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Review

Emotional perception: Meta-analyses of face and natural scene processing

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ABSTRACT

Functional imaging studies of emotional processing typically contain neutral control conditions that serve to remove simple effects of visual perception, thus revealing the additional emotional process. Here we seek to identify similarities and differences across 100 studies of emotional face processing and 57 studies of emotional scene processing, using a coordinate-based meta-analysis technique. The overlay of significant meta-analyses resulted in extensive overlap in clusters, coupled with offset and unique clusters of reliable activity. The area of greatest overlap is the amygdala, followed by regions of medial prefrontal cortex, inferior frontal/orbitofrontal cortex, inferior temporal cortex, and extrastriate occipital cortex. Emotional face-specific clusters were identified in regions known to be involved in face processing, including anterior fusiform gyrus and middle temporal gyrus, and emotional scene studies were uniquely associated with lateral occipital cortex, as well as pulvinar and the medial dorsal nucleus of the thalamus. One global result of the meta-analysis reveals that a class of visual stimuli (faces vs. scenes) has a considerable impact on the resulting emotion effects, even after removing the basic visual perception effects through subtractive contrasts. Pure effects of emotion may thus be difficult to remove for the particular class of stimuli employed in an experimental paradigm. Whether a researcher chooses to tightly control the various elements of the emotional stimuli, as with posed face photographs, or allow variety and environmental realism into their evocative stimuli, as with natural scenes, will depend on the desired generalizability of their results.

Contents

The majority of functional magnetic resonance imaging (fMRI) studies of emotion have used visual stimuli, most often employing pictures of expressive human faces or natural scenes to elicit

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emotional reactivity. The use of emotional faces and scene images has yielded a considerable amount of data, and here we seek to identify the similarities and distinctions in blood oxygen level dependent (BOLD) signal that is associated with these classes of eliciting stimuli, using a coordinate-based meta-analysis technique, through which a comparison can be made between fMRI studies using faces and those using scenes. fMRI studies of emotional processing typically contain a neutral control condition (unexpressive face, or non-emotional scene) that theoretically serves to remove simple effects of visual perception, thus revealing the emotional process. Here we seek to identify potential differences that may remain in comparisons of emotional face and emotional scene perception, to aid in data interpretation across published reports. Perhaps more importantly, we seek to identify the brain regions consistently activated during visual perception of emotional stimuli, whether via the expressive face or the evocative scene.

Human faces are ubiquitous visual stimuli that consistently engage multiple bilateral regions of the brain. While the essential neural structures of face perception are not absolutely clear, the principal components of the human neural system for face perception include the inferior occipital gyrus (IOG), the superior temporal sulcus (STS), and the anterior fusiform gyrus or 'fusiform face area' (FFA; Haxby et al., 2002; Kanwisher et al., 1999; Puce et al., 1996). The perception of emotionally expressive faces results in greater activation in the FFA, as well as increased activity in bilateral amygdala (Breiter et al., 1996; Morris et al., 1998; Vuilleumier et al., 2001, 2003, 2004). In addition to the theoretical interest in socioemotional processing, the inherently equivalent perceptual characteristics of posed human faces and general availability have led to the widespread use of expressive face stimuli as a means to operationalize emotional perception in the MR scanner.

Standardized emotional and non-emotional natural scene photographs are also commonly employed in studies of emotional perception in neuroimaging studies. Commonly reported areas of the brain activated by emotional, relative to neutral, natural scene photographs include the extrastriate occipital and inferotemporal cortex, superior parietal visual areas, the amygdala, insula, anterior cingulate, superior frontal gyrus, and medial prefrontal cortex (Bradley et al., 2003; Britton et al., 2006; Hariri et al., 2002b; Northoff et al., 2004; Sabatinelli et al., 2005, 2007, 2009).

While predictions concerning a large-scale comparison of emotional face and scene processing are tentative, the structures listed in Haxby's (2002) model of face processing (IOG, STS, FFA) may be more commonly reported in the studies using face stimuli, relative to scene stimuli. Conversely, structures associated with visual processing of objects, such as the lateral occipital cortex (Grill-Spector et al., 2001), and structures associated with spatial processing of elements at varying points in space, such as intraparietal sulcus, frontal eye fields (Astafiev et al., 2003; Corbetta and Shulman, 2002), and parahippocampal place area (PPA; Epstein et al., 1999, Walther et al., 2009) may be more prevalent in emotional scene studies. With regard to emotional processing, the amygdala is reported to be engaged during the perception of arousing (both pleasant and unpleasant) face and scene stimuli, though the majority of face studies have employed fearful expressions. Two studies (Britton et al., 2006; Hariri et al., 2002a,b) have directly compared both face and scene stimuli, and report greater amygdala reactivity in response to fearful face stimuli, therefore the current meta-analyses may maintain this finding.

Methods

Article selection

Articles published between 1995 and 2009 were identified using specific keyword searches in the PubMed database. The following search string was used to locate articles related to emotional face processing: ("1995/01/01"[Publication Date]: "2009/12/31"[Publication Date]) AND ((face OR facial OR FFA OR expression) AND (emotion* OR mood OR motivation OR affective OR fear* OR valence OR pleasantness) AND (fMRI OR neuroimag* OR "functional MRI" OR "functional magnetic resonance imaging")). Similarly, publications involving emotional scene processing were obtained with the search string: ("1995/01/01"[Publication Date]: "2009/12/31"[Publication Date]) AND (emotion* OR affective OR fear* OR valence) AND (fMRI OR neuroimag* OR "functional MRI" OR "functional magnetic resonance imaging") NOT ((face OR facial OR FFA OR express* OR Ekman OR kdef)). Articles were then removed from the resulting pool if they did not meet any of the following criteria: Journal article available in English, use of adult (19- to 44-year-old) human subjects with a sample size of at least five, linked full text available, and whole-brain analyses with reported Montreal Neurological Institute (MNI) or Talaraich coordinates. Articles were also excluded if analyses were limited to a special population, but were included if data was separately reported for a matched control group. After close examination of experimental design and analyses, a small proportion of articles were excluded, as they were highly specific in purpose, or did not report contrasts of emotional and non-emotional stimuli.

Contrast selection

All contrasts reflected the statistically significant, whole brain clusters that were active during emotional, relative to neutral stimuli, whatever stimuli or task was employed. In cases where multiple contrasts were reported, the most basic emotional versus neutral contrast was chosen, e.g., passive viewing instead of embedded task conditions (see Table 1).

Activation likelihood estimation (ALE) procedure

Activation likelihood estimation (Turkeltaub et al., 2002; Laird et al., 2005) is a coordinate-based quantitative meta-analysis method that identifies consistent brain activation locations elicited across studies employing a similar task. In ALE, activation foci (reported coordinates) are treated as probability distributions centered at the reported coordinates. Activation probabilities are then calculated for each standard-space voxel to construct ALE maps for contrasts of interest. To determine the reliability of the ALE map, null-distributions are generated by permutation tests in which all the foci in the actual meta-analysis are randomly redistributed, and null-ALE scores are computed. A statistical test of values in the observed ALE distribution is then performed by comparing them with values in a null distribution to assign P values to the observed (experimental) values. Here we used GingerALE 2.0 (http://www.brainmap.org), a 10 mm spatial filter kernel, and a $p<.001$ False Discovery Rate threshold for the 5000-iteration permutation tests of face and scene ALE maps. Each resulting map was thesholded at 250 µl and a $p<.001$ alpha level. A detailed description of the ALE process and analysis procedures can be found on the Brainmap website (http://www.brainmap.org/ale/manual.pdf).

Results and discussion

Article inclusion

The final meta-analysis study pool (total $n=2748$, see Table 1) included 100 reports of emotional face processing and 57 reports of emotional scene processing. The total number of foci (Talairach or converted MNI coordinates) entered into the ALE analysis was 1444 for face studies and 1029 for scene studies. The total gender breakdown was slightly biased toward females (55% of total), with women making up 51% of emotional face studies, and 60% of emotional scene studies.

Table 1
Studies included in the face and scene meta-analyses.

Year	1st author	Stimuli	Subjects
1998	Phillips	Face	6M/0F
1998	Whalen	Face	8M/0F
2000	Critchley	Face	9M/0F
2000	Narumoto	Face	8M/3F
2001	Dolan	Face	4M/8F
2001	Gorno-Tempini	Face	5M/5F
2001	Iidaka	Face	6M/6F
2001	Phelps	Face	6M/6F
2001	Thomas	Face	6M/0F
2001	Vuilleumier	Face	6M/6F
2001	Williams	Face	11M/0F
2001	Wright	Face	8M/0F
2002	Feinstein	Face	0M/9F
2002a	Gur	Face	7M/7F
2002b	Gur	Face	10M/4F
2002a	Hariri	Face	5M/7F
2002b	Hariri	Face	6M/6F
2002	Iidaka	Face	6M/6F
2002	Morris	Face	6M/6F
2002	Pessoa	Face	13M/8F
2002	Wright	Face	8M/8F
2002	Yang	Face	6M/11F
2003	Abel	Face	8M/0F
2003	Carr	Face	7M/4F
2003	Gunning-Dixon	Face	4M/4F
2003	Iidaka	Face	3M/3F
2003	Lange	Face	9M/0F
2003	Phillips	Face	8M/0F
2003	Surguladze	Face	5M/4F
2003	Vuilleumier	Face	6M/7F
2004	Benuzzi	Face	7M/7F
2004	Etkin	Face	13M/13F
2004	Hennenlotter	Face	5M/4F
2004	Lennox	Face	6M/6F
2004	Phillips	Face	8M/0F
2004	Sato	Face	10M/12F
2004	Schroeder	Face	10M/10F
2004	Straube	Face	4M/6F
2004	Vuilleumier	Face	7M/6F
2004	Williams	Face	15M/7F
2005	Botvinick	Face	0M/12F
2005	Critchley	Face	6M/9F
2005	Del-Ben	Face	12M/0F
2005	Fenker	Face	6M/14F
2005	Fischer	Face	12M/12F
2005	Hennenlotter	Face	6M/6F
2005	Ishai	Face	8M/5F
2005	Liddell	Face	11M/11F
2005	Moriguchi	Face	6M/10F
2005	Reinders	Face	7M/8F
2005	Tessitore	Face	6M/6F
2005	Williams	Face	5M/8F
2006	Brown	Face	21M/37F
2006	Chakrabarti	Face	12M/13F
2006	Drabant	Face	51M/50F
2006	Fitzgerald	Face	10M/10F
2006	Ishai	Face	6M/6F
2006	Meriau	Face	0M/23F
2006-a	Williams	Face	7M/6F
2006-b	Williams	Face	7M/8F
2006-a	Wright	Face	6M/12F
2006-b	Wright	Face	6M/6F
2007	Burklund	Face	6M/13F
2007	Engell	Face	7M/5F
2007	Furl	Face	3M/9F
2007	Habel	Face	0M/14F
2007	Malhi	Face	0M/10F
2007	Rauch	Face	10M/10F
2007	Rubino	Face	10M/18F
2007	Salloum	Face	11M/0F
2007	Scheuerecker	Face	5M/7F
2007	Thielscher	Face	10M/15F
2007	van der Gaag	Face	8M/9F
2008	Andersson	Face	7M/9F
2008	Beaver	Face	9M/13F
2008	Canli	Face	4M/11F
2008	Fu	Face	8M/11F
2008	Hall	Face	16M/8F
2008	Hermans	Face	0M/12F
2008	Jackson	Face	20M/15F
2008	Jogia	Face	5M/7F
2008	Lee	Face	2M/13F
2008	Michalopoulou	Face	5M/4F
2008	Miskowiak	Face	7M/5F
2008	Nomi	Face	7M/7F
2008	Payer	Face	9M/3F
2009	Amting	Face	13M/6F
2009	Dominguez-Borràs	Face	0M/17F
2009	Gentili	Face	4M/4F
2009	Harrison	Face	16M/0F
2009	Jimura	Face	13M/21F
2009a	Kim	Face	8M/6F
2009b	Kim	Face	9M/12F
2009	Kleyn	Face	26M/0F
2009	Passamonti	Face	5M/7F
2009	Preibisch	Face	17M/0F
2009	Reker	Face	0M/33F
2009	Schulz	Face	16M/8F
2009	Suslow	Face	28M/23F
2009	Trautmann	Face	0M/16F
2001	Beauregard	Scene	10M/0F
2001	Garavan	Scene	0M/11F
2002	Gray	Scene	6M/8F
2002	Karama	Scene	20M/20F
2002	Ochsner	Scene	0M/15F
2003	Eugene	Scene	0M/10F
2003	Mourao-Miranda	Scene	6M/2F
2003	Mouras	Scene	9M/0F
2003	Shapira	Scene	3M/5F
2003	Stark	Scene	9M/10F
2003	Wicker	Scene	14M/0F
2003	Wrase	Scene	10M/10F
2004	Cahill	Scene	12M/11F
2004	de Gelder	Scene	4M/3F
2004	Fichtenholtz	Scene	9M/13F
2004	Lee	Scene	5M/5F
2004	Phan	Scene	6M/6F
2004	Stark	Scene	24M/0F
2004	Takahashi	Scene	9M/6F
2004	Wright	Scene	4M/4F
2005	Goldin	Scene	0M/13F
2005	Heinzel	Scene	10M/3F
2005	Petrovic	Scene	0M/15F
2005	Schafer	Scene	20M/20F
2005-a	Schienle	Scene	0M/63F
2005-b	Schienle	Scene	0M/13F
2005	Takahashi	Scene	13M/0F
2006	Baumgartner	Scene	0M/9F
2006	Bermpohl	Scene	8M/9F
2006	Erk	Scene	0M/14F
2006	Garrett	Scene	4M/5F
2005	Hutcherson	Scene	0M/28F
2006	Kensinger	Scene	11M/10F
2006	Mather	Scene	6M/10F
2006	Mather	Scene	6M/4F
2006	Nitschke	Scene	10M/11F
2006	Schienle	Scene	0M/20F
2006	Siessmeier	Scene	13M/0F
2007	Blair	Scene	10M/12F
2007	Hermann	Scene	0M/10F
2007a	Herwig	Scene	16M/18F
2007b	Herwig	Scene	6M/10F
2007	Kim	Scene	0M/10F
2007	Ogino	Scene	10M/0F
2007	Stark	Scene	34M/32F
2007	Sterpenich	Scene	9M/12F
2008	Kensinger	Scene	12M/25F
2008	Kim	Scene	7M/5F
2008	Leclerc	Scene	5M/12F
2008	Mataix-Cols	Scene	17M/20F
2008	Mitchell	Scene	12M/9F

Table 1 (*continued*)

Year	1st author	Stimuli	Subjects
2008	Straube	Scene	3M/11F
2008	Talmi	Scene	6M/5F
2008	Wendt	Scene	0M/32F
2009	Akitsuki	Scene	12M/14F
2009	Demaree	Scene	0M/6F
2009	Van Marle	Scene	0M/27F

Columns include year of publication, first author, stimulus class, and gender breakdown of subject sample, M = male, F = female. See reference section for full citation.

Emotional activation: Faces and scenes

An overlay of emotional face and scene ALE maps is shown in Fig. 1. Blue clusters represent significant emotional face processing areas, red clusters represent significant emotional scene processing areas, and purple areas represent the overlap of emotional face and scene processing. All foci meeting criterion identified in ALE analyses for emotional face and emotional scene studies are listed in Tables 1 and 2.

This meta-analysis of 157 fMRI studies sought to compare 2 widely used classes of stimuli in the investigation of emotional processing, namely posed expressive faces, and natural scene photographs. The analysis intended to compare only the effects of emotional arousal, after effective removal of the basic effects of face and scene perception. Therefore only significant emotion-driven clusters (e.g., emotional face > neutral face, emotional scene > neutral scene) were included in the analyses. If the task subtraction method common in the neuroimaging literature extends to this comparison of emotional processing, then effects of stimulus emotionality should be consistent across faces and scenes. However, if emotion-related brain activity is moderated by the demands of the specific visual media, face- and scene-specific emotion activation may be present.

As is often the case, the results are equivocal, as there is both considerable overlap, partial overlap, and exclusivity in the resulting meta-analytic clusters. Perhaps not surprisingly, a comparison of emotional face clusters and emotional scene clusters reveals the greatest overlap in the amygdala, the multimodal subcortical structure most consistently associated with emotional processing in the fMRI literature. Both emotional stimulus types also prompted reliable BOLD signal in regions of medial prefrontal cortex, inferior frontal cortex, inferior temporal cortex, and extrastriate occipital cortex. However, the spatial extent of clusters within these regions varied considerably, such that in most clusters, generally minor overlap is evident across face and scene clusters. In addition, several cortical and subcortical clusters were unique to one class of stimuli. Thus while the brain regions driven by face and scene emotionality are generally consistent, within-region variance is substantial. An overarching result of the meta-analysis therefore suggests that, despite within-study contrasts controlling for the basic elements of visual stimuli (neutral faces or scenes) the particular class of stimuli has a considerable impact on the resulting emotion effects. Beyond the amygdala, emotion evoked by a fearful face is associated with a distinct pattern of brain activity relative to emotion evoked by a fearful scene. In the following sections we will provide a brief overview of the background literature supporting the role of the major cluster locations identified in the two meta-analyses presented here.

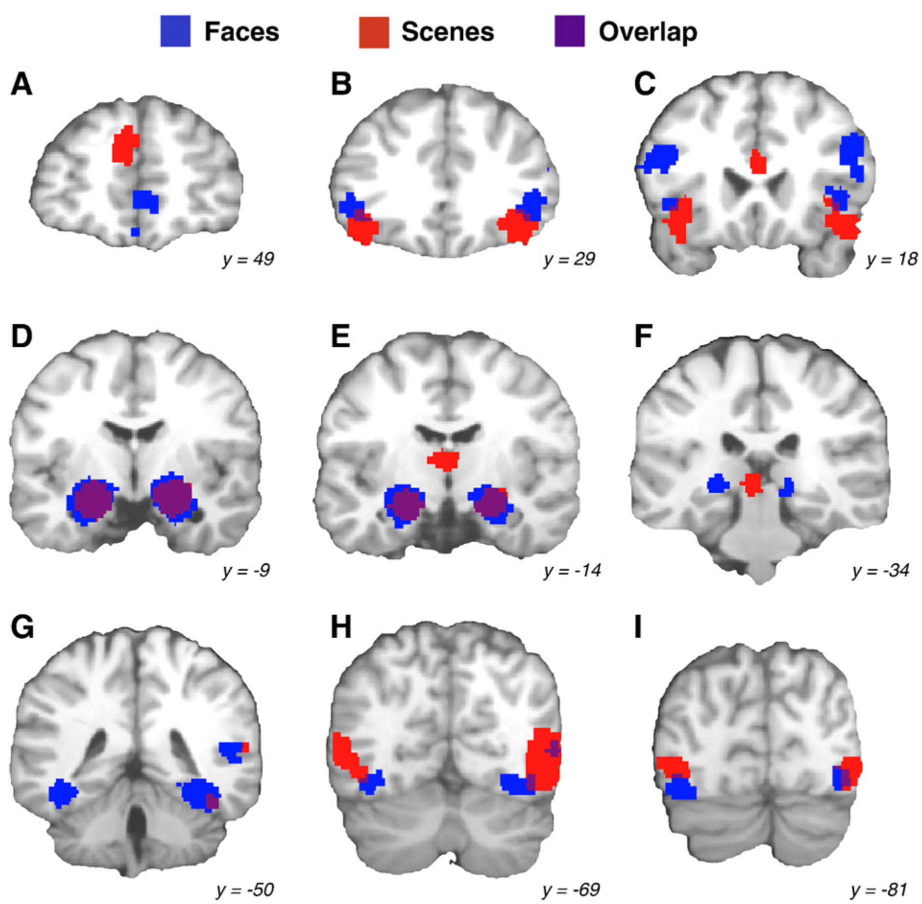

Fig. 1. Clusters resulting from an ALE analysis of 100 emotional face processing studies are shown in blue, clusters resulting from an ALE analysis of 57 emotional scene processing studies are shown in red, and the overlap of the two analyses is shown in purple, overlaid on a standardized structural volume. The neurological convention is used (right lateralized clusters are located on the right side of the slice).

Table 2
Clusters derived from meta-analysis of emotional face>neutral face contrasts.

x	*y*	*z*	Structure
4	47	7	Medial Prefrontal Ctx
42	25	3	R Inferior Frontal Gyrus
−42	25	3	L Inferior Frontal Gyrus
48	17	29	R Middle Frontal Gyrus
−42	13	27	L Middle Frontal Gyrus
−2	8	59	Superior Frontal Gyrus
20	−4	−15	R Amygdala
−20	−6	−15	L Amygdala
−20	−33	−4	L Parahippocampal Gyrus
14	−33	−7	R Parahippocampal Gyrus
53	−50	4	R Middle Temporal Gyrus
38	−55	−20	R Fusiform Gyrus
−40	−55	−22	L Fusiform Gyrus
38	−76	−16	R Post. Fusiform Gyrus
−40	−78	−21	L Post. Fusiform Gyrus

MNI coordinates and structure of clusters identified in the 100-study meta-analysis of emotional face studies.

Emotional face processing

Table 2 lists the clusters of activity identified by the ALE analysis of emotional face perception, and includes regions implicated in the Haxby model of face processing (Gobbini and Haxby, 2007; Haxby et al., 2002), specifically the anterior fusiform gyrus, middle/superior temporal gyrus, and inferior occipital gyrus. Reliable BOLD signal in basic face processing areas is evoked by emotional face perception, despite a non-emotional (or less emotional) face comparison condition. Emotionality thus increases activation in much of the basic circuit of face perception.

The fusiform gyrus, particularly the anterior region as it nears the parahippocampal gyrus, has been consistently associated with the perception of human faces (Haxby et al., 2000; Puce et al., 1995; Kanwisher et al., 1999), and has been shown to be more active during expressive (e.g., fearful) face processing than neutral faces (Morris et al., 1998, Vuilleumier et al, 2001, 2004). This region of inferotemporal cortex has been associated with the processing of color, face-like objects, and learned semantic categories (Bartels and Zeki, 2000; Chao et al., 1999; Gauthier et al., 2003; Grill-Spector et al., 2004; Kanwisher and Yovel, 2006). The meta-analytic finding of anterior fusiform gyrus and parahippocampal gyrus activity during emotional face perception is therefore in keeping with the literature, and replicates the hypothesized role of this region across 100 fMRI datasets.

Several studies have reported superior/middle temporal gyrus (MTG) activity during emotional scene perception (Bremner et al., 1999; Proverbio et al., 2009; Schafer et al., 2005), as well as during the discrimination of expressive faces (Batty & Taylor, 2003; Blair et al., 1999). Effects of hemisphere in the MTG have been mixed, with studies of expressive face perception reporting bilateral activity (Fusar-Poli et al., 2009), right-lateralized MTG activity (Blair et al., 1999; Chakrabarti et al., 2006; Morris et al., 1998) and left-lateralized MTG activity (Critchley et al., 2000). The current meta-analysis implicates the right MTG as reliably active during emotional face perception, although significant activity in this region was associated with both face and scene stimulus types.

While outside the basic model of face perception proposed by Haxby et al. (2002), several studies have shown that the inferior frontal gyrus (IFG) can be activated by expressive face processing (Carr et al., 2003; Montgomery and Haxby, 2008; Fusar-Poli et al., 2009). Bilateral inferior frontal clusters were identified in both emotional face and emotional scene meta-analyses, with face-specific areas centered superior and lateral to scene-specific regions of IFG, bordering orbitofrontal cortex. This offset will again require within-subject experimentation to clarify.

Middle frontal gyrus (MFG) has also been shown to be activated by facial expressions of emotion (Fusar-Poli et al., 2009), perhaps especially by expressions of disgust (Kitada et al., 2010). MFG may play a role in emotion regulation (Eippert et al., 2007; Ochsner et al., 2002), via the orbitofrontal cortex, and it dense connections with the amygdala (McDonald, 1998).

The medial and ventromedial prefrontal cortex (mPFC) has a well-established role in emotional processing, particularly with regard to reward (Knutson et al., 2003; Phillips et al., 2003; Philips et al., 2008; Sabatinelli et al., 2007). This meta-analysis necessarily combines activation sites across a number of experimental designs that often include secondary tasks. Considering the role of prefrontal structures ascribed to emotion regulation phenomena (Philips et al., 2008; Ochsner and Gross, 2007) the identification of clusters in this region across both face and scene meta-analyses is predictable.

The amygdala has a well-established role in the emotional discrimination of faces and natural scenes (Fusar-Poli et al., 2009; Sabatinelli et al., 2009; Zald, 2001). In both face and scene emotion meta-analyses, bilateral amygdala activation is evident across the entire structure. The greater extent of the amygdala clusters apparent in the emotional face stimuli may be a result of the added role of the amygdala in facial recognition and identification (Davis and Whalen, 2001; Adolphs, 2002).

Emotional scene processing

Listed in Table 3, clusters identified in the meta-analysis that are specifically associated with emotional scene (relative to face) perception include the lateral occipital cortex (LOC), orbitofrontal cortex(OFC),the dorsal anterior cingulate cortex (ACC), and sub-cortical structures including the pulvinar and the medial dorsal nucleus of the thalamus (MDNT).

The lateral occipital cortex (LOC) has been associated with object perception (Grill-Spector et al., 2001) and emotional scene processing (Bradley et al., 2003; Sabatinelli et al., 2004, Sabatinelli, 2007). Both emotional faces and scenes reliably activate posterior extrastriate cortex, yet face-specific areas are centered inferior, and extend anterior to the scene-specific areas, which occupy a broad area of middle and lateral occipital cortex. The role of lateral occipital "complex" in object processing (Grill-Spector et al., 2001; Lerner et al., 2001) is consistent with this distinction between faces and scenes, in that objects are often depicted in scene stimuli, and not included in the controlled backgrounds of posed face photographs.

Both emotional faces and emotional scenes elicited activity in inferior frontal gyrus, yet clusters associated with emotional scene studies are situated more ventrally in what is commonly referred to as orbitofrontal cortex (OFC). The OFC has a well-described role in emotional perception and evaluative processing (Cardinal et al., 2002;

Table 3
Clusters derived from meta-analysis of emotional scene>neutral scene contrasts.

x	*y*	*z*	Structure
−4	52	31	Medial Prefrontal Ctx
36	25	−3	R Orbitofrontal Ctx
−38	25	−8	L Orbitofrontal Ctx
2	19	25	Anterior Cingulate
22	−3	−17	R Amygdala
−20	−6	−17	L Amygdala
0	−15	10	MDN Thalamus
−2	−31	−7	Pulivinar
59	−44	9	R Superior Temporal Gyrus
40	−54	−12	R Fusiform Gyrus
−28	−70	−14	L Fusiform Gyrus
46	−68	−4	R Lateral Occipital Ctx
−48	−72	−4	L Lateral Occipital Ctx

MNI coordinates and structure of clusters identified in the 57-study meta-analysis of emotional scene studies.

Phillips et al., 2003; Rolls, 2004), and its contribution to the processing of emotional information contained in natural scenes is consistent with the literature. Inferior frontal clusters associated with facial emotion studies is also well supported in the literature (Adolphs, 2002; Haxby et al., 2002), however the superior and lateral location of the bilateral clusters relative to those associated with emotional scene studies is as yet undocumented. Clarifying the possibility of emotional stimulus specificity in OFC/inferior frontal gyrus regional activation will necessitate explicit experimental designs.

Emotional scene studies led to activity in a dorsal region of the anterior cingulate cortex (ACC) that falls in a transition area between hypothesized 'emotional' and 'cognitive' subsections (Bush et al., 2000). Again, this region of cortex is well documented in emotional tasks. Considering the early reports of ACC involvement in facial emotional tasks (Morris et al., 1998; Blair et al., 1999), it is unexpected that meta-analysis of 100 emotional face studies did not yield a cluster of ACC activity.

The pulvinar of the thalamus plays a critical role in visual scene discrimination (Desimone et al., 1990; Michael and Desmedt, 2004; Snow et al., 2009). It receives input from visual cortex (e.g.: V1 and extrastriate cortex) and is connected with the prefrontal cortex, posterior parietal cortex, and superior colliculus (Shipp, 2003). Demanding visual tasks such as attention shifting (Yantis et al., 2002), spatial selective attention (Kastner et al., 2004; LaBerge and Buchsbaum, 1990) and complex visual discrimination (Cotton and Smith, 2007) consistently activate the human pulvinar. Thus the current identification of pulvinar recruitment during emotional scene processing is consistent with the perceptual distinctions between homogeneous face stimuli, and heterogeneous scene stimuli.

The meta-analysis of emotional scene processing studies led to a cluster of activation in the medial dorsal nucleus of the thalamus (MDN). The MDN shows strong connectivity to the bilateral dorsolateral prefrontal cortex, the superior temporal gyrus, and occipital regions, are as hypothesized to function as a thalamo-cortico-thalamic loop of the lateral orbitofrontal and dorsolateral prefrontal cortices (Buchsbaum et al., 2006), and thus may represent a component of sensory-planning integration. The MDN is also associated with "selective engagement" and attention, and has a close linkage to visuospatial deficits present in schizophrenia (Crosson, 1999; Mitelman et al., 2005).

Location vs. effect size meta-analysis

The activation likelihood estimation (ALE) is a coordinate-based meta-analysis method. With this method, each study in the analysis is summarized by a set of locations of peak activations. Relative to image-based meta-analysis, in which the complete original datasets or statistical maps are required, the ALE method is much more practical, as the input data can be easily obtained from published reports. However, the simple coordinate locations offer considerably less information (Salimi-Khorshidi et al., 2009), which cannot be quantified. We cannot control for the chosen statistical method or thresholding technique across studies, and it is difficult to gauge the influence of this limitation on the results of the meta-analyses. We can only hope that the large number of studies included here will serve to compensate for the variability of individual study methods, and enable meaningful interpretation.

Unequal study contribution/variance

Although our selection criteria identified a large number of studies employing faces and scenes, a greater proportion of reports (60%) used face stimuli. To ensure that the differences in cluster location across face and scene meta-analyses were not an artifact of the unequal number of contributed coordinate points, a second ALE analysis was conducted using a randomly chosen subset of face studies that equaled that number of scene studies. The results of this subsampled face meta-analysis were highly consistent with the total sample comparison, and thus the apparent differences across face and scene meta-analyses reported here is not an artifact of the greater number of available studies using face stimuli.

Stimulus heterogeneity/homogeneity

One inherent issue in the comparison of these two types of visual stimuli is the homogeneity of faces relative to scenes. By design, image sets of expressive faces are composed to minimize variation across exemplars. For example, the orientation and visual angle of the face in the photograph is held constant. Natural image sets depict a range of content reflecting the variability of our natural environment, and thus are inherently heterogeneous. Therefore the brain activity that might be evoked by these types of stimuli will differ in range as well as pattern. In the ALE method, adjacent or overlapping activation foci lead to higher overall value of activation likelihood in the union of all foci in the final ALE map. Therefore, when comparing the resulting probability distribution to the null distribution, unions calculated from nearby foci are more likely to meet the threshold for significance. As face stimuli are by design consistent in their composition, they likely elicited similar patterns of activation in the brain, whereas heterogeneous scene stimuli might be expected to show more distributed patterns of activation. Ultimately, therefore, the meta-analyses presented here will demonstrate both the brain areas that are unique to processing emotional faces and emotional scenes, as well as differences that may result from the increased perceptual heterogeneity of natural scenes, relative to face stimuli.

Discrimination of facial emotion vs. emotional perception

Another issue that may complicate the comparison of emotional face and scene processing is the communicative role of facial expressions. The expressive face is a social signal, meant to convey the state of the sender, as well as alert the receiver to motivationally relevant events or contexts (Adolphs, 2002). Scene processing is more unilateral, observational, and while humans are certainly commonly included in the composition of emotionally arousing scenes, the interaction is indirect, and the social aspect is secondary. This distinction may moderate the interpretation of differences in brain activation evoked by emotional faces and scenes.

In summary, the meta-analyses of emotional activity elicited by expressive faces and natural scenes resulted in extensive overlap in clusters, coupled with offset and unique regions of reliable activity. The area of greatest overlap is the amygdala, followed by regions of medial prefrontal cortex, inferior frontal/orbitofrontal cortex, inferior temporal cortex, and extrastriate occipital cortex. Emotional face-specific clusters were identified in regions known to be involved in face processing, including anterior fusiform gyrus and middle temporal gyrus, and emotional scene studies were associated with lateral occipital cortex, as well as pulvinar and the medial dorsal nucleus of the thalamus. One global result of the meta-analysis reveals that a class of visual stimuli (faces vs. scenes) has a considerable impact on the resulting emotion effects, even after removing the basic visual perception effects through subtractive contrasts. This highlights a potential area of misinterpretation of subtractive fMRI data; even after contrast with a well-chosen control for simple perceptual processing (a neutral face with an emotional face, a neutral scene with an emotional scene), media-specific activation may remain. This activation could be interpreted as reflecting purely emotional information—while in fact the particular location of activation in part reflects the researcher's choice of stimuli. Pure effects of emotion may thus be difficult to identify for a particular class of stimuli employed in an experimental paradigm. Whether a researcher chooses to tightly control the various elements of the emotional stimuli, as with posed face photographs, or allow variety and environmental realism into their evocative stimuli, as with natural scenes, will depend on the desired generalizability of their results. Moreover, activation data resulting from control condition contrasts should be conservatively interpreted as independent from the underlying media of presentation.

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