Research Report

A ROLE FOR THE HUMAN AMYGDALA IN RECOGNIZING EMOTIONAL AROUSAL FROM UNPLEASANT STIMULI

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Abstract—*Functional neuroimaging and lesion-based neuropsychological experiments have demonstrated the human amygdala's role in recognition of certain emotions signaled by sensory stimuli, notably, fear and anger in facial expressions. We examined recognition of two emotional dimensions, arousal and valence, in a rare subject with complete, bilateral damage restricted to the amygdala. Recognition of emotional arousal was impaired for facial expressions, words, and sentences that depicted unpleasant emotions, especially in regard to fear and anger. However, recognition of emotional valence was normal. The findings suggest that the amygdala plays a critical role in knowledge concerning the arousal of negative emotions, a function that may explain the impaired recognition of fear and anger in patients with bilateral amygdala damage, and one that is consistent with the amygdala's role in processing stimuli related to threat and danger.*

Studies in humans provide strong evidence for neural systems that are specialized for the recognition of certain emotions. Some of the clearest evidence comes from studies of patients with damage to the amygdala, a brain structure long thought to play an important role in emotion. Bilateral amygdala damage disproportionately impairs the recognition of unpleasant emotions, especially fear, in facial expressions (Adolphs, Tranel, Damasio, & Damasio, 1994, 1995; Broks et al., 1998; Calder et al., 1996; Young et al., 1995). These findings are consonant with functional imaging studies in normal individuals, which have shown increased neural activity within the amygdala when subjects are viewing facial expressions of fear (Breiter et al., 1996; Morris et al., 1996).

However, amygdala damage in humans also causes lesser impairments in recognition of highly arousing emotions that are similar to fear, such as anger (e.g., Adolphs et al., 1994, 1995; Young et al., 1995). The data so far are thus compatible both with the idea that there are neural systems specialized for processing specific basic emotions (e.g., fear) and with the idea that there are neural systems specialized for processing highly arousing, unpleasant emotions, of which fear and anger may be two instances. A direct dissociation on the basis of arousal has been demonstrated in rats: Amygdala lesions interfere with avoidance of water that has been paired with electric shock (a highly arousing, unpleasant stimulus), but do not interfere with avoidance of water that has been made to taste bitter (an unpleasant, but not highly arousing stimulus; Cahill & McGaugh, 1990). Also, the amygdala plays a key role in conditioned fear in both humans and rats (Bechara et al., 1995; LeDoux, 1996), as well as in fearful and aggressive behaviors (Davis, 1992; Kling, 1986), further suggesting that the amygdala may be critical to process a class of emotions that are highly arousing and related to threat and danger.

We hypothesized that the human brain contains neural systems specialized to recognize emotional arousal in negatively valenced stimuli, and that the amygdala is one key component of such systems. We tested this hypothesis by asking a rare subject with complete, selective bilateral amygdala damage to rate emotional stimuli explicitly with respect to the two attributes of arousal and valence.

MATERIALS AND METHODS

Subjects

We studied a rare individual, SM046, who has complete, bilateral damage restricted to the amygdala. Her neuroanatomical and neuropsychological profiles have been described in detail (Adolphs et al., 1994, 1995; Tranel & Hyman, 1990). SM046 is a 31-year-old woman with a high school education who has focal bilateral amygdala damage resulting from Urbach-Wiethe disease, a hereditary disease whose phenotype appears in infancy or early childhood.

Twenty-four (for rating faces) or 18 (for rating sentences) normal control subjects were also studied in order to provide normative data on the tasks. All had a high school education, and none had any history of neurological or psychiatric disease (age: 48 ± 15; Verbal IQ of 103 ± 10 on Blair & Spreen's, 1989, National Adult Reading Test–Revised). All participants gave informed consent, and the study was approved by the Human Subjects Committee of the University of Iowa.

Tasks

We asked subjects to rate stimuli on two distinct attributes of emotion: valence (pleasantness-unpleasantness) and arousal. Subjects rated each stimulus on a 9-point scale with respect to the emotion depicted. Our rating instrument consisted of a one-dimensional grid onto which the subject placed an "x"; this was a simplified version of a previously developed rating instrument called the "Affect Grid," which has demonstrated reliability and construct validity (Russell, Weiss, & Mendelsohn, 1989). Subjects were told that for the valence scale, ratings greater than 5 corresponded to feelings that were more pleasant than neutral, and ratings less than 5 corresponded to feelings that were less pleasant than neutral. Similarly, for the arousal scale, subjects were told that ratings greater than 5 corresponded to higher energy-arousal-wakefulness than one's average arousal state, and ratings lower than 5 corresponded to lower energy-arousal or greater sleepiness-relaxation than one's average arousal state. Subjects were told that any given level of arousal could be either a pleasant or an unpleasant emotion.

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Facial expressions of emotion

Subjects were shown 39 slides depicting prototypical expressions of basic emotions (from Ekman & Friesen, 1976). There were 6 slides each for happiness, surprise, fear, anger, disgust, and sadness, and 3 neutral expressions (the stimuli were identical to those used in Adolphs et al., 1994, 1995). Slides were shown in random order, one at a time, without time limit. Subjects were asked to rate how they thought the person in each slide was feeling with respect to both arousal and valence, rated in counterbalanced order. Subject SM046 participated in three replications of this experiment.

Lexical stimuli

Subjects were read 30 sentences (five clear depictions of each basic emotion) and the six words denoting the six basic emotions. All stimuli were read to subjects in a neutral tone of voice. The sentences depicted either a person's actions (e.g., "Jody giggled and laughed") or events (e.g., "Tom's wife and children had all died in the car crash") but did not provide any verbal label of the emotion. Subjects were asked to rate how they thought a person would feel when experiencing the emotion denoted by the given label or when experiencing the given situation of the sentence. Again, subjects rated both valence and arousal. Subject SM046 participated in three replications of this experiment. All subjects were able to name the correct emotion in all sentences.

Discrimination of emotional facial expressions

To investigate SM046's basic visual perception, we assessed her ability to discriminate faint emotional expressions from neutral expressions, for all six basic emotions. This task required two-alternative forced-choice discriminations between 80 pairs of a single neutral face paired with 80 images that were linear morphs between the neutral face and facial expressions of emotion. Percentiles were calculated from the data obtained from normal control subjects (N = 28).

RESULTS

SM046 had no visuoperceptual impairment that might account for her performances on the experimental tasks. Her Performance IQ (Wechsler Adult Intelligence Scale–Revised) was 90, and she had no difficulty perceiving and copying complex visual figures (e.g., Rey Osterrieth complex figure score: 30; normal range: 30 ± 3.4) or matching different views of an individual's face (Benton Facial Recognition task: 71st percentile; Benton, Hamsher, Varney, & Spreen, 1983). She was able to discriminate fine differences between emotional expressions (see Methods) at better than the 60th percentile for all emotions but sadness (40th percentile). She had no impairments in language function (Tranel & Hyman, 1990).

Ratings of Valence and Arousal in Facial Expressions

When shown facial expressions of emotion, normal subjects reliably rated the emotions sadness, anger, disgust, and fear as unpleasant, and happiness as pleasant. Sad and neutral faces received relatively low ratings of arousal, and faces expressing fear, anger, happiness, and surprise received high ratings of arousal. These results are in close agreement with other data from normal subjects (Russell, 1980; Russell et al., 1989).

SM046 rated the valence of emotional facial expressions normally. Her ratings of valence were within 2 standard deviations of the control mean for all six basic emotions. By contrast, she was severely impaired in her ratings of arousal, differing from the control mean by more than 4 standard deviations for certain emotional facial expressions (Fig. 1). We calculated for each face the difference between SM046's arousal rating and the mean rating given to that face by the 24 normal control subjects (Fig. 2). This analysis showed clearly that she assigned abnormally low arousal ratings to negatively valenced emotions. The two negative emotions that control subjects judged to be the most arousing, fear and anger, were given the most abnormal ratings by SM046. The specificity of the impairment is especially striking when comparing pleasant and unpleasant emotions that are both highly arousing. For example, SM046's ratings of the arousal of surprise were within the normal range, whereas her ratings of fear were severely impaired.

We wanted to examine the possibility that the disproportionate impairments in rating the arousal of anger and fear might result simply from a larger variance in the ratings given by SM046. The large negative deviations of her ratings from control ratings in the case of fear and anger could have resulted in part from the fact that it simply was possible to deviate more from normal ratings on these emotions than it was possible to deviate on other emotions. To address this issue, we calculated the difference measure that would be obtained if a subject generated random ratings. As Figure 2 shows, the expected difference of random ratings from normal ratings (gray curve) is also lowest for anger and fear. However, SM046 often gave lower ratings of arousal to negative emotions than would be the case if she were giving random ratings, as also borne out by the fact that her mean arousal ratings of negative emotions were less than 5 (less arousing than neutral; Fig. 1). It thus appears that SM046 judged negative emotions to exhibit abnormally low levels of arousal.

Ratings of Valence and Arousal in Lexical Stimuli

SM046 showed a severe impairment in her ability to recognize the arousal signaled by sentences and by words denoting negative emotions (Fig. 3). She rated sentences depicting anger or fear as "relaxing," ratings that were typically more than 5 standard deviations below the mean for the normal control subjects. For two of the sentences depicting fear, every normal subject gave arousal ratings of 9 (the highest possible rating), whereas SM046 gave ratings of 6 (to the sentence "As the car was speeding down the mountain, Mike stepped down to find that he had no brakes") and 3 (to the sentence "Sally waved her hands in the air and yelled for help, as the boat was sinking"). However, she gave normal ratings of valence to all emotions.

DISCUSSION

We report here a subject with selective bilateral amygdala damage who showed a specific impairment in judging various classes of stimuli that signal unpleasant emotions: an inability to recognize their arousal, with a spared ability to recognize their valence. The data provide further detail to previously reported impairments in the ability of subjects with bilateral amygdala damage to recognize certain negative facial expressions, especially fear and anger. It is not the case that bilateral amygdala damage impairs all knowledge regarding such emotional expressions; rather, it impairs the knowledge that they are

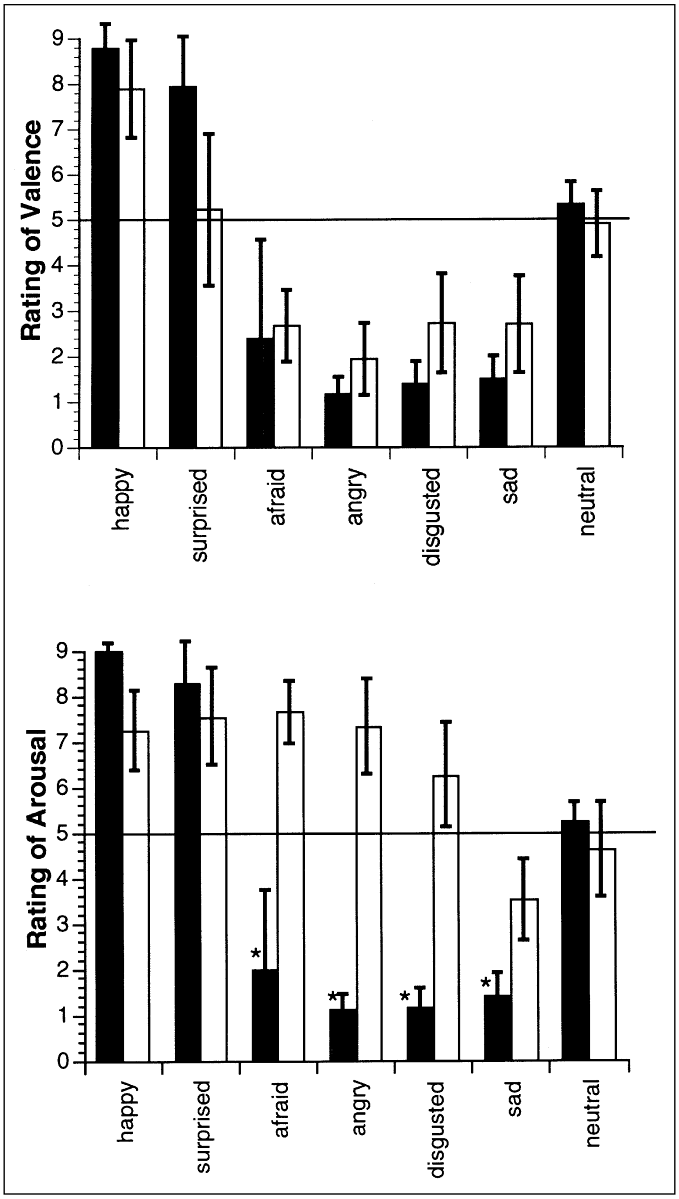

Fig. 1. Mean ratings of arousal and valence for 39 facial expressions of emotion. Data were averaged for all faces that express the same emotion (6 of each basic emotion; 3 neutral). Means and standard deviations are shown for 24 normal control subjects (white bars) and for subject SM046 (black bars; three experiments). An asterisk indicates that SM046's ratings were more than 2 standard deviations below the control mean. Ratings greater than 5 denote more pleasant, or more arousing, emotions than neutral; those less than 5 denote more unpleasant, or more relaxing, emotions than neutral; neutral itself was given a rating of 5 (horizontal line).

arousing. This interpretation may explain impaired recognition of fear in subject SM046 (Adolphs et al., 1994, 1995), and it may account also for impaired recognition of fear and anger in other subjects with bilateral amygdala damage (Broks et al., 1998; Calder et al., 1996; Young et al., 1995).

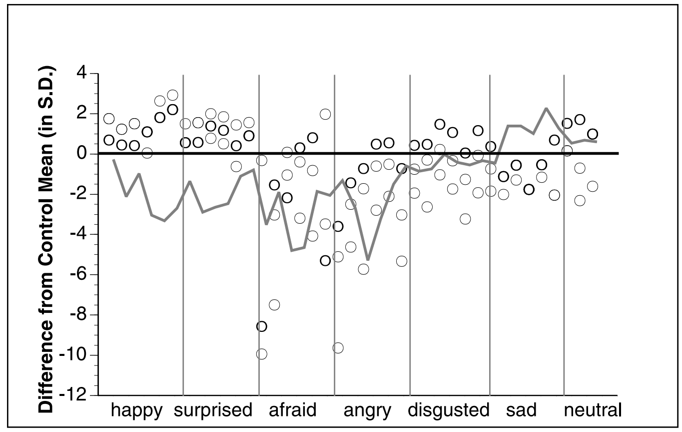

Fig. 2. Comparisons between 24 normal control subjects and SM046 in rating the magnitude of arousal signaled by 39 facial expressions. Each circle plots the difference between SM046's arousal rating and the control subjects' mean arousal rating for a given face in *SD* units. The stimuli are rank-ordered on the *x*-axis according to their perceived similarity (Adolphs et al., 1994, 1995); expressions of emotions judged to be more similar are adjacent on the axis. The solid gray curve indicates the measure expected for completely random ratings; that is, it represents the expected (average) difference of random ratings from the control subjects' mean ratings, calculated as (5 – mean normal rating)/*SD*.

It is interesting to note that SM046 is able to recognize most individual unpleasant emotions other than fear, and that she can correctly retrieve considerable knowledge about unpleasant emotions, including fear (cf. Adolphs et al., 1995). She also shows an apparently normal emotional response, both in terms of subjective experience and in terms of physiological measures, to some emotional stimuli. In particular, she rated her emotional experience of an unpleasant, arousing slide show normally (Adolphs, Cahill, Schul, & Babinsky, 1997), and she shows normal skin conductance response to auditory startle stimuli (which could also be classified as arousing and unpleasant; Bechara et al., 1995). The present finding thus suggests a rather specific role for the human amygdala in emotion: not in emotional experience, and not in emotional response to unconditioned stimuli, but rather in a particular domain of knowledge about emotions.

Additional investigations will be needed to determine whether the impairment we report is due primarily to impaired acquisition or to impaired retrieval of knowledge. We (Adolphs, in press; Adolphs, Damasio, Tranel, & Damasio, 1996; Hamann et al., 1996) and other researchers (Phelps & Anderson, 1997) have conjectured that the human amygdala may be more crucial for the acquisition of knowledge regarding emotions than for subsequent retrieval. Prior case studies hinted that amygdala damage can impair recognition of fear in facial expressions if the damage is sustained early in life, but not if it is sustained in adulthood (Adolphs et al., 1994; Hamann et al., 1996; see also Anderson, LaBar, & Phelps, 1996), and both functional imaging (Cahill et al., 1996) and lesion studies (Adolphs et al., 1997; Cahill, Babinsky, Markowitsch, & McGaugh, 1995) have demonstrated the human amygdala's involvement in encoding declarative knowledge regarding emotionally arousing material. In the present case, SM046 acquired her amygdala damage early in life, possibly as early

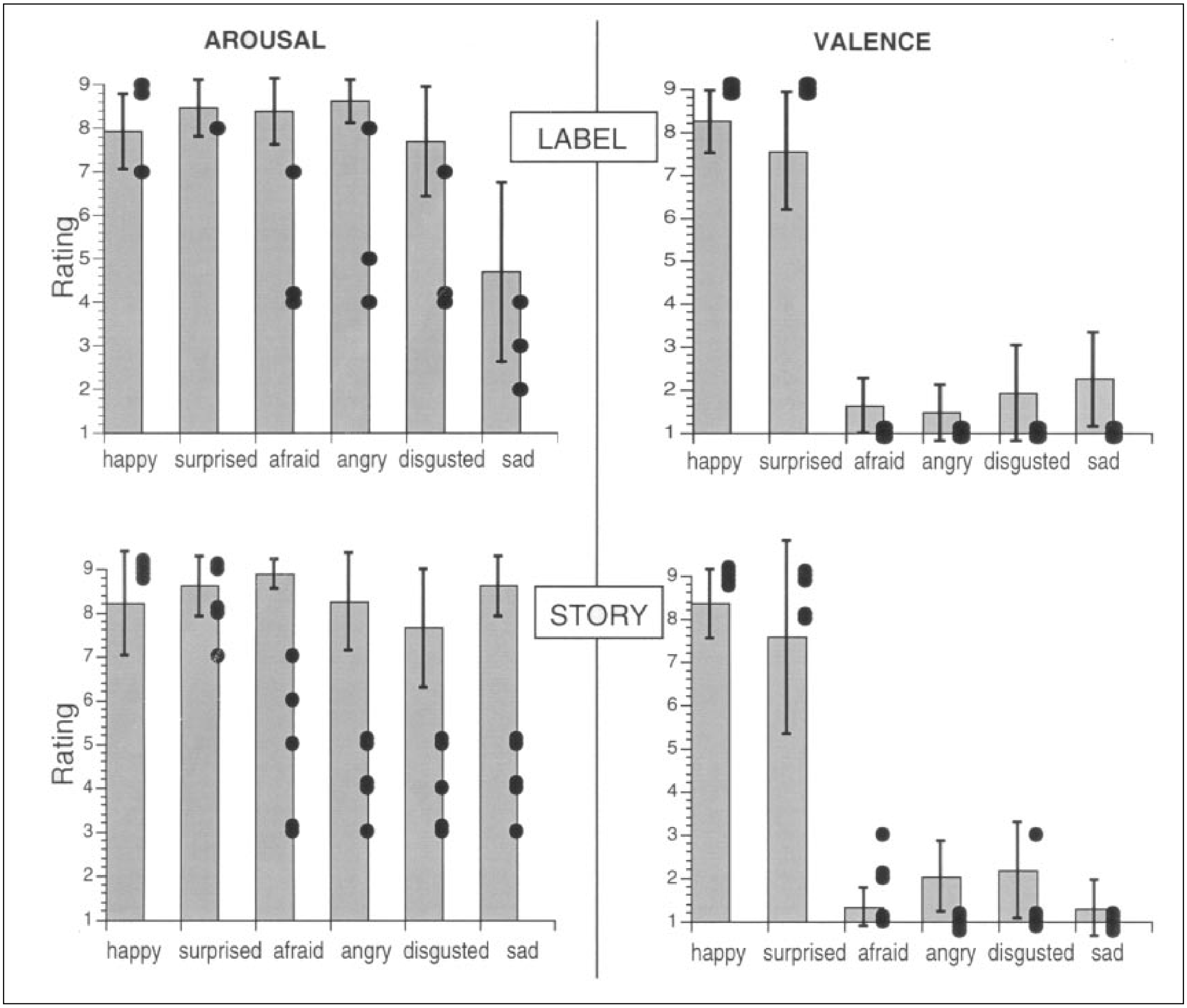

Fig. 3. SM046's (filled circles; three experiments) and normal control subjects' (bars; $N = 18$; mean ± *SD*) ratings of emotional sentences and words depicting basic emotions. The words were the labels "happy," "surprised," "afraid," "angry," "disgusted," and "sad." The 30 sentences (5 for each basic emotion) depicted either a situation typical of an emotion (e.g., "The alley was very dark, and the footsteps behind Linda were getting louder") or a behavior typically associated with an emotion (e.g., "Jody giggled and laughed"), but there was no mention of the label of the emotion. Ratings greater than 5 denote more pleasant, or more arousing, emotions than neutral; those less than 5 denote more unpleasant, or more relaxing, emotions than neutral.

as at birth. One explanation of the findings is thus that SM046 never acquired normal conceptual knowledge concerning the arousal of unpleasant emotions, and is hence unable to retrieve such knowledge on the experimental tasks. This possible role for the amygdala in declarative knowledge may bear some analogy to the established role of the hippocampus (Zola-Morgan & Squire, 1990): Both structures may be important in regard to the acquisition, but not the retrieval, of declarative knowledge; and both structures may participate in the consolidation of long-term memory stores over the course of many years (Rempel-Clower, Zola, Squire, & Amaral, 1996), for example, during development. In the case of the amygdala, this role may be both more specific (pertaining to stimuli that signal threat or danger) and less direct (pertaining to modulation of declarative memory systems rather than direct encoding; McGaugh, Cahill, & Roozendaal, 1996). A role for the amygdala in acquiring declarative knowledge for arousing, unpleasant stimuli would parallel its demonstrated role in acquiring conditioned autonomic responses that have been associated with an aversive startle stimulus. It thus appears that the amygdala is important both in associative and in declarative forms of emotional memory (Adolphs, in press; Cahill & McGaugh, 1998).

Evolutionary explanations have been offered for a variety of apparently domain-specific cognitive processes, including retrieval of knowledge about concrete entities (e.g., Caramazza & Shelton, 1998) and reasoning about social exchange (Cosmides & Tooby, 1992). Although the generally post hoc nature of evolutionary explanations requires cautious interpretation, one plausible scenario is that relatively modular neural systems evolved to deal with situations of potential danger and threat. Both the requirement for speed and the need to trigger a particular class of behaviors may make specialized systems advantageous. Highly arousing, negatively valenced stimuli, which could be expected to pose rather imminent threats to the organism's survival, are those for which a particular class of rapid response is imperative. It is for such stimuli that the amygdala's role in behavioral and somatic response is clearest from animal studies. The present findings from a human subject indicate that the amygdala's role may encompass yet a third component triggered by such stimuli: retrieval of specific types of declarative knowledge.

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