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Hemispheric asymmetry for emotional stimuli detected with fMRI

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CURRENT brain models of emotion processing hypothesize that positive (or approach-related) emotions are lateralized towards the left hemisphere, whereas negative (or withdrawal-related) emotions are lateralized towards the right hemisphere. Brain imaging studies, however, have so far failed to document such hemispheric lateralization. In a functional magnetic resonance imaging (fMRI) study, 14 female subjects viewed alternating blocks of emotionally valenced positive and negative pictures. When the experience of valence was equated for arousal, overall brain reactivity was lateralized towards the left hemisphere for positive pictures and towards the right hemisphere for negative pictures. This study provides direct support for the valence hypothesis, under conditions of equivalent arousal, by means of functional brain imaging. *NeuroReport* 9: 3233–3239 © 1998 Lippincott Williams & Wilkins.

Key words: Affect; Emotion; Human; Imaging; Laterality

Introduction

One of the most influential models of hemispheric asymmetry in emotion is the valence hypothesis. This hypothesis is grounded in clinical and EEG data[1] and posits that the experience or expression of emotional valence is lateralized across the hemispheres of the brain. Positive (or approach-related) emotions are thought to be lateralized towards the left and negative (or withdrawal-related) emotions towards the right frontotemporal regions of the brain. Direct support for the valence hypothesis by functional imaging studies has, however, remained elusive: imaging studies report activation patterns that are either bilateral or inconsistent with the valence hypothesis, when comparing valenced emotional and neutral states.[2,3]

The failure of imaging studies to replicate observations by clinical and EEG measures may be due to differences in study design or methodology.[4] Most importantly, previous imaging studies were not explicitly designed to test the valence hypothesis and have only assessed brain activation in response to negative versus neutral stimuli, precluding the opportunity to compare laterality patterns in both valence conditions. It is therefore not clear whether a given laterality pattern would be specific to negatively valenced affect or to affect in general, regardless of valence. Furthermore, a comparison between negative and neutral emotion states may be less sensitive to detecting brain laterality than a comparison between negative and positive states.

The comparison between negative and neutral conditions also confounds two dimensions of emotional experience, valence and arousal. Valence refers to the degree to which an emotion is pleasant or unpleasant, whereas arousal refers to the intensity of that emotion. The negative test condition is not only significantly different from the neutral control condition in valence but also arousal, which may be controlled by different neural systems.[5] In the absence of efforts to control for arousal,[1] it is difficult to draw firm conclusions on brain laterality for the experience of emotional valence.

The present fMRI study was designed explicitly to test the valence hypothesis, using positively and negatively valenced pictures controlled for arousal. We predicted that viewing pictures that were different in valence but not arousal would produce left-lateralized activation for positive and right-lateralized activation for negative stimuli in frontal and temporal regions.

Materials and Methods

Subjects: Fourteen right-handed healthy female volunteers (mean age 25.6 years, range 19–42 years) participated in this study.

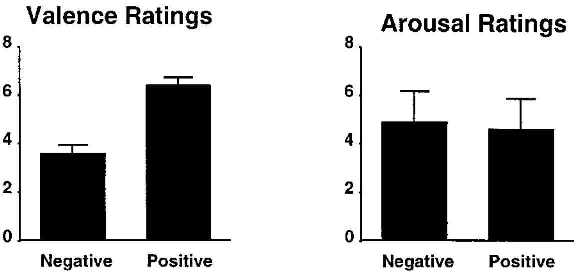
Emotion stimuli and manipulation check: Participants were scanned while viewing alternating sets of negative and positive pictures selected from a standardized set of pictures (IAPS).[6] Positive pictures included images of a happy couple, puppies, foods like ice cream and brownies, and urban sunsets. Negative pictures included images of angry or crying people, spiders, guns and a cemetery. The pictures were intended to be different in valence, but not in arousal. Stimuli were presented in five alternating blocks of four pictures each. The order of positive and negative blocks was counterbalanced across subjects. Each picture was presented for 7500 ms, with an interstimulus interval of 1125 ms. Total scan time was 345 s. As a manipulation check, subjects were shown the same sequence of stimuli immediately after scanning and asked to rate how each picture made them feel when they first saw it in the scanner. The visual scale that was used[6] ranged from 1 (unhappy) to 9 (happy) for ratings of emotional valence and from 1 (calm) to 9 (excited) for ratings of emotional arousal, with 5 representing a neutral rating in both dimensions.

MRI: Data were acquired in a 1.5 T GE Signa MR imager, which was used to measure blood oxygen level-dependent (BOLD) contrast.[7] For structural images, 16 coronal slices 3 mm in thickness were imaged, using a T1-weighted flow-compensated spin-warp sequence (TR = 500 ms, minimum TE). Functional images were obtained using a $T2^*$-sensitive 3-D gradient echo spiral sequence with four interleaves (TR = 90 ms, TE = 40 ms, flip angle 22°, FOV 36 cm, in-plane resolution 2.35 mm^2, acquisition time 4.32 s/frame, number of frames 80).[8] A whole-head coil was used for all subjects. Head movement was minimized using a bite-bar with each subject's dental impression. Standard algorithms for motion analysis[9] and correction[10] were used. Individual functional activation maps were based on a correlation between the signal intensity of each pixel and a reference function which was computed by convolving a square-wave at the task frequency (alternating blocks of negative and positive pictures) with a data-derived estimate of the hemodynamic response function[11] and spatially smoothed at fwhm = 4.8 mm. Average brain activation maps were then constructed and displayed by projection onto an averaged T1-weighted anatomical image of each slice. The resulting averaged functional maps were then intensity thresholded at $p < 0.05$ (two-tailed) and each slice was subjected to a cluster analysis procedure[12] to correct for multiple statistical comparisons, using a spatial extent threshold that yielded a $p < 0.05$ significance level over the entire image (taking into account the 4.8 mm FWHM spatial smoothing and the 2.35 mm inherent resolution of the images, a smoothness FWHM of $(4.8^2 + 2.35^2)^{1/2} = 5.3$ mm was used for the cluster analysis procedure).

Results

Subject ratings of emotional valence and arousal: Examination of the subjects' ratings indicated that there were two different subgroups. For one group, the aim of varying valence while holding arousal constant was achieved. Figure 1 (top panel) shows data from those subjects ($n = 8$) who experienced the negative and positive picture sets as significantly different in valence (mean ± s.d: negative, 3.51 ± 0.43; positive, 6.34 ± 0.37; t = 26.19, $p < 0.0001$), but not in arousal (negative, 4.81 ± 1.33; positive, 4.53 ± 1.30; t = 1.18, $p = 0.28$). Thus, for these subjects the experience of emotional valence was controlled for arousal. Figure 1 (bottom panel) shows data from the other group of subjects ($n = 6$) who experienced the picture sets as significantly different not only in valence (negative, 3.16 ± 0.34; positive, 7.02 ± 0.84; t = 8. 18, $p < 0.0005$), but also in arousal (negative, 6.02 ± 1.12; positive, 4.12 ± 1.43; t = 5.62, $p < 0.005$); they rated the negative pictures as more arousing than the positive pictures.

Arousal Equal (N=8)



Arousal Confounded (N=6)

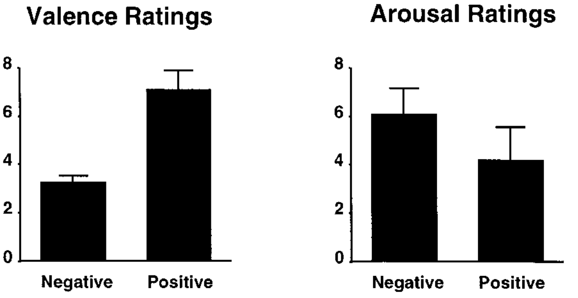


FIG. 1. Mean subject ratings of emotional valence and arousal for negative and positive pictures. Each subject rated each picture individually. Unpaired *t*-tests were performed for each subject to determine whether negative and positive pictures were rated significantly differently with respect to valence and arousal. Eight subjects gave ratings indicating a significant difference in valence, but not arousal, between negative and positive pictures (group 'Arousal Equal', top panel). Six subjects gave ratings indicating a significant difference in valence, and also in arousal, between negative and positive pictures (group 'Arousal Confounded', bottom panel).

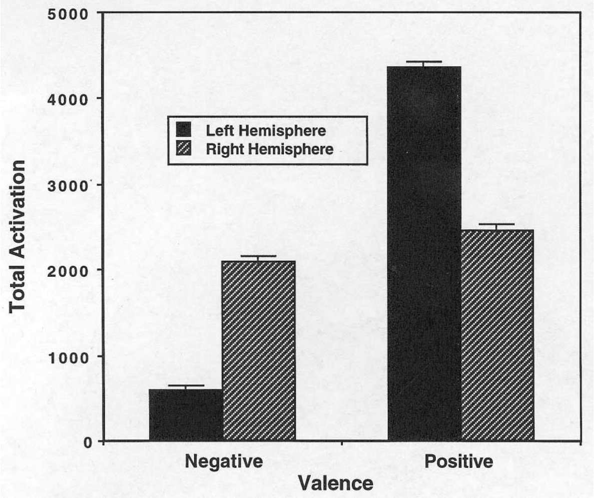


FIG. 2. Total activation in response to positive and negative emotional pictures. Subjects in the 'Arousal Equal' group exhibited more brain reactivity to positive than to negative pictures in the left hemisphere (summed weighted activation, as computed by area × average z-score: 4347.33, s.d. = 75.75) than in the right (summed weighted activation, as measured by area × average z-score: 2456.04, s.d. = 74.76). These subjects also exhibited more brain reactivity to negative than to positive pictures in the right hemisphere (summed weighted activation, as computed by area × average z-score: 2089.55, s.d. = 73.47) than in the left (summed weighted activation, as measured by area × average z-score: 593.44, sd = 55. 39).

For subjects whose experience of emotional valence was equated for arousal, the left hemisphere was dominant in responding to positive pictures while the right hemisphere was dominant in responding to negative pictures. The global asymmetry was measured in two ways. First, the summed weighted activation (area of significant pixel clusters × average z-score of these pixel clusters) in response to positive and negative pictures was calculated in each hemisphere. As can be seen from Fig. 2, most of the total activation seen in response to negative pictures was seen in the right hemisphere (78% in the right, 22% in the left), while most of the total activation seen in response to positive pictures was seen in the left hemisphere (64% in the left, 36% in the right). The second way to quantify global asymmetry was to count the number of regions (clusters) of significant pixels in each hemisphere. Significantly more clusters were present in the left than the right hemisphere in response to positive pictures ($\chi^2(1) = 10.83$, $p < 0.001$), and significantly more clusters were present in the right than the left hemisphere in response to negative pictures ($\chi^2(1) = 6.64$, $p < 0.01$). Clusters in the right *vs* left hemisphere were not significantly different from each other with respect to the number of pixels in each cluster or the average z-score of these pixels.

Figure 3 shows the composite brain activation map for those subjects whose experience of emotional valence was controlled for arousal. Overall brain reactivity to positive, relative to negative, pictures was lateralized towards the left hemisphere, with more clusters of significant activation in the left than right frontal and temporal gyri. This pattern of activation was not exclusively lateralized to the left hemisphere, however: loci of significant activation in response to positive stimuli were also seen in the right hemisphere in cingulate, inferior frontal, and superior temporal

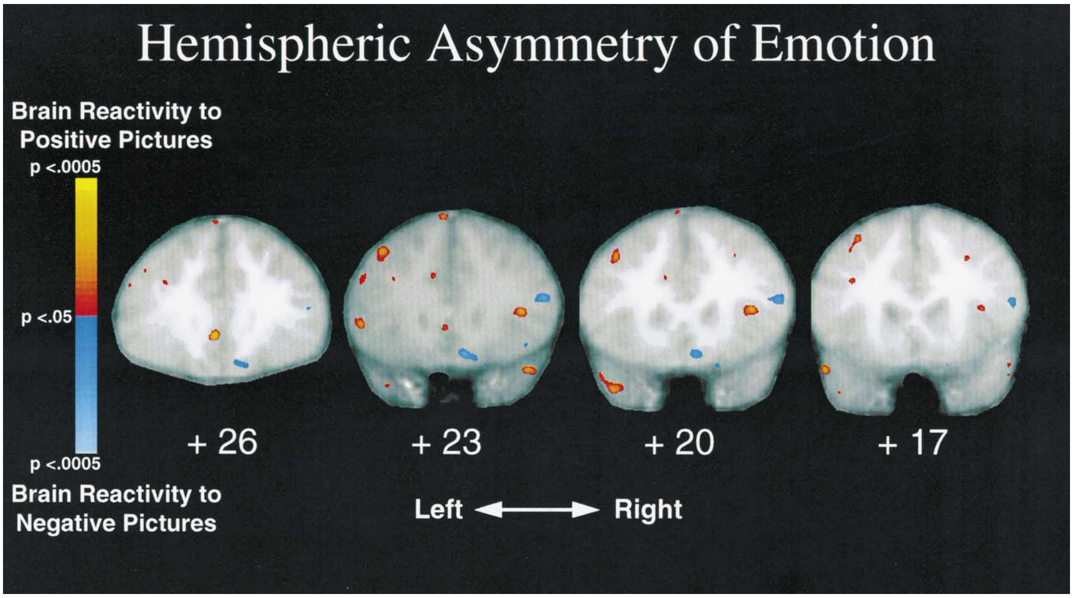


FIG. 3. Loci of activation in response to positive and negative emotional pictures. Shown are coronal slices and significant ($p < 0.05$) activation loci. Loci colored in red represent regions of significant activation in response to positive, relative to negative, pictures. Loci colored in blue represent regions of significant activation in response to negative, relative to positive, pictures.

gyri. Overall brain reactivity to negative, relative to positive, pictures was lateralized towards the right hemisphere, particularly in the inferior frontal gyrus and gyrus rectus.

A complete listing of significant activation loci for these subjects (and the remaining, arousal-confounded subjects) is provided in Table 1.

Discussion

This study demonstrated lateralized brain reactivity to emotional stimuli consistent with the valence hypothesis, when subjects' emotional experience was controlled for arousal. Significant activation in response to positive, relative to negative, stimuli was seen most consistently in the left middle frontal gyrus, as well as middle and superior temporal gyri. Significant activation in response to negative, relative to positive, stimuli was seen in the right inferior frontal and gyrus rectus.

This laterality pattern is consistent with earlier evidence from clinical studies. For example, damage to the left hemisphere has been associated with depressive symptomatology while damage to the right hemisphere has been associated with indifference or positive affect such as euphoria, laughter and optimism.[13] Hemispheric inactivation by injection of sodium amobarbital produces laughter and elated mood more frequently after right-hemisphere injection and crying more frequently after left-hemisphere injection.[14]

The laterality pattern observed here is also consistent with a large body of EEG studies, reviewed in Ref. 1. For example, subjects with stable (across 3 weeks) and extreme left frontal baseline activation reported more positive and less negative dispositional affect than subjects with extreme right frontal activation. Subjects with right-lateralized brain baseline electrical activity report more negative affect in response to negative film clips than left-lateralized subjects. Individuals also exhibit greater left frontal activation in response to positive film clips and greater right frontal activation in response to negative film clips. Subjects who are subclinically or clinically

Table 1. Areas of significant activation.

Group	Location	x	y	z	Volume	Mean z
Arousal Equal						
Positive pictures	left precentral gyrus	–48	–9	39	355	2.25
	left middle frontal gyrus, BA 6	–17	–7	62	453	2.12
	left middle frontal gyrus, BA 6	–34	6	51	1495	2.18
	left middle temporal gyrus, BA 21	–59	1	–15	363	2.22
	right superior temporal gyrus, BA 38	50	11	–24	264	2.13
	right inferior frontal gyrus	35	19	11	499	2.21
	left superior temporal gyrus, BA 38	–40	18	–28	409	2.16
	left middle frontal gyrus	–38	20	39	430	2.21
	left middle frontal gyrus, BA 8	–21	33	41	266	2.09
	right anterior cingulum	11	33	21	913	2.25
Negative pictures	right inferior frontal gyrus, BA 44	56	10	18	272	–2.1
	right subcallosal gyrus	7	20	–12	426	–2.2
	right inferior frontal gyrus	49	19	17	554	–2.2
	left anterior cingulum	–13	31	5	280	–2.2
	right gyrus rectus	0.4	34	–16	516	–2.4
Arousal Confounded						
Positive pictures	right temporal lobe	47	–8	–38	306	2.39
	right middle frontal gyrus	16	–7	62	498	2.19
	left caudate	–18	0	22	2458	2.31
	left superior temporal gyrus, BA 22	–54	–2	–2	4639	2.39
	right insula	33	6	11	578	2.09
	right superior temporal gyrus	60	–2	–1	6139	2.36
	left lenticular nucleus	–8	7	–3	679	2.12
	right superior temporal gyrus, BA 38	39	15	–31	2687	2.26
	right uncus	30	3	–20	8608	2.29
	right frontal lobe	19	28	35	619	2.16
		2	31	–7	750	2.12
Negative pictures	left inferior frontal gyrus, BA 47	–48	20	–10	567	–2.4
	left inferior frontal gyrus	–51	31	–8	270	–2.2
	right anterior cingulum	16	28	12	272	–2.1

The table lists loci of significant brain activation in response to positive (relative to negative) and negative (relative to positive) emotional pictures. To determine the 3D coordinates of each cluster, the method of Xiong *et al.*[12] was used on the activation volume. Regions are identified by name of location, Brodmann's area (BA), and coordinates in the brain atlas of Talairach and Tournoux.[42] x = distance in mm to the right (+) or left (–) of midline; y = distance anterior (+) or posterior (–) to the anterior commissure; z = distance superior (+) or inferior (–) to a horizontal plane through the anterior commissure.

depressed exhibit significantly less left frontal activation than nondepressed subjects. This finding of left hypofrontality has also been corroborated by a number of PET imaging studies.[15,16]

The activation pattern we observed was not completely lateralized. This finding is also consistent with a number of other studies. For instance, one study reported that inactivation of the left hemisphere produced depression-like responses 63% of the time, but euphoria-like responses 37% of the time.[14] Importantly, when these observations were controlled for speech lateralization, inactivation of the language-dominant hemisphere still produced euphoria-like responses 29% of the time. Thus, the lack of complete laterality cannot be ascribed to variability in language lateralization. Inactivation of the right hemisphere produced euphoria-like responses 83% and 93% of the time in two studies cited by Lee and colleagues,[14] but also produced depression-like responses 17% and 7% of the time, respectively. Thus, both positive and negative emotional responses can be produced by the hemisphere that is non-dominant for that particular emotional valence.

The EEG literature also reports incomplete lateralization. This is most apparent when the reported laterality data are recalculated using the laterality index formula (L–R)/(L+R).[17] Using this formula, one finds that the reported left-lateralized midfrontal activation of anxiety repressors[18] is represented by a laterality index of –0.048. Thus, the reported laterality rests on a difference of brain activation of $< 5\%$ between the left and right hemispheres. Similar calculations show that left-lateralized frontal activation reported for joyful expressions in infants[19] is represented by a laterality index of –0.125. Right-lateralized frontal activation reported for sad expressions[19] is represented by a laterality index of 0.227. Thus laterality for emotional valence is not absolute by fMRI, inactivation, or EEG.

The regions identified in this study are consistent with some other functional imaging studies of emotion. For instance, Paradiso and colleagues reported increased blood flow in left superior temporal gyrus in elderly subjects who experienced happiness.[20] Pardo and colleagues reported significant (albeit bilateral) activation in inferior frontal and orbitofrontal regions in women who experienced self-induced sadness.[21]

The functional significance of the activation loci is unclear. Previous work has recognized the role of the dorsolateral prefrontal cortex and anterior cingulate in attention[22,23] and it is possible that activation of these structures reflects attention towards valenced stimuli. Activation of the medial prefrontal region has been suggested to reflect the conscious experience of emotion, monitoring or modulation of emotion, inhibition of emotional expressions or emotionally relevant decision making.[24,25] In future work, more specific emotion-related tasks will be needed to specify different roles of these structures in emotion-related processes.

Interestingly, we found no significant amygdala activation in response to negative stimuli, despite its well-documented role in the processing of other emotional visual stimuli such as facial affective expressions.[26,27] It is not clear whether this is due to lacking statistical power (only two of 16 sampled slices contained pixels located in the amygdala), the nature of the stimulus set (e.g. facial emotional expressions present in both conditions), or the fact that the amygdala may not play a significant role in the experience of negative affect. Amygdala activation in response to negative scenes (as opposed to facial expressions) has been documented by some investigators.[28,29] On the other hand, Cahill and colleagues[30] did not observe significant activation of the amygdala while subjects were watching a set of negative film clips, compared to neutral film clips, even though subjects rated films as negative. Studies investigating phobic fear[31,32] or re-experience of traumatic experiences[33] have also failed to detect amygdala activation. Finally, patients with bilateral damage to the amygdala rate negative emotional stimuli comparable to normal controls.[34] Thus, there is evidence consistent with the view that negative affect can be experienced in the absence of amygdala activation.

Subjects who experienced negative and positive stimuli as different in valence as well as arousal exhibited a very different brain activation pattern. The most striking feature of this pattern was the strongly right-lateralized activation in the temporal lobe in response to positive stimuli. We speculate that these subjects may have reacted to low-arousal positive stimuli with greater introspection or efforts to retrieve autobiographical memories, compared to high-arousal negative stimuli. Low-arousal positive stimuli may have been perceived as 'emotionally ambiguous', especially when compared to high-arousal negative stimuli, and may have prompted efforts to imbue them with emotional significance by other means, such as introspection or autobiographical memory. Autobiographical memory has been shown to be processed in right temporal regions.[35]

The fact that two groups of subjects can display different laterality and activation patterns, depending on their experience of arousal, highlights the fragility of hemispheric laterality in emotional processes. Indeed, most imaging studies of emotion have reported either bilateral brain activation or laterality patterns contradicting the valence hypothesis (reviewed in Ref. 4). For example, Fredrikson and colleagues[36] used an aversive unconditioned stimulus

(US) in a classical conditioning experiment and reported bilateral or left-lateralized blood flow changes as a result of the procedure. In the first study to use personal recollection as a means of mood induction in normal volunteers,[21] subjects who remembered a sad event exhibited increased bilateral, rather than right-lateralized, activation in the frontal regions. However, because the control condition was rest rather than neutral recollection, it has been argued that the pattern of laterality may be related to memory rather than affect.[37] Later studies that included a neutral control condition were either consistent[38] or inconsistent[3] with the valence hypothesis. Other studies using a more experimenter-controlled approach to emotion induction, such as film clips or pictures, reported largely bilateral activity patterns in response to the stimuli.[2,33]

These previous imaging studies may have failed to replicate laterality patterns from the clinical and EEG literature for several reasons.[4] First, most studies assessed brain activation only in response to negatively valenced stimuli and used neutral stimuli as a control condition. However, hemispheric asymmetry may be more sensitively detected by contrasting a negative versus a positive emotional state. For example, hemispheric asymmetry is reported when EEG recordings associated with happiness and disgust are compared, but not when happiness is compared to baseline.[39] Second, variability in subjective emotional experiences may have obscured laterality patterns. For example, several studies used autobiographical memory to induce emotional states. Such memories may contain more than just the target emotion, perhaps even conflicting emotions, which may produce ambiguous laterality patterns. Third, few studies have explicitly measured both valence and arousal in manipulation checks. Valence and arousal are often regarded as distinct dimensions of emotional experience[40] and are likely controlled by different neural systems.[5] These neural systems may interact with each other, making it imperative to control for arousal when comparing two differently valenced states.[1]

Conclusion

This study used fMRI to demonstrate a pattern of laterality in emotional processing that is consistent with the valence hypothesis. This finding is based on the inclusion of at least two valenced states, experimenter-controlled choice of stimuli, and careful consideration of individual differences in emotional experience, particularly the experience of emotional arousal. Indeed, future studies should focus on the role of arousal, contrasting high- and low-arousal conditions for positive and negative stimuli. These efforts may help to determine the nature of the interrelation between neural systems involved in the experience of valence and arousal, respectively. Furthermore, the advancement of new statistical approaches, such as single-trial fMRI,[41] will make it possible to produce brain activation maps on the basis of performance, such as subjects' ratings or ability to recall, and may thus further improve our understanding of the neural basis of individual differences in emotional processes. This effort can also help to illuminate the functional significance of activation loci in both the dominant and non-dominant hemispheres, as subjects can be scanned with single-trial fMRI while performing a range of tasks related to emotion processing.

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