the left medial prefrontal cortex ($T_{1,16}=4.94$; $P<0.0001$) (Fig. 5) remained active even without attention, along with a smaller region in the right medial prefrontal cortex ($T_{1,16}=3.74$; $P<0.0009$). The maintained discrimination of emotion and neutral words during inattention suggests that in certain cortical regions processing of emotion demonstrated the signature of automaticity.

Attention Condition

Region	BA	voxels	(x,y,z)	t_{1,16}	p<
L Middle Temporal Gyrus	21	961	-58, -42, -4	4.78	0.0002
L Superior Temporal Gyrus	22/39	(same cluster)	-44, -54, 20	4.24	0.0004
R Middle Temporal Gyrus	21	862	54, -16, -20	4.94	0.0001
R Superior Temporal Gyrus	22/39	(same cluster)	56, -56, 8	4.03	0.0005
L Inferior Prefrontal Cortex	44/45	292	-38, 16, -16	4.60	0.0002
R Insula/R Inferior Prefrontal	44/45	20	46, 8, -12	3.15	0.004
Ventromedial Prefrontal	8, 9,10	964	0, 40, -20	5.61	0.0001
Dorsomedial Prefrontal	8, 9,10	(same cluster)	4, 60, 16	5.03	0.0001
Superior Frontal	8, 9,10	(same cluster)	-20, 52, 20	4.04	0.0005
Posterior Cingulate	23	105	-2, -48, 20	4.02	0.0005
Anterior Cingulate	24	33	-4, 24, 24	3.81	0.0008

Inattention Condition

Region	BA	voxels	(x,y,z)	t_{1,16}	p<
L Anterior Middle Temporal	21	64	-62, -18, -12	5.10	0.0001
L Inferior Prefrontal Cortex	44/45	339	-52, 30, 8	4.46	0.0002
L Medial Prefrontal Cortex	8,9	246	-12, 54, 12	4.94	0.0001
R Medial Prefrontal Cortex	8,9	62	36, 60, 4	3.74	0.0009

Table 1: Regions of activation for emotional versus neutral word stimuli during attention and inattention conditions.

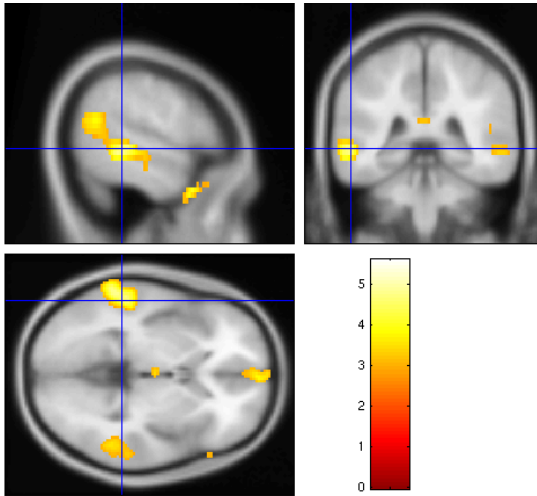


Figure 1

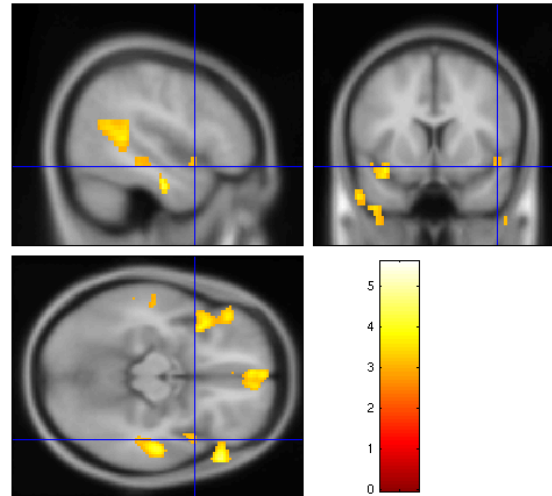


Figure 2

Figure 1: Attention condition (emotional versus neutral words): contiguous activation in left and right middle temporal gyri, extending to superior temporal gyrus

Figure 2: Attention condition (emotional versus neutral words): activation in the left inferior prefrontal cortex (LIPFC), right insula/IPFC, and medial prefrontal cortex

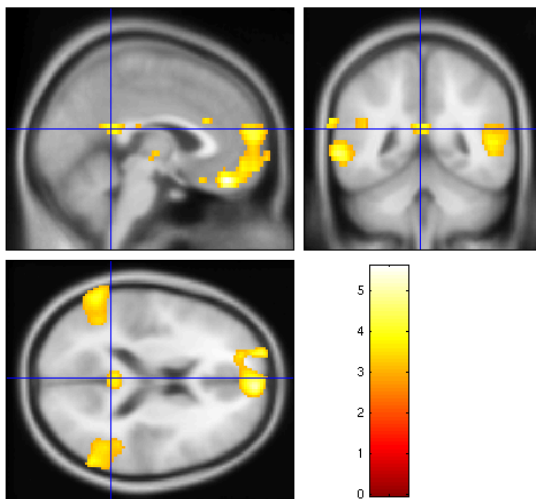


Figure 3

Figure 3: Attention condition (emotional versus neutral words): activation in the left and right superior temporal gyrus, posterior and anterior cingulate, and contiguous activation in the ventro- and dorso- medial prefrontal cortex, extending to the superior frontal cortex

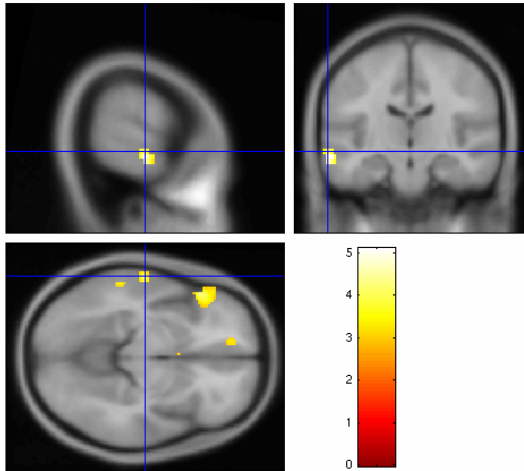


Figure 4

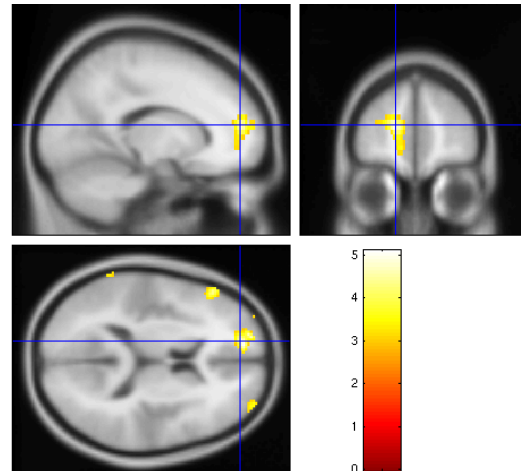


Figure 5

Figure 4: Inattention condition (emotional versus neutral words): activation in the left anterior middle temporal cortex, and the left inferior prefrontal cortex

Figure 5: Inattention condition (emotional versus neutral words): activation in the left medial prefrontal cortex, and the left inferior prefrontal cortex

Discussion

While previous studies have suggested that the cortex is highly dependent on attention, we find that the emotional quality of a word stimulus takes precedence over attention in certain cortical regions. Similar regions are activated with and without attention in the MTG and the LIPFC while processing emotional versus neutral words. The activations during reduced attention in the left anterior MTG are a smaller subset of the larger, bilateral activation in the MTG while attending to the same stimuli, suggesting attentional independence in this semantic processing region. Activation in the LIPFC in both the attention and inattention conditions suggests altered semantic retrieval of emotional words. Furthermore, the medial prefrontal cortex (MPFC), a region traditionally associated with emotion processing (Bechara et al., 1994, 2000; Angrilli et al., 1999; Cardinal et al., 2002), remained active in both conditions to emotional compared to neutral words. The lack of reduction in activation during conditions of reduced awareness challenges the notion that the cortex is reliant on attention for processing; thus, these findings support the principle of automaticity in cortical processing of affectively significant events. Further, we find that automaticity extends to cortical regions not specific to emotion processing (i.e., word processing regions).

Amygdala and Cortical Representations

How have cortical representations been changed to allow for such automaticity? Words, like a majority of events in our modern lives, belong to a class of items that are acquired over the course of an individual's lifetime. They do not hold "biologically prepared" representations in our brains, as snakes, lions and other predators might

(Öhman & Mineka, 2001), and thus need to be acquired and integrated into our brain architecture.

Whereas the brain is not preferentially responsive to neutral words, we find it differentially activates to emotional words. Some now believe that the amygdala is involved in this process of affecting cortical change and sensitivity to emotionally arousing stimuli (Anderson & Phelps, 2001). The amygdala has been cited as critical for enhancing the processing of emotionally significant stimuli in cortical areas (Morris et al., 1998; Anderson & Phelps, 2001). The result of these arousal-based cortical modifications is to decrease the resource dependence of processing in these regions.

Behavioral paradigms, such as the attentional blink, support this notion. The attentional blink is an experimental condition where subjects are presented with two successive masked target stimuli, separated by a temporal interval of variable duration. Subjects fail to recognize the presentation of the second stimulus if they have to perform a task on the first and if the inter-stimulus interval is between 100-400 ms (Kanwisher, 2001). However, studies show that when emotionally arousing words are presented, the “blink” is substantially diminished -- healthy subjects are more accurate at reporting these arousing compared to neutral words. These results demonstrate that emotionally arousing words depend less on attention to reach awareness. On the other hand, patients with amygdala lesions do not show enhanced perception of emotionally arousing stimuli under conditions of limited attention (Anderson & Phelps, 2001). Given that amygdala damage decreases the enhanced awareness effect but does not impair comprehension of emotional words, we infer that the amygdala itself is not involved in encoding the emotional meaning of words, only in influencing subsequent perceptual awareness. If the amygdala

causes the change in cortical representations, then its involvement in altering the sensitivity of word processing regions to emotionally arousing verbal stimuli probably occurs during the course of language acquisition and development. After the cortex sensitizes, it may not need the amygdala or attention for enhanced processing.

Perhaps this is why the present study did not find amygdala activation among the results, as our native English speakers had already long ago acquired the verbal stimuli presented. Studies suggest that the amygdala is responsible for modulation of memory storage, but is not the site of memory formation (Packard et al., 1994; Cahill & McGaugh, 1998). For example, when subjects view emotionally arousing stimuli (positively or negatively valenced), the amygdala and hippocampus (traditionally known for its role in memory formation) work together in long-term memory storage (Hamann et al., 1999). However, it is unknown whether the amygdala is involved when subjects recall or review those previously stored memories. In conjunction with evidence of spared comprehension of emotionally arousing words in patients with amygdala damage, these findings implicate the amygdala in changing the cortical representations of emotionally arousing events, but not in accessing them. This could explain why we see enhanced activation in cortical word processing regions, but not in the amygdala, in the present study.

Cortical Emotion Processing

Attention is usually a prerequisite for perception; however, multiple studies have shown that little to no attention is needed for processing emotionally significant events (Whalen et al., 1998; Anderson & Phelps, 2001; Vuilleumier et al., 2001; Vuilleumier et al., 2002.) The distinction between attention and inattention is critical when we consider

the hostile environment in which mammals evolved. Both positively and negatively arousing stimuli were important for survival, for locating food and mating partners, and for avoiding predators (Öhman et al., 2001). The reproductive potential of animals was influenced by the ability to identify such salient elements in the environment quickly, by automatic scanning and analysis of peripherally located events. Traditionally, the amygdala functions in automatic perception, as it effectively distinguishes the emotionally salient and the benign, even when an individual's attention is absent.

However, neural correlates of emotion also reside in the cortex. The medial prefrontal/orbitofrontal regions play a critical role in emotion processing (Bechara et al., 1994, 2000; Angrilli et al., 1999; Cardinal et al., 2002). Orbitofrontal (OFC) lesion patients are impaired in making emotionally reactive decisions and resemble amygdala-lesion patients in their affect-lacking judgments (Bechara et al., 2000). For example, when engaged in a gambling game with two different decks of cards, a "safe" one with which the player wins or loses money in small amounts and a "risky" one that involves large amounts, normal subjects quickly come to prefer the safe deck and develop a physiological response when they choose the risky deck. OFC-lesioned patients do not preferentially opt to play with the safe deck, and they do not exhibit a physiological response when they choose the risky deck (Bechara et al., 2000). An emotion-related sensing mechanism seems to be extinct in cases involving OFC-lesions.

The anterior cingulate cortex (ACC) has been cited as important for encoding emotional responses, as well (Lane et al., 1997; Cardinal et al., 2002). Garavan et al. (2000) have shown that the ACC is responsive to cocaine-associated cues in cocaine users, and to emotionally evocative sexual images in normal subjects. In addition,

Maddock et al. (2003) have shown posterior cingulate activation to emotional words. Accordingly, areas of the neocortex appear to play a critical role in emotion processing, as well.

Consistent with previous research, we have also found cortical activations in emotion processing regions. When subjects were paying explicit attention to emotional versus neutral words, we found ventro- and dorso- medial prefrontal cortex, posterior and anterior cingulate activations. Furthermore, in the inattention condition (emotional versus neutral words), areas of the dorsomedial prefrontal cortex remained active. This suggests that cortical representations for emotionally evocative stimuli have been changed in some, but not all, emotion processing regions -- some have been sensitized to be automatically responsive to emotional stimuli while others remain dependent on attention. For instance, since regions such as the anterior and posterior cingulate may represent more cognitive and attention demanding aspects of emotional evaluations, this could explain why we do not see activation in these regions during conditions of reduced attention in the present study.

Emotional Attention

The reason behind the greater activation patterns in emotional compared to neutral events may reflect either top-down or bottom-up processing changes. A top-down theory of processing would propose that an emotional stimulus incites greater interest in the viewer than does a neutral stimulus, and consequently, the viewer pays more attention to it. Greater attention generates greater corresponding brain activity when viewing these stimuli. This theory would suggest that the active brain regions were not responding to the emotional quality of the stimulus, but to the subject's volitional

attention. In the present study, we tested this by manipulating attention while presenting emotional and neutral verbal stimuli in the visual field. The results indicate that even when a participant's attention is reduced, there continue to be some regions active in both traditional word and emotion processing regions of the brain. This implies that greater activation to emotional words was not simply a function of paying more attention to them; rather, these brain regions have been "fine-tuned" for emotional responsiveness, reflecting enhanced bottom-up processing of affective content. Corresponding cortical representations appear to be sensitized to heighten responsiveness, irrespective of attention.

However, not all word processing regions exhibit such automaticity. It appears that emotional content has only played a role in changing the representation of neural substrates at the semantic processing level but not in lower-end orthographic representations. During the inattention condition, enhanced processing of emotionally arousing words only remained in the left anterior MTG and the LIPFC, from the multiple activations in the left and right MTG, STG and IPFC during the attention condition, already noted for contributions in semantic processing (Pugh et al., 1997; Kiehl et al., 1999; Poldrak et al., 1999; Fiebach et al., 2002). However, the visual word form area (VWFA) in the inferior temporal lobe was not differentially active to emotionally arousing words. Research shows that the VWFA is equally responsive to words and pseudo-words, suggesting that it operates in sublexical, orthographic and not in semantic representation (Cohen et al., 2000; Dehaene et al., 2001). Considering that sublexical representations are common to both emotionally arousing and more neutral words, it would be surprising to find that emotional value influences responsiveness in the VWFA.

For instance, it is unlikely that the sublexical graphemes “ca,” “nc” and “er” from the word “cancer” exhibit enhanced cortical representation because they also are building blocks of many other words, such as (ca)ndy, bou(nc)e and bart(er). Thus, such orthographic processing is unlikely to be enhanced by emotional significance of the whole word unit. This could explain why cortical representations appear to be sensitized to the emotional quality of words and prepared for automaticity at the semantic, but not at the orthographic, level in the present study.

Future studies may examine critical cross-cultural differences in how emotion influences neural representations of language. In ideographic languages such as Chinese, where there is a one-to-one mapping between orthographic and semantic meaning, emotional significance may influence perceptual awareness and attentional dependence from sublexical graphemic to semantic word processing regions.

In sum, the present study provides evidence that attentional dependence is not a fundamental feature of cortical processing. Similarly, automaticity is not restricted to amygdala processing of biologically prepared events; rather, it extends to cortical representations of events with acquired affective significance, as well.

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