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Can theories of visual representation help to explain asymmetries in amygdala function?

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Abstract Emotional processing differs between the left and right hemispheres of the brain, and functional differences have been reported more specifically between the left and right amygdalae, subcortical structures heavily implicated in emotional processing. However, the empirical pattern of amygdalar asymmetries is inconsistent with extant theories of emotional asymmetries. Here we review this discrepancy, and we hypothesize that hemispheric differences in visual object processing help to explain the previously reported functional differences between the left and right amygdalae. The implication that perceptual factors play a large role in determining amygdalar asymmetries may help to explain amygdalar dysfunction in the development and maintenance of posttraumatic stress disorder.

Keywords Amygdala · Visual cortex · Emotion · Hemisphere · Laterality

The cerebral hemispheres differ in their processing of emotional information, and modern neuroimaging techniques have begun to explore precisely which neural structures are involved in these hemispheric asymmetries. The amygdalae are subcortical structures located bilaterally in the temporal lobes that play roles in diverse emotional processes (Zald, 2003). Recently, several meta-analyses of amygdalar activation have confirmed that the left and right amygdalae function differently, but these findings were not consistent with previous theories for emotional asymmetries in general, or with previous theories of amygdalar asymmetries in particular (Table 1). We propose that bottom-up perceptual processes heavily influence the amygdalae, and that hemispheric asymmetries in visual object processing can help to provide a parsimonious explanation of amygdalar asymmetries.

This review is organized into five sections: In the first section, we review differences in emotional processing between the two cerebral hemispheres (including the amygdala). The second section reviews functional asymmetries specific to the amygdalae, and the third reviews hemispheric asymmetries in visual object processing. In the fourth section, we describe ways in which visual object processing asymmetries may help to explain the amygdalar asymmetries, and the final section provides an example of how a consideration of perceptual factors can provide insight regarding amygdalar *dys*function in posttraumatic stress disorder (PTSD).

Theories of emotion asymmetry

Emotional asymmetries in humans

For a century, researchers have hypothesized that the left and right hemispheres of the brain process emotion differently (Mills, 1912, cited in Murphy, Nimmo-Smith, & Lawrence, 2003). Three major theories have been proposed to characterize the differences in emotional processing between hemispheres in humans: right-hemisphere dominance, valence lateralization, and motivation lateralization.

Right-hemisphere dominance theory The earliest theories of emotional lateralization proposed that the right hemisphere (RH) is more efficient at affective processing than the left hemisphere (LH), providing a complement to the LH’s language and “cognitive” abilities (Harrington, 1995). A variety of experimental paradigms and measures have been used to provide evidence for the RH dominance theory. For

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Table 1 Previous descriptions of functional hemispheric asymmetries in the human amygdalae

Asymmetry Type	Left Amygdala Function	Right Amygdala Function	Reference(s)
Language-related	Activated by language-based stimuli	Activated by image-based stimuli	Markowitsch (1998), Gläscher and Adolphs (2003)
Language-related	Verbally instructed threat	Image-apparent threat	Phelps et al. (2001)
Masking-related	Detailed, sustained analysis	Shallow, rapid analysis	Markowitsch (1998), Gläscher and Adolphs (2003)
Masking-related	Used for explicit/conscious evaluation of emotion	Used for implicit evaluation of emotion	Markowitsch (1998), Gläscher and Adolphs (2003)
Habituation-rate	Slow neural habituation	Fast neural habituation	Wright et al. (2001)
Gender-related	More active in females	More active in males	Cahill (2006)

example, the left half of a face—whose musculature is controlled by the right hemisphere—is more expressive (Sackeim, Gur, & Saucy, 1978), affective prosody in speech is more easily detected when presented to the left ear (hence, mostly to the RH) than to the right ear (hence, mostly to the LH; Erhan, Borod, Tenke, & Bruder, 1998), and emotional stimuli elicit stronger physiological responses when presented to the left visual field (LVF; hence, directly to the RH) than to the right visual field (RVF; hence, directly to the LH; Spence, Shapiro, & Zaidel, 1996).

Valence lateralization theory Eventually, evidence accumulated that the LH also plays a prominent role in emotional processing. The valence lateralization theory asserts that the LH is more efficient at processing positively valenced affect than is the RH, and that the RH is more efficient at processing negatively valenced affect than is the LH (Davidson, 1992). Lesions of the LH prefrontal cortex (PFC) or LH basal ganglia correspond to an increased likelihood of depressive symptoms (Morris, Robinson, Raphael, & Hopwood, 1996), whereas a lesion of the RH frontal operculum (Starkstein et al., 1989), a complete RH hemispherectomy, or lesions to unspecified locations in the RH (Sackeim et al., 1982) increase the likelihood of cheerfulness and euphoric symptoms. Similarly, in nonlesioned patients, individual differences in threat sensitivity are positively associated with resting-state neural activity, as indexed by the inverse of alpha-band electroencephalography (EEG) at right anterior electrodes (Coan & Allen, 2004; Sutton & Davidson, 1997). Source-estimate analysis has indicated that this EEG effect is due to activation of right dorsolateral PFC (dlPFC; Shackman, McMenamin, Maxwell, Greischar, & Davidson, 2009). Conversely, individual differences in reward sensitivity are positively associated with neural activity at left anterior electrodes (Coan & Allen, 2004; Sutton & Davidson, 1997), which are presumably linked to activation within left PFC. Finally, divided-visual-field paradigms—which use lateralized stimulus presentation to facilitate processing in the RH (via brief presentation in the LVF) or LH (via brief presentation in the RVF)—have provided behavioral evidence that the speed with which either hemisphere processes positively or negatively valenced emotional images is consistent with valence lateralization (Davidson, Mednick, Moss, Saron, & Schaffer, 1987; Maxwell, Shackman, & Davidson, 2005).

Motivation lateralization theory More recently, the valence lateralization theory has been modified to a *motivation* lateralization theory, by which the LH is more efficient at processing approach-related affect and the RH is more efficient at processing withdrawal-related affect (Harmon-Jones, 2003). This theory is largely indistinguishable from the valence lateralization theory, because approach and withdrawal behaviors are typically elicited by stimuli with positive and negative valences, respectively. However, Berkman and Lieberman (2010) deconfounded stimulus valence and motivation with a novel task in a functional magnetic resonance imaging (fMRI) study. Their participants read about the fictional *Nochmani* culture, in which people enjoy eating insects but are disgusted by eating meat, and then categorized pictures of food as edible or inedible to the *Nochmani*. In this task, the stimuli could have a positive valence to the participant but evoke a withdrawal action (e.g., indicating that a pleasing picture of meat is inedible) or have a negative valence and an approach response (e.g., indicating that a displeasing picture of an insect is edible). Activation in left dlPFC was greater for trials that emphasized approach-related behavior (i.e., “edible” objects, regardless of valence), and activation was stronger in right dlPFC for trials that emphasized withdrawal-related behavior (i.e., “inedible” objects, regardless of valence), supporting the motivation lateralization theory. Additional support for the motivation lateralization theory has come from studying anger, because it is negatively valenced but *approach* related. An association between RH function and anger would provide evidence for the valence lateralization hypothesis; however, Harmon-Jones (2004a, b) reported that anger was associated with LH EEG activity, providing evidence that the asymmetries in emotional function are more closely linked to motivation than to valence.

Emotional asymmetries in nonhumans

The lateralization of affective processes is not unique to humans or primates. Pigeons (Güntürkün & Kesch, 1987), chicks (Rogers, 2000), black-winged stilts (Ventolini et al., 2005), and several species of toad (Robins & Rogers, 2004; Vallortigara, Rogers, Bisazza, Lippolis, & Robins, 1998) are more likely to initiate feeding behaviors for food stimuli processed in the LH. Conversely, toads (Lippolis, Bisazza, Rogers, & Vallortigara, 2002; Vallortigara et al., 1998), chameleons (Deckel, 1998), chicks (Rogers, 2000), and baboons (Casperd & Dunbar, 1996) are more likely to exhibit defensive behaviors when threats are processed in the RH.[1]

This particular pattern of emotional asymmetry is found in quite diverse species, suggesting that it provides an important general benefit and is not a peculiarity of the primate cortex that may be attributable to a specific environmental niche or language abilities. However, one could question how asymmetrically organized emotional systems are capable of benefiting an organism. In fact, one may intuit that a brain with highly lateralized emotional systems would perform suboptimally because, for example, it diminishes the reward responsiveness in one visual field and threat responsiveness in the other. However, Güntürkün et al. (2000) reported that pigeons with greater visual-field asymmetries for feeding (i.e., better performance distinguishing grain from grit when using the RVF/LH than the LVF/RH) were also more efficient at foraging. This suggests that pigeons with less lateralization in feeding behaviors were less efficient at foraging overall. Rogers, Zucca and Vallortigara (2004) manipulated the degree of brain lateralization in chicks by varying their exposure to light or dark prior to hatching—the chick embryo is positioned such that the left eye is occluded late in development, and exposure to light at this time results in stronger lateralization. The light-exposed chicks were more efficient at foraging and more accurate at detecting a predator while foraging. This indicates that lateralization facilitates foraging behavior *and* facilitates the simultaneous operation of approach- and withdrawal-related processes (e.g., foraging for food while remaining vigilant to threat).

Asymmetries in amygdala activation

There is support for all three of the major theories of emotional asymmetry, so it is important to determine which regions of the brain may be responsible for which asymmetry patterns. Simply specifying that a process differs between the left and right hemispheres does not provide a desirable level of anatomical specificity, given that meta-analysis of neuroimaging studies can identify asymmetries in emotional processing in specific brain regions within each hemisphere (Wager, Phan, Liberzon, & Taylor, 2003). Particular emphasis has been placed on exploring the asymmetries in the amygdala because of its involvement in many emotional processes (Zald, 2003). The amygdala's reputation as a "fear center" or "threat detector" would imply greater involvement in processing negative affect and/or withdrawal-related behavior, so each of the three aforementioned theories of emotional asymmetry should predict relatively greater responsiveness of the RH amygdala than the LH amygdala. However, neuroimaging meta-analyses have indicated that effects are reported more frequently within the *left* than the right amygdala (Fusar-Poli et al., 2009; Murphy et al., 2003; Wager et al., 2003). If traditional theories of emotional asymmetries fail to explain differences in functional activity between the two amygdalae, what could provide an explanation?

Hypotheses for hemispheric asymmetries in amygdalar function

Previous hypotheses of functional differences between the left and right amygdalae (Table 1) can be grouped into four general families: language-related differences, masking-related differences, habituation-rate differences, and gender effects. It is important to note that these hypotheses are not mutually exclusive, and some researchers have suggested that asymmetries are actually due to a combination of these differences (Gläscher & Adolphs, 2003; Markowitsch, 1998).

Language-related differences One hypothesis is that the left amygdala is more responsive than the right amygdala to stimuli requiring linguistic processing (Markowitsch, 1998). This would imply that the left amygdala is more easily activated by written or spoken words and by initiating an emotional response to stimuli whose emotional value was learned linguistically rather than through experience. Phelps et al. (2001) instructed participants that a particular stimulus was predictive of future punishment, and they found that this instructed-threat stimulus evoked greater activity in the left amygdala, in contrast to traditional fear-conditioning studies that have implicated regions throughout the RH (Hugdahl, 1995).

Masking-related differences Markowitsch (1998) also proposed that the left amygdala is involved in "explicit,

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[1] Some reports have indicated an RH benefit for approach-related behaviors that require the discrimination of conspecifics, such as agonistic contact in toads (Vallortigara et al., 1998) and courtship behavior in black-winged stilts (Ventolini et al., 2005). The subsequent sections will provide an account of how this may occur because of an RH perceptual benefit for discriminating object exemplars (i.e., conspecifics).

language-related or feature-extracting processes" and that the right amygdala is involved in "imagery-related, pictorial and fast or shallow" processing (Markowitsch, 1998, p. 240). These functional differences could be described generally as a difference in the temporal characteristics of processing, in that the left amygdala is involved with slower processes and the right amygdala is involved with faster processes. This is consistent with lesion data in which damage to the left amygdala reduced the correlation between the skin-conductance response (SCR) magnitudes of the concious rating of an image's arousal, whereas damage to the right amygdala was associated with reduced SCR to simply viewing emotional images (Gläscher & Adolphs, 2003). This theoretical account proposes that the left amygdala is more involved with slower, explicit emotion appraisal processes, and that the right amygdala is more involved with faster, implicit "threat detection" types of processes. A common experimental manipulation for testing the temporal characteristics of processing is to limit the processing time for a stimulus by applying a mask. The right amygdala is more active than the left amygdala for emotional visual stimuli that have been masked to limit concious awareness and/or explicit processing (Morris, Öhman, & Dolan, 1998, 1999).

Habituation-rate differences An alternative explanation is that different rates of neural habituation occur for the two amygdalae. Wright et al. (2001) repeatedly presented the same emotionally expressive face (happy or fearful) to participants in an fMRI scanner and measured the evoked amygdalar response as a function of stimulus repetition. The activity evoked by the fearful face relative to the happy face did not change with repetition in the left amygdala, whereas the evoked fearful response decreased with repetition in the right amygdala (i.e., the response habituated). It may be important to note that this study used facial stimuli exclusively, which rely more on RH representation (Haxby, Hoffman, & Gobbini, 2000; Herrington, Taylor, Grupe, Curby, & Schultz, 2012), so the absence of left amygdala habituation could be attributed to a less robust perceptual input from ipsilateral visual areas. Moreover, the habituation was not linked to a behavioral or physiological change, making the interpretation difficult. If the physiological arousal evoked by the stimulus did not change after habituation, the implication would be that the right amygdala was developing a more efficient representation for a frequently encountered stimulus. Alternatively, if arousal decreased during the habituation, additional tests would be necessary after a period of rest to determine whether the effect was due to a transient fatigue effect or a more permanent "unlearning" of emotional significance.

Gender-based asymmetries Finally, amygdalar asymmetries may depend in part on gender (Cahill, 2006). In females, the left amygdala is activated more than the right amygdala at rest (Kilpatrick, Zald, Pardo, & Cahill, 2006) or during the encoding of emotional memories (Cahill et al., 2001), and the converse is true for males. Savic and Lindström (2008) extended this finding by demonstrating an interaction with sexual orientation. Heterosexual females and homosexual males have greater resting-state connectivity between the left amygdala and outside areas than between the right amygdala and outside areas, whereas heterosexual males and homosexual females have greater resting-state connectivity between the right amygdala and outside areas than between the left amygdala and outside areas. This pattern of different amygdala lateralizations for males and females has also been found in rats (Sullivan, Dufresne, & Waldron, 2009).

Meta-analyses of amygdalar asymmetries

Several meta-analyses of neuroimaging results have been performed, and they can be used to test which theories of amygdalar asymmetry are supported by the body of published neuroimaging data. The number of studies, the meta-analytic techniques, and the statistical tests have differed for each report, so the methods and results from each meta-analysis are reviewed separately.

Wager et al. (2003) This meta-analysis did not focus specifically on the amygdala or the theories of emotional asymmetry listed in Table 1, but it did pioneer the use of meta-analysis of neuroimaging results to investigate emotional processes. It used a vote-counting technique to determine the relative frequencies of significant effects in 65 fMRI and PET studies. Vote-counting is a simple technique for meta-analysis, performed by tallying the number of times that researchers report significant activity in a particular brain region, and then testing whether the significant effects are more or less likely under different experimental conditions.

Studies investigating withdrawal-related affect have reported significance more frequently in both amygdalae than have studies investigating approach-related affect. Moreover, studies using withdrawal-related or negative emotional content reported significant activity in the *left* amygdala more frequently than in the right amygdala, contradicting the predictions from the RH dominance, valence lateralization, and motivation lateralization theories. Across all brain regions, males had more lateralized responses to emotional stimuli than did females, but the predicted gender differences in lateralization were not found between the amygdalae per se. Rather, the sublenticular area surrounding the amygdala demonstrated the rightward asymmetry for males and leftward asymmetry for females predicted by the gender asymmetry theory.

Baas, Aleman and Kahn (2004) This meta-analysis focused specifically on amygdalar asymmetries and tested several of the hypothesized functional differences in Table 1. A total of

54 fMRI and PET studies were analyzed with a vote-counting approach. The stimuli used in each of the experiments were classified as pictorial, language-related, or "other" (i.e., memory recall or nonlinguistic sounds) to test the role of linguistic content on each amygdala. The uniformity of stimuli was used to test the effects of neural habituation—if the same stimuli were repeated over the course of the task, habituation should be greater than in a study in which different stimuli were used. The task demands for each experiment were classified as elaborative if one had to read words to ascertain emotional value, if mood was induced, or if emotional reappraisal was required. Experiments that instructed participants to attend to the emotional aspects of the task were labeled as explicit; otherwise, the experiment was categorized as containing implicitly processed emotion. Baas et al. found no evidence for the language-related, masking-related, or habituation-rate hypotheses. However, they did find that significant amygdalar activation was more frequent in the left amygdala than the right overall, but that none of the differences in experimental stimuli or task parameters affected that asymmetry.

Costafreda, Brammer, David and Fu (2008) The nonsignificant effects reported for most factors on amygdalar asymmetries in Wager et al. (2003) and Baas et al. (2004) may have been due to methodological factors that limited statistical power. Costafreda et al. performed a more sensitive meta-analysis by expanding the corpus of data to include 385 fMRI and PET studies and using a logistic regression to test for differences in the probabilities of significant effects. This regression approach is a significant improvement over the previous methods, because it accounts for the relationships between experimental parameters to reduce potential confounds (e.g., in Baas et al.'s analysis, seven out of ten studies using elaboration also had uniform stimuli). With the benefit of additional studies and this improved methodology, the researchers tested whether stimulus masking or linguistic demands affected the likelihood of asymmetric amygdalar activity. Costafreda et al. found that activation was more likely in the left amygdala than the right, consistent with an overall LH amygdala bias. But if visual stimuli were masked to limit explicit or sustained processing, the right amygdala was more likely to be activated than the left. If linguistic stimuli were used (i.e., the stimuli were written words, spoken, or internal dialogue), the left amygdala was more likely than the right to be activated.

Sergerie, Chochol and Armony (2008) The previous meta-analyses relied on vote counting, which is used to measure how certain experimental parameters affect the likelihood of statistical significance, but not how experimental parameters affect the *strength* of activation (i.e., effect size). Sergerie, Chochol, and Armony performed a meta-analysis to replicate those of Wager et al. (2003) and Baas et al. (2004) with a larger corpus of data (148 fMRI and PET studies); however, they replaced the vote-counting technique with an approach that compared effect sizes across studies.

First, significant effects were overall more likely in the left amygdala than in the right, consistent with the previous meta-analyses. However, the *effect sizes* did not differ between the left and right amygdalae. Second, a comparison of blocked and event-related designs indicated hemispheric differences in amygdalar activation: Significant activity was reported more frequently in the left than in the right amygdala when using blocked designs, but not when using event-related designs. This may suggest different effects of task set on the two amygdalae, because blocked designs require less task or process switching over time than do event-related designs. Alternatively, event-related designs may minimize the opportunity for slow and sustained activation in the left amygdala. Third, language-related stimuli evoked marginally stronger effects in the left amygdala than did pictorial stimuli, consistent with the analyses by Costafreda et al. (2008). Finally, a positive correlation between the effect size of amygdala activation and the proportion of the participants who were male suggested that amygdala activation is strong in males, even though statistically significant effects were not more common in studies with a higher proportion of males. However, no tests of gender-based lateralization were reported.

Summary of amygdalar meta-analyses

LH bias in amygdala activation The meta-analyses have indicated that reliable differences exist in activation of the left and right amygdalae (summarized in Table 2), but the only consistent finding across all of the meta-analyses was that significant effects were more common in the left than in the right amygdala overall (Baas et al., 2004; Costafreda et al., 2008; Sergerie et al., 2008; Wager et al., 2003; for additional evidence, see also Fusar-Poli et al., 2009; Murphy et al., 2003). This is inconsistent with the RH dominance theory of emotion asymmetry, and several of the analyses performed specific tests to demonstrate that the activation of the amygdalae are not consistent with the valence or motivation lateralization theories (Sergerie et al., 2008; Wager et al., 2003).

Language-related asymmetries Costafreda et al. (2008) and Sergerie et al. (2008) concluded that LH amygdala activity was more likely than RH amygdala activity during language-based emotional processing, consistent with the hypotheses formed by Markowitsch (1998) and Gläscher

Table 2 Summary of neuroimaging meta-analyses of hemispheric asymmetries in amygdalar function

Meta-Analysis	Found Evidence for Language Differences	Found Evidence for Masking Differences	Found Evidence for Habituation-Rate Differences	Found Evidence for Gender Effects	Found Evidence for a Left Amygdala Bias
Wager et al. (2003)				✓	✓
Baas et al. (2004)					✓
Costafreda et al. (2008)	✓	✓			✓
Sergerie et al. (2008)	✓		✓		✓

and Adolphs (2003). The tests of language-based effects in these meta-analyses were restricted to experiments in which a participant read or listened to words; thus, these findings are also informative that experiments with verbally instructed threats result in greater left than right amygdala activity (Phelps et al., 2001).

Masking-related asymmetries Costafreda et al. (2008) reported that masking a visual stimulus resulted in a greater likelihood of activation of the right than of the left amygdala. This suggests that masks that degrade the stimulus or limit the amount of time available for processing disrupt activation in the right amygdala to a lesser degree than activation in the left amygdala.

Habituation-rate asymmetries The Baas et al. (2004) analysis tested whether the use of repeated stimuli affected amygdalar asymmetries, but it did not reveal a significant effect. However, Sergerie et al. (2008) reported that blocked designs, in which amygdalar processing would be sustained in emotional conditions, evoke more activity from the left amygdala than from the right. This is consistent with the prediction that the activity in the right amygdala habituates more rapidly than activity in the left amygdala when habituation is enabled by a blocked design.

Gender-based asymmetries Wager et al. (2003) provided evidence of gender differences in amygdala lateralization consistent with those hypothesized by Cahill (2006; Cahill et al., 2001): Females exhibit more activity near the left amygdala, and males exhibit greater activity near the right amygdala. The only other meta-analysis to address gender effects did not test whether gender interacted with amygdala lateralization (Sergerie et al., 2008). However, this should not be interpreted as evidence against the existence of gender-based asymmetries in amygdala functioning. The gender-based amygdala asymmetry has generally been reported in studies of long-term memory, so it may be inappropriate to expect it to appear in a general meta-analysis. Moreover, the effect may have been obscured by experiments that did not explicitly account for important variables relevant to the gender effect (e.g., sexual orientation; see Savic & Lindström, 2008).

Conclusions

This review has indicated that amygdala activation does not correspond to any of the traditional theories of hemispheric asymmetry for emotion (i.e., RH dominance, valence lateralization, or motivation lateralization). However, partial support was found for each of the hypothesized functional differences between the amygdalae (i.e., language-related, masking-related, habituation-rate, and gender differences), and a strong consensus indicated that the left amygdala is more frequently activated than the right overall. An unparsimonious explanation for these findings would be that several hypotheses could each be credited with partially explaining some of the observed asymmetries. Alternatively, in the rest of this article, we will propose a unifying hypothesis: Specifically, hemispheric asymmetries in perceptual processing may be responsible for hemispheric asymmetries in the amygdalae, in a manner that may provide a parsimonious explanation for the observed results.

Asymmetries in visual object processing

The human amygdalae process information from most sensory modalities (Zald, 2003), mapping perceptual inputs to affective values (Rolls, 2005); however, they are particularly responsive to visual input (Phan, Wager, Taylor, & Liberzon, 2002). Visual information enters through the basolateral nucleus of the amygdala (BLA) via projections from the thalamus and the anterior portion of inferotemporal cortex (IT; Freese & Amaral, 2009), and the medial portion of the BLA projects back onto the ventral visual stream to modulate ongoing processing (Freese & Amaral, 2009; Sabatinelli, Lang, Bradley, Costa, & Keil, 2009; Vuilleumier, 2005). The BLA receives most visual input from the ipsilateral hemisphere (McDonald, 1998), so the existence of a hemispheric asymmetry in the ventral visual stream's perceptual representations could easily manifest itself "downstream" in the amygdala. This section reviews asymmetries in visual object processing, and the subsequent section describes how these asymmetries may account for the observed functional differences between the left and right amygdalae.

Hemispheric asymmetries in recognizing categories and identifying exemplars

Object perception is complicated by the conflicting demands to be able to both categorize and individuate objects effectively. In many situations, the ability to recognize the abstract category to which a visual object belongs is important (e.g., when scanning a desk to quickly find a pen to write with). In other situations, the ability to identify the specific exemplar to which a visual object corresponds is paramount (e.g., when trying to find the individual pen that was a gift from a friend). These abilities place contradictory demands on the visual system. For efficient abstract category recognition, it is useful to learn the visual features that maximize *between-category* variations, and minimize within-category variations. In contrast, for efficient specific exemplar identification, it is useful to learn the visual information that maximizes *within-category* variation for distinguishing exemplars.

A resolution to the contradictory demands would allow dissociable neural subsystems to underlie the abilities to abstractly categorize objects and to specifically identify exemplars (Marsolek, 1999, 2004; Marsolek & Burgund, 1997, 2008). An abstract-category subsystem operates more effectively in the LH than in the RH, and a specific-exemplar subsystem operates more effectively in the RH than in the LH. This pattern of asymmetries has been observed in divided-visual-field experiments (e.g., Marsolek, 1999; Marsolek & Burgund, 2008; Marsolek, Nicholas, & Andresen, 2002), fMRI studies (Koutstaal et al., 2001; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003), performance following unilateral brain damage (e.g., Beeri, Vakil, Adonsky, & Levenkron, 2004; Vaidya, Gabrieli, Verfaellie, Fleischman, & Askari, 1998), differential effects of the neuromodulator serotonin (Burgund, Marsolek, & Luciana, 2003), and selective disruption via repetitive transcranial magnetic stimulation (Pobric, Schweinberger, & Lavidor, 2007). It is important to note that these asymmetries in visual category recognition and exemplar identification can affect the object representations used by other cognitive processes. For example, the visual asymmetries extend to how categories and exemplars are stored in working memory (Marsolek & Burgund, 2008).

Parts-based and whole-based processing strategies

The abstract-category (AC) and specific-exemplar (SE) subsystems utilize different processing strategies to accomplish their different goals. To effectively categorize objects, an abstract-category subsystem uses a parts-based processing strategy to represent the smaller features of larger whole objects that are diagnostic of an object's category, even when visually dissimilar objects belong to the same category (Marsolek, 1995; Marsolek & Burgund, 2003). In contrast, to effectively individuate objects, a specific-exemplar subsystem uses a whole-based strategy to represent the visually distinctive whole configurations that distinguish even very similar objects (Marsolek & Burgund, 2003; Marsolek, Schacter, & Nicholas, 1996).

A virtue of this theory is that both relatively parts-based and relatively whole-based representations are posited, because both kinds of representations enable benefits for different purposes. It has been argued that the two kinds of representations provide two complementary methods for representation in any system, with the parts-based strategy enabling effective generalization to novel objects, and the whole-based strategy enabling effective discrimination of similar inputs (Hummel, 2000, 2003). In addition, the effects of expertise have been investigated in studies in which participants learn new categories of preexperimentally novel artificial figures (e.g., Greebles). After expertise has been gained for effectively distinguishing visually similar shapes, whole-based representations are used that enable greater automaticity in performance (Gauthier & Tarr, 1997, 2002; Gauthier, Williams, Tarr, & Tanaka, 1998). The neuroimaging evidence supports the hypothesis that the two kinds of representations are asymmetric. Attending to local image features (i.e., to the small parts in hierarchical figures, such as the small letter Ss that form a larger letter H) increases activity in the LH, but attending to global image features (i.e., to the wholes in hierarchical figures, such as the larger letter H that is formed by small letter Ss) increases activity in the RH (Fink et al., 1996; Han et al., 2002).

Effects of stimulus masking

The effects of stimulus degradation (e.g., masking) on object processing are more pronounced in the LH than in the RH (Christman, 1989; Sergent & Hellige, 1986), which may be related to the different representational strategies used by the AC and SE subsystems. The whole-based representations used in a SE subsystem are more distributed than the parts-based representations used in an AC subsystem (Marsolek & Burgund, 1997), which could confer greater robustness to stimulus noise and degradation to the representations in the RH (Marsolek & Burgund, 2003). Repetition-priming effects measured in a divided-visual-field paradigm support the hypothesis that an AC subsystem operates more effectively in the LH than in the RH, and this asymmetry is influenced by stimulus degradation (Marsolek, 1999; Marsolek & Hudson, 1999). Moreover, an effect similar to masking and stimulus degradation may occur in situations in which attention is heavily restricted. Consistent with the findings that the LH is more sensitive than the RH to stimulus degradation, priming within an AC subsystem is reduced when attention is directed away from the prime stimulus, relative to when attention is directed toward the prime stimulus (Hummel, 2000, 2003; Stankiewicz & Hummel, 2002; Stankiewicz, Hummel, & Cooper, 1998).

Relationship between visual and amygdalar asymmetries

Processing in sensory cortices can be modulated by emotional factors (Curby, Johnson, & Tyson, 2012; Diamond & Weinberger, 1986; Edeline & Weinberger, 1992; Maxwell, Shackman, McMenamin, Greischar, & Davidson, 2011; Vuilleumier, 2005), and perceptual factors are relevant to understanding emotional processes (Larson, Aronoff, Sarinopoulos, & Zhu, 2009; Larson, Aronoff, & Stearns, 2007; McMenamin et al., 2012; Vuilleumier, Armony, Driver, & Dolan, 2003). Despite the reciprocal influences between emotional and perceptual systems, relatively few attempts have been made to connect the hemispheric asymmetries in emotion to the hemispheric asymmetries in perception.

Kensinger and Choi (2009) presented emotional and nonemotional object images in the left and right visual fields and then tested memory for the objects in a surprise memory test. Combining the observed asymmetries for processing visual object categories and exemplars with the asymmetries for processing affective valence or motivation, one can predict that (a) memory for object exemplars should be greater when they are presented directly to the RH than to the LH, particularly for objects with negative or withdrawal-related emotional value, and (b) memory for object categories should be greater when they are presented directly to the LH than to the RH, particularly for positive or approach-related stimuli. The hypothesized results were found, indicating that asymmetries in object representation and emotional processing interact during memory encoding.

Cahill and van Stegeren (2003) linked gender-based asymmetries in amygdalar function to hemispheric differences in local/global processing by testing whether the way in which emotion modulates memory is relatively more local in females and relatively more global in males. Participants listened to a short, emotion-provoking story accompanied by a slide show, and then their memory for the story was assessed in an unexpected memory test. Memory for local information was assessed as memory for details that were peripheral to the central aspects of the narrative, and memory for global information was assessed as memory for the central aspects of the narrative. Half of the participants received a beta-blocker (a substance that blocks the amygdala’s memory-modulating function) prior to the story to reduce the effect of the emotionality of the stories on memory for them. Relative to a placebo group, the participants in the beta-blocker group exhibited impaired memory for the local information when they were female and impaired memory for the global information when they were male.

These studies connected emotional and perceptual asymmetries, but neither tested the specific question of whether amygdalar asymmetries can be explained by asymmetries in object representation. In a previous section, we reviewed hypotheses of amygdalar asymmetry and grouped them into five families—an overall LH activation bias, language-related effects, masking-related effects, habituation-rate effects, and gender-based asymmetries. Each of these hypotheses was partially supported by neuroimaging meta-analyses. Below, we revisit each of these hypotheses and explore how each may arise because of differences in object representation across hemispheres.

Overall LH bias and language-related asymmetries explained by perceptual input

Emotional associations formed for object categories—which are represented effectively in the LH—may generalize to novel stimuli and situations, whereas emotional associations formed for object exemplars—which are represented effectively in the RH—may not generalize as widely. This may explain why significant activation was reported more frequently in the left than in the right amygdala in all of the meta-analyses. However, Costafreda et al. (2008) specifically reported that *linguistic* stimuli resulted in more frequent activation of the left than of the right amygdala, consistent with a leftward lateralization for the visual analysis of linguistic stimuli (e.g., the visual word-form area; Vigneau, Jobard, Mazoyer, & Tzourio-Mazoyer, 2005). In addition, the perceptual processing of linguistic stimuli is usually categorical in nature, in that the goal is to recognize the word category to which each input belongs, not the specific exemplar to which each input corresponds (e.g., a word in a particular font and style; Marsolek, 2004). Moreover, the activation of the left amygdala for verbally instructed threats (Phelps et al., 2001) may depend on the ability of analytic representations in the LH to effectively generalize to novel (i.e., not previously seen) objects.

Masking-based asymmetries explained by perceptual input

From their meta-analysis, Costafreda et al. (2008) reported that the right amygdala is more frequently activated than the left amygdala in studies in which visual stimuli are masked. This supports the previous hypothesis that the right amygdala is specialized for rapid or implicit emotional processing (Gläscher & Adolphs, 2003; Markowitsch, 1998). The cause of this asymmetry may arise from asymmetries in the effects of stimulus masking during visual object processing. In particular, the finding that stimulus degradation has a greater effect on stimuli presented to the LH than to the RH suggests that masking disrupts visual processing in the LH, and subsequently in the left amygdala, more than visual processing in the RH, and subsequently in the right amygdala.

Habituation-rate asymmetries explained by perceptual input

Different habituation rates have also been hypothesized as being critical for the functional differences between the amygdalae, such that the right amygdala habituates faster than the left amygdala (Sergerie et al., 2008; Wright et al., 2001). Why would this be found? Reduced activation in the amygdalae after repeated stimulus presentation may be a consequence of repetition priming in perceptual systems, which generally manifests as reductions in neural activity (Grill-Spector, Henson, & Martin, 2006). Repetition-priming effects for the SE subsystem are larger behaviorally (Marsolek, 1999) and neurally more widespread (Koutstaal et al., 2001; Simons et al., 2003) than those for the AC subsystem, so the reduced activity in the right amygdala after repeated presentations may be due to a larger degree of suppressed input from RH visual areas. Alternatively, the habituation effects may reflect an unlearning of emotional relevance because reward or punishment is not delivered with the emotional stimulus in a habituation study; less evidence is needed to learn that a particular object exemplar is irrelevant, but learning irrelevance for an entire object category should take longer. Therefore, the observation that repeated stimulus presentation reduces activity in the right, and not the left, amygdala may reflect faster unlearning of threat in a SE subsystem than in an AC subsystem.

Gender-based asymmetries explained by perceptual input

Gender differences in amygdala lateralization were partially confirmed by Wager et al.'s (2003) meta-analysis: Regions surrounding the left amygdala were activated more frequently than regions surrounding the right amygdala in female participants, and vice versa in male participants. As was discussed in Cahill and van Stegeren (2003), this may not reflect differences in amygdala function, but instead reflect different biases toward local and global feature processing in females and males, respectively (Kramer, Ellenberg, Leonard, & Share, 1996; Roalf, Lowery, & Turetsky, 2006). If so, the explanation for gender-based asymmetries is in line with perceptual asymmetries in which parts-based representations are used in an AC subsystem in the LH, and whole-based representations are used in an SE subsystem in the RH. These perceptual asymmetries, combined with different gender biases, may explain the gender-based asymmetries in amygdala activation.

Effects of perceptual asymmetry on posttraumatic stress disorder

If amygdalar function is partially determined by perceptual factors, it is reasonable to explore whether perceptual factors also play a role in amygdalar *dys*function. As an example, this section illustrates how consideration of perceptual factors may help to form novel ideas about the origin and maintenance of PTSD.

PTSD occurs for some individuals following exposure to a traumatic event and manifests itself as a vivid reexperiencing of the trauma (e.g., flashbacks), emotional numbing or avoidance, and hyperarousal (American Psychiatric Association, 2000). A study of Vietnam War veterans with (n = 193) and without (n = 52) head trauma reported that none of the veterans with amygdalar damage (i.e., 0 out of 15) developed PTSD, but 48 % of those without head trauma (i.e., 25 out of 52) did develop PTSD (Koenigs et al., 2007). This suggests that intact amygdalae are critical for the development and/or maintenance of PTSD, complementing reports that indicate increased amygdalar activity at rest and during a variety of cognitive tasks for individuals with PTSD (Bremner, 2007).

The increased amygdalar activity in PTSD may be due to reduced top-down inhibition from the ventromedial prefrontal cortex (vmPFC), corresponding to impaired fear extinction (Koenigs & Grafman, 2009). However, the acquisition and maintenance of PTSD is also dependant on bottom-up associative learning in the amygdalae (Ehlers & Clark, 2000), suggesting a critical role for perceptual representations in the development of PTSD symptoms. This section advances the hypothesis that the overgeneralization of fear responses in PTSD, and possibly in other affective disorders (Lissek et al., 2008; Lissek et al., 2009; Schechtman, Laufer, & Paz, 2010), may be partially explained by an overreliance on the AC object recognition subsystem during the traumatic event.

Parts-based representation for traumatic memory

Traumatic memories are different from typical episodic memories because they are difficult to recall voluntarily, but when triggered, are experienced as a fragmented sensory experience that approximates "reliving" the trauma (i.e., a flashback). These memories are predominately visual and highly disorganized, making them difficult to verbalize until many flashbacks allow the fragmented events to be combined into a coherent narrative (Foa, Molnar, & Cashman, 1995; Koss, Figueredo, Bell, Tharan, & Tromp, 1996; van der Kolk & Fisler, 1995; van der Kolk, Hopper, & Osterman, 2001). The inability to voluntarily recall traumatic memories, and the fact that their content is accurate and stable over time (van der Kolk & Fisler, 1995), distinguish them from "flashbulb memories" for emotional events, which are easily recalled voluntarily, but are often inaccurate and unstable (Talarico & Rubin, 2003).

Experiencing peritraumatic psychological dissociation—described as "a compartmentalization of experience: elements of the experience are not integrated into a unitary whole, but stored in memory as isolated fragments" (van der Kolk & Fisler, 1995, p. 510)—is strongly associated with the strength of subsequent PTSD symptoms (Koopman, Classen, Cardenta, & Spiegel, 1995; Marshall & Schell, 2002). Brewin (2001) proposes two distinct representations for traumatic memory—a situationally accessible memory (SAM) that stores the original, "dissociated" sensory impressions, and a verbally accessible memory (VAM). Flashbacks are triggered whenever a stimulus matches a sensory fragment in the SAM, but the spatial and temporal structure of the SAM contents are learned during flashbacks and stored as more complex, structured memories in the VAM. Eventually, the simple sensory fragments in the SAM that trigger flashbacks are coalesced into more complex memories in the VAM, providing a consciously accessible narrative of the trauma.

The present theory may help to explain these findings. The fragmented quality of traumatic memory and the phenomenology of peritraumatic dissociation suggests that traumatic memories may rely on parts-based perceptual representations with poorly bound features, possibly like those that are normally used in an AC subsystem.

LH involvement in PTSD

Provocation of PTSD symptoms activates the left amygdala more than the right (Liberzon et al., 1999; Shin et al., 2004), and it activates the LH ventral visual stream more than the RH ventral visual stream (Shin et al., 1999). These findings are consistent with the hypothesized overuse of an AC subsystem. Also consistent is the finding that the prevalence of PTSD among females—who have more left-lateralized amygdala function than men (Cahill, 2006)—is roughly twice that of men (Stein, McQuaid, Pedrelli, Lenox, & McCahill, 2000). In addition, fMRI data indicate that females with PTSD have greater LH amygdala activation during the acquisition phase of fear conditioning than do non-PTSD females (Bremner et al., 2005).

Three lines of research seem to provide putative evidence against the importance of the LH for the development of PTSD. First, S. D. Smith, Abou-Khalil and Zald (2008) performed a case study on a single individual who had had her left amygdala lesioned to treat epilepsy, but who developed PTSD after trauma later in life. This study may not invalidate the hypothesis that AC representations are critical for the development of PTSD, because it is unknown whether the typical asymmetrical organization of the AC and SE subsystems was preserved in that single case study after years of severe epilepsy and a unilateral lesion.

Second, deficits in verbal—but not spatial—explicit memory accompany PTSD (Bremner, 2007). Verbal and spatial working memory systems tend to be lateralized to the LH and RH, respectively (E. E. Smith, Jonides, & Koeppe, 1996), so the verbal working memory deficit suggests that LH processing is deficient. One could argue that this LH deficit contradicts the proposed overreliance on LH perceptual representations in PTSD; however, working memory systems can operate independently of the implicit long-term memory systems (Gabrieli, Fleischman, Keane, Reminger, & Morrell, 1995) and the fear memory systems (Bechara et al., 1995) involved in PTSD development.

Finally, PTSD patients sometimes demonstrate changes in right-amygdala activity that correspond to the severity of PTSD symptoms. Rauch et al. (2000) measured amygdalar activity for masked fearful versus happy faces in participants with and without PTSD. Collapsed across groups, a difference in the activity elicited by fearful and happy faces was observed in the left amygdala, but a difference between the PTSD and non-PTSD groups was restricted to the right amygdala. Moreover, the magnitude of the fear-minus-happy effect in the right amygdala correlated positively with PTSD symptom severity. The correlation between symptom severity and right-amygdala function was replicated in two of the aforementioned symptom provocation studies (Liberzon et al., 1999; Shin et al., 2004) and in an fMRI study (Armony, Corbo, Clément, & Brunet, 2005). Armony et al. presented masked or unmasked emotional faces, and the fearful-minus-happy effect in the right amygdala correlated positively with PTSD symptom severity for masked faces; however, the right-amygdala effect for unmasked faces was negatively correlated with symptom severity. These findings may not contradict the proposal that an AC subsystem is critical to the development and expression PTSD; instead, they may illustrate that participants with strong symptoms are likely to show effects bilaterally. And, perhaps more importantly, they may indicate that the use of facial stimuli (which engage more SE processing than do other objects) likely biases the results away from LH involvement.

Serotonergic involvement in the abstract-category system and PTSD

A final link between visual asymmetries and PTSD may be made via the neuromodulator serotonin. According to our hypothesis, provoking PTSD symptoms overactivates the left amygdala in part because the AC subsystem is overused in PTSD patients. Increasing brain serotonin levels helps to treat PTSD symptoms (Hidalgo & Davidson, 2000; Seedat et al., 2002) by reducing amygdalar activity (Harmer, Mackay, Reid, Cowen, & Goodwin, 2006). The reduction in amygdalar activity may be direct or may be due in part to reduced use of the AC subsystem, according to our hypothesis. If so, increasing serotonin levels in normal participants might also decrease the use of the AC subsystem. Evidence in line with this hypothesis has been observed in a repetition-priming study (Burgund et al., 2003). Participants with increased serotonin levels (i.e., tryptophan augmentation) exhibited only SE priming effects, but participants with decreased serotonin levels (i.e., tryptophan depletion) exhibited only AC priming effects. This suggests that overactivation of the left amygdala in PTSD may be alleviated by increased serotonin in part through a reduction of the overreliance on an AC subsystem in the LH.

Future directions

Amygdalar hyperactivation is common for individuals with PTSD, accompanying symptoms that include fragmented, parts-based memories of the trauma and a reliance on LH processing. These symptoms could stem from serotonergic depletions that result in overreliance on parts-based representations in an AC subsystem. Future research will be needed to test whether individual differences in the strength of the AC and SE processing subsystems mediate the relationships between 5-HT, dissociative processing, fragmented traumatic memories, and overgeneralization of fearful stimuli. Testing these hypotheses may help identify additional risk factors, diagnostic tools, and treatment methods for PTSD.

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