Impaired Judgments of Sadness But Not Happiness Following Bilateral Amygdala Damage

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Abstract

■ Although the amygdala's role in processing facial expressions of fear has been well established, its role in the processing of other emotions is unclear. In particular, evidence for the amygdala's involvement in processing expressions of happiness and sadness remains controversial. To clarify this issue, we constructed a series of morphed stimuli whose emotional expression varied gradually from very faint to more pronounced. Five morphs each of sadness and happiness, as well as neutral faces, were shown to 27 subjects with unilateral amygdala damage and 5 with complete bilateral amygdala damage, whose data were compared to those from 12 brain-damaged and 26 normal controls. Subjects were asked to rate the intensity and to label the stimuli. Subjects with unilateral amygdala damage performed very comparably to controls. By contrast, subjects with bilateral amygdala damage showed a specific impairment in rating sad faces, but performed normally in rating happy faces. Furthermore, subjects with right unilateral amygdala damage performed somewhat worse than subjects with left unilateral amygdala damage. The findings suggest that the amygdala's role in processing of emotional facial expressions encompasses multiple negatively valenced emotions, including fear and sadness. ■

INTRODUCTION

A number of lesion and functional imaging studies have demonstrated the amygdala's role in processing emotional facial expressions, but its precise importance for certain emotions remains debated. In particular, while there are consistent data to implicate the amygdala in perception and judgments of fear (Whalen et al., 2001; Broks et al., 1998; Breiter et al., 1996; Calder et al., 1996; Morris et al., 1996; Adolphs, Tranel, Damasio, & Damasio, 1994, 1995; Adolphs, Tranel, et al., 1999), only some studies have argued also for a role in processing other negative emotions, especially sadness (Schmolck & Squire, 2001; Adolphs, Tranel, et al., 1999; Blair, Morris, Frith, Perrett, & Dolan, 1999). Additional data to suggest that the amygdala may be involved in processing sad expressions come from findings that it is activated during the feeling of sadness (Schneider et al., 1997; Drevets et al., 1992)—although this finding does not demonstrate the amygdala's involvement in perception of sadness specifically, it nonetheless suggests that abnormal processing related to the emotion sadness may be a feature of amygdala dysfunction (in the same way that fear conditioning, phobias, and fear recognition all depend on the amygdala). While there are no data from lesion studies to support the idea that the amygdala is involved in processing happy expressions, some functional imaging studies have provided evidence for such a role (Yang et al., 2002; Breiter et al., 1996). One recent study in fact found amygdala activation (compared with neutral faces) when viewing expressions of fear, anger, sadness, or happiness (Yang et al., 2002). These findings challenge the notion that the amygdala is specialized to process expressions of fear.

It is important to note that the disproportionate activation to fear compared with other emotions, seen in most studies, does not rule out some (lesser) activation to other emotions. Thus, activations to emotional expressions when contrasted with neutral (Yang et al., 2002) may be compatible with activation selectively to fear, when that emotion is contrasted with any other emotion. One way of investigating these issues would be to parametrically vary the intensity of each emotion using computer-generated morphs between neutral and emotional expressions. Using such morphs might also provide a more sensitive task for detecting possible impairments following amygdala damage. Subjects with such damage may be able to produce correct performances on some tasks if the stimulus provides a sufficiently intense prototypical feature—such as a broad smile to signal happiness (Adolphs, 2002).

Clarification of the above controversies would contribute substantially to the theoretical frameworks used to interpret the data. One view considers the amygdala a component of a neural system for the rapid, automatic evaluation of stimuli that signal potential threat or danger in the environment, of which fearful expressions may be signals (Adolphs, Russell, & Tranel, 1999; Adolphs, Tranel, et al., 1999). Others view the amygda-

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la's role as processing signals of distress (Blair et al., 1999), thus including fear and sadness, or processing signals that indicate potentially important environmental information that must be disambiguated (Whalen et al., 2001), thus pointing to both fear and surprise, and perhaps additional emotions (Yang et al., 2002). Yet other data support the ideas that the amygdala may be more generally involved in withdrawal-related behaviors (Anderson, Spencer, Fulbright, & Phelps, 2000), which would include multiple negatively valenced emotions, or that it processes the dimension of emotional arousal, independently of valence (Anderson et al., 2003).

These controversies have persisted in part because the majority of lesion and of functional imaging studies have focused on the amygdala's role in processing facial expressions of fear, and in processing other fear-related information. That role is supported by most of the studies. By contrast, far fewer studies have systematically examined the amygdala's role in processing other emotions. Another reason for the inconsistent findings regarding the amygdala's role in judgments of other emotions may be that different stimuli and different tasks have been used in various studies. It is thus possible that some studies were simply more sensitive to possible impairment, whereas others had insufficient sensitivity to detect such impairment, or that different tasks and methods of analysis reveal different patterns of impairment (Schmolck & Squire, 2001; Rapcsak et al., 2000).

To investigate the above issue in more detail, we generated morphs between a prototypical neutral expression and prototypical expressions of sadness or happiness, thus including stimuli that varied in terms of their sensitivity to judgments of the intended emotion (cf. Figure 1). Each of these faint morphs thus generated a series of (typically monotonically increasing) performances (depicted as the variously colored lines in Figures 2 and 3). To address the role of the amygdala, we tested five different subject groups. A normal control group was used to provide a reference for all other comparisons. Subjects with amygdala damage consisted of three groups: those with unilateral left and unilateral right amygdala damage due to neurosurgical temporal lobectomy, and those with bilateral amygdala damage (Table 1). In addition, we included a brain-damaged control group, comprised by subjects whose brain damage spared the amygdala.

To obtain a detailed assessment of emotion judgment, and to permit comparisons to previous studies, we used the two tasks that have been most common in the literature: rating of the stimulus on all the emotions, and a forced-choice labeling task in which subjects chose the word best suited to describe the emotion shown. We chose our stimuli such that their discriminability from neutral ranged between 80% and 100%, thus focusing on stimuli that were just sufficiently different from neutral that they could be reliably discriminated most of the time by normal subjects. The accuracy with which the final set of stimuli can be discriminated from a neutral face by normal subjects is given in Table 2, together with the mean rating given to the stimulus on each emotion. The mean accuracies in labeling the stimuli by normal subjects are given in Table 3.

RESULTS

Ratings Task

We first asked subjects to rate the morph stimuli on a scale of 1–10 with respect to the intensity of each of the basic emotions. This task has been used in a number of prior studies (Schmolck & Squire, 2001; Adolphs et al., 1995; Adolphs, Tranel, et al., 1999), circumvents the issue of what emotion response options are available to subjects (by explicitly asking them to rate every individual emotion), and provides a fine-grained assessment of sensitivity to the intensity of specific individual emotions signaled by the face stimuli.

Subjects with bilateral amygdala damage gave raw ratings to several of the sad morphs that were more than 2 SD different from the mean ratings given by brain-damaged controls. Every subject with bilateral amygdala damage showed this pattern, and none except AP showed any such impairment for happy morphs. However, different raw ratings could arise from both an impairment in the ability to judge that a morph stimulus was different from a neutral expression, or from different baseline ratings for that emotion, even for neutral stimuli. To take into account subjects' baseline ratings

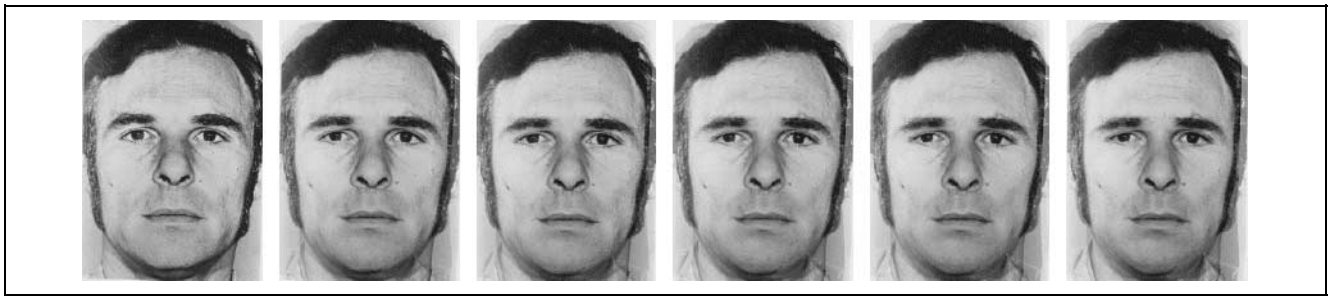

Figure 1. Examples of morph stimuli used. From left to right: morphs between neutral and increasing sadness.

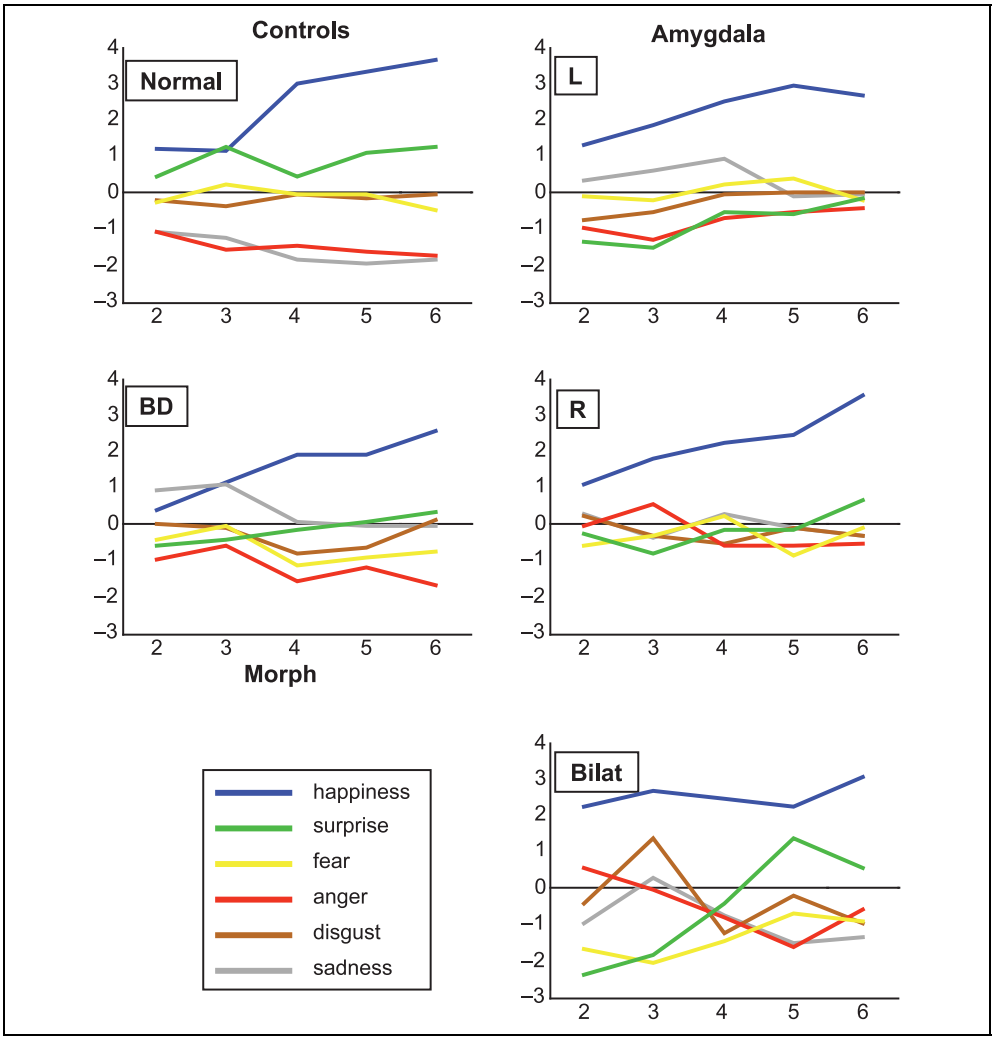

Figure 2. Ratings for happy morphs. The mean rating difference (from ratings given to neutral faces) is shown for increasing morphs of happiness, for each subject group. The differently colored lines show the ratings given on the different emotion labels (see legend). BD = brain-damaged controls with lesions sparing the amygdala; L = unilateral left amygdala damage group; R = unilateral right amygdala damage group; Bilat = complete bilateral amygdala damage group.

given to neutral faces, we subsequently calculated all rating scores as differences from ratings given to neutral faces (see Methods).

For morphs of happiness, all subject groups showed a similar pattern of a gradual increase in their ratings as a function of increasing happiness of the morph stimulus (Figure 2). Subjects with amygdala damage did not differ noticeably from brain-damaged controls.

Both normal and brain-damaged groups showed very similar rating curves for sad morphs (Figure 3), featuring a gradual increase in sad ratings together with a slight decrease on happy ratings, and a low level of ratings also on nonintended emotions of negative valence. No major deviations from these overall patterns were seen in subjects with unilateral amygdala damage, although subjects with unilateral left damage did show a surprisingly high sensitivity to sadness, exhibiting higher-than-normal ratings of intensity. However, those with bilateral amygdala damage showed a rather different pattern, with lower overall ratings on sadness together with higher ratings on intruding, nonintended emotions. Especially notable are the high ratings on disgust, and also somewhat higher ratings on happiness.

A 5 by 5 repeated-measures ANOVA on the ratings of sadness given to the sad morphs, with factors of subject group (NC, BDC, left, right, bilateral) and morph degree, showed a significant effect of both morph degree, $F(4,341) = 4.0$, $p < .005$ and group, $F(4,341) = 8.1$, $p < .0001$. To have a conservative statistic that did not depend on the assumptions of parametric statistics, we next applied Mann–Whitney U tests to all pairwise comparisons between groups, and Bonferroni corrected for multiple comparisons. The only significant contrasts were between subjects with unilateral left amygdala damage and all other groups (subjects with left amygdala damage scored higher), and between subjects with bilateral amygdala damage and normal controls ($p < .05$). Identical analyses for happy ratings given to the happy morphs showed no significant effects.

To ensure that differences in the group ratings shown in Figures 2 and 3 were not the result of different sample sizes in the groups (especially the small sample size of the bilateral amygdala damaged group), we also calculated mean rating curves from randomly drawn subsets of brain-damaged controls. When subsets of $n = 5$ were used, a sample size identical to that of the bilateral

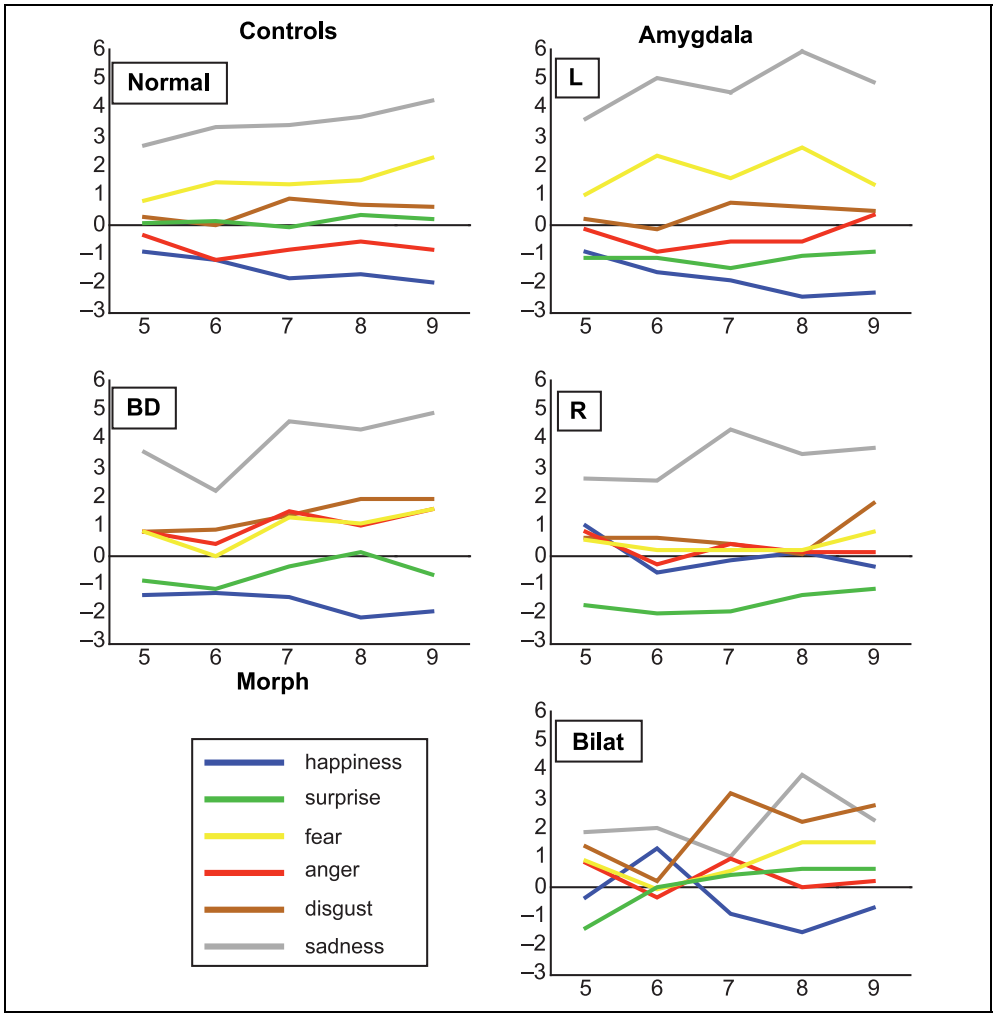

Figure 3. Ratings for sad morphs. The mean rating difference (from ratings given to neutral faces) is shown for increasing morphs of sadness, for each subject group. The differently colored lines show the ratings given on the different emotion labels (see legend). BD = brain-damaged controls with lesions sparing the amygdala; L = unilateral left amygdala damage group; R = unilateral right amygdala damage group; Bilat = complete bilateral amygdala damage group.

amygdala subjects, we still obtained curves that were essentially the same as those of the entire brain-damaged group. Thus, the abnormal mean ratings given by subjects with bilateral amygdala damage when rating sad morphs (Figure 3) did not result simply from the smaller sample size of this group.

To obtain a quantitative measure of these patterns, we calculated correlations between each subject's rating profile and the mean normal control rating profile for a given stimulus (Adolphs et al., 1995; Adolphs, Tranel, et al., 1999). When the magnitude of this correlation was plotted as a function of the increasing morph for each emotion, we obtained plots that corroborated the above patterns (Figure 4): Subjects with bilateral amygdala damage showed abnormal patterns of ratings to morphs of sadness (notably morphs 7 and 8), but not happiness.

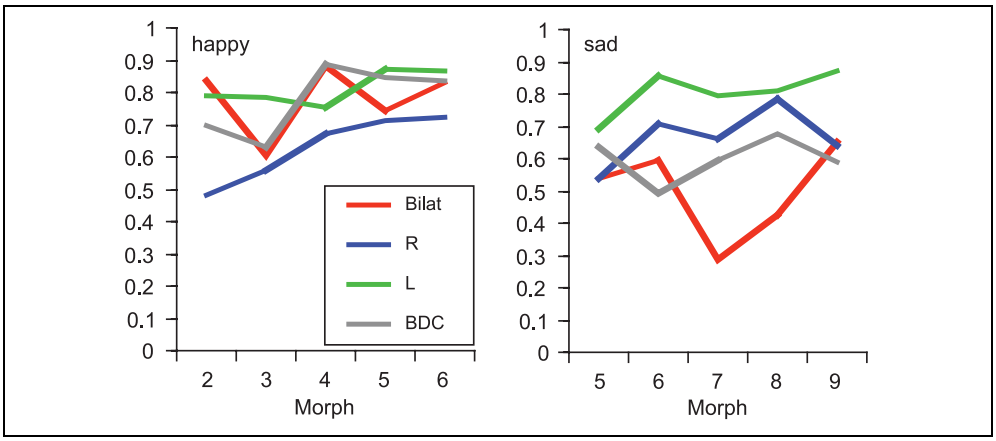

Figure 4. Correlations with normal Ratings. Correlations for happy (left) and sad (right) morphs are shown for each subject group (differently colored lines). Mean correlations for a group were calculated from the averaged *z*-transformed correlations for individuals. BD = brain-damaged controls with lesions sparing the amygdala; L = unilateral left amygdala damage group; R = unilateral right amygdala damage group; Bilat = complete bilateral amygdala damage group.

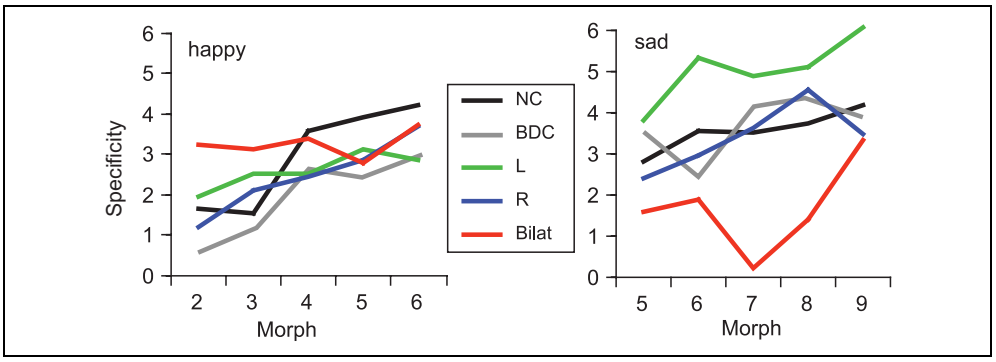

Figure 5. Specificity of ratings. Specificity was calculated as the difference between ratings on the emotion shown (e.g., ratings on "sad" when shown sad morphs) and the mean of ratings on all the other emotions (ratings on other emotion labels when shown the sad morphs). Specificity scores are shown for happy (left) and sad (right) morphs for each subject group (differently colored lines). BD = brain-damaged controls with lesions sparing the amygdala; L = unilateral left amygdala damage group; R = unilateral right amygdala damaged group; Bilat = complete bilateral amygdala damage group.

The abnormally low correlations for sadness in subjects with bilateral amygdala damage reflect what is apparent from Figure 3: They are less specific in their ratings of the emotion. Whereas other subject groups make a distinction between sadness and other emotions, subjects with bilateral amygdala damage do not. Whereas the ratings of subjects in all other groups correlated significantly ($p < .05$) with normal ratings, those of 3/5 of the subjects with bilateral amygdala damage did not. One can derive a specificity index from these ratings, by calculating the rating difference between ratings given on the correct label, sad, and on other, incorrect labels. Such a specificity calculation corroborates the impaired ability of subjects with bilateral amygdala damage to judge sadness as distinct from other emotions (Figure 5). A further observation evident from Figures 4 and 5 was that, as a group, subjects with right unilateral amygdala damage were somewhat more impaired than were subjects with left unilateral amygdala damage, a finding broadly consistent with prior lesion studies (Adolphs, Tranel, & Damasio, 2001; Anderson et al., 2000).

A final question of interest was whether the abnormal pattern of ratings given by subjects with bilateral amygdala damage might result from less consistency within each subject (more "noise" in each individual's data), or from ratings given by each subject that were consistently abnormal. Three of the five subjects with bilateral amygdala damage had repeated the task, as had seven brain-damaged controls. We therefore calculated consistency measures between the two datasets for each subject. We found that subjects with bilateral amygdala damage did not differ in their consistency from brain-damaged controls, either in the labels they assigned to stimuli, or in the ratings that they gave them (Table 4; all consistency measures for subjects with bilateral amygdala damage are within a standard deviation of the mean consistency measures for brain-damaged controls).

Labeling Task

Another commonly used task (Schmolck & Squire, 2001; Broks et al., 1998; Calder et al., 1996) asks subjects to choose one word from a list of the basic emotions. This task introduces the additional complexity that there are not equally many confusable response options available for each target emotion (for instance, happiness is the only unambiguously positive emotion, whereas there are many negatively valenced emotions that can potentially

Table 1. Background Neuropsychology

	Age	*Education*	*Sex*	*PIQ*	*VIQ*	*Benton*	*BDI*
BDC	59 ± 11	12 ± 2	5 women/7 men	100 ± 13	92 ± 12	46 ± 4	6 ± 9
R Amy	36 ± 10	14 ± 2	3 women/8 men	106 ± 18	95 ± 14	44 ± 4	5 ± 3
L Amy	36 ± 10	13 ± 2	9 women/7 men	103 ± 11	95 ± 14	44 ± 3	6 ± 5
Bilat	49 ± 13	14 ± 2	1 woman/4 men	92 ± 18	94 ± 12	43 ± 3	1 ± 1

Means and *SD* are shown for brain-damaged controls (BDC), and subjects with unilateral (R, L) and bilateral (Bilat) amygdala damage on age, education (in years), sex distribution, performance and verbal IQ (PIQ, VIQ, from the Wechsler Adult Intelligence Scale, Revised), facial discrimination (Benton, from the Benton Faces Task, all in the normal range), and depression (BDI, Beck Depression Inventory, none severely depressed).

Table 2. Characterization of Stimuli in Terms of Discriminability and Emotion Ratings

Stimulus	*Morph Number*	*Discrim.*	*Happy*	*Sad*	*Disgust*	*Anger*	*Fear*	*Surprise*
Happy	2	0.79	**4.58**	2.38	1.50	1.88	1.46	2.00
Happy	3	0.88	**4.54**	2.19	1.35	1.38	1.92	2.77
Happy	4	0.93	**6.35**	1.62	1.65	1.50	1.69	2.00
Happy	5	0.93	**6.73**	1.50	1.54	1.35	1.65	2.62
Happy	6	0.97	**7.04**	1.65	1.65	1.27	1.23	2.81
Sad	5	0.89	2.42	**6.19**	1.96	2.65	2.46	1.58
Sad	6	0.95	2.15	**6.81**	1.69	1.77	3.15	1.65
Sad	7	0.98	1.54	**6.85**	2.62	2.12	3.04	1.46
Sad	8	0.99	1.65	**7.19**	2.38	2.35	3.23	1.85
Sad	9	0.98	1.42	**7.65**	2.27	2.15	3.96	1.69
Neutral	0	N/A	3.23	3.50	1.27	2.81	1.58	1.50
Neutral	0	N/A	3.38	3.42	2.04	3.27	1.85	1.38
Neutral	0	N/A	3.46	3.38	1.77	2.81	1.65	1.69

Mean discriminability (proportion correctly discriminated from a neutral face), and mean ratings on emotion labels given by normal controls are shown. Numbers in bold type indicate ratings on the intended emotion label.

be confused with one another; Adolphs, 2002). On the other hand, the task can also be considered easier, because it requires only a categorical response rather than the more detailed ratings on all the different emotions that the above rating task required.

When subjects were asked to match stimuli to the best label from a list of the six basic emotion words, labeling for sad and happy morphs showed very similar patterns in all subject groups (data not shown). The intended emotion was labeled the highest proportion of the time, and in general labeling provided more discrimination between emotions than did rating. This effect would be expected, since labeling forces subjects to choose a single label, whereas ratings encourage them to assign multiple emotions to a single stimulus. Particularly notable was the entirely intact ability of

Table 3. Characterization of the Stimuli in Terms of Labeling

Stimulus	*Morph*	*Label: happy*	*Surprise*	*Afraid*	*Angry*	*Disgust*	*Sad*
Happy	2	**0.65**	0.12	0.04	0.08	0	0.12
Happy	3	**0.65**	0.15	0.04	0	0.04	0.12
Happy	4	**0.92**	0	0.04	0	0.04	0
Happy	5	**0.81**	0	0.08	0.04	0.04	0.04
Happy	6	**0.81**	0.04	0	0	0.12	0.04
Sad	5	0.12	0	0.08	0.12	0.08	**0.62**
Sad	6	0.15	0	0.12	0	0.04	**0.69**
Sad	7	0	0	0.04	0	0.04	**0.92**
Sad	8	0	0.04	0.08	0.04	0.12	**0.73**
Sad	9	0.04	0.04	0	0.04	0.08	**0.81**
Neutral	0	0.42	0.04	0.08	0.15	0.12	0.19
Neutral	0	0.27	0	0	0.31	0.15	0.27
Neutral	0	0.5	0.08	0	0.19	0.04	0.19

Mean proportion of stimuli that received a given label by normal controls are shown. Bold type shows proportion labeled as intended emotion.

Table 4. Consistency Measures for Three Subjects With Bilateral Amygdala Damage (SM, JM, and RH), Compared With Brain-damaged Controls (BDC mean)

Subject	*Emotion*	*Label*	*Happy*	*Sad*	*Disgust*	*Anger*	*Fear*	*Surprise*
SM	happy	0	2.2	0.2	0	0	0	0
	sad	0	1.4	2.2	0	0	0	0
JM	happy	0	2.4	0.2	0	0	0	3
	sad	4	2	2.6	3.2	1.8	0.8	4.4
RH	happy	0	1.2	1.4	1.8	2	1.6	1.8
	sad	2	1	0.8	1.8	1.6	1.8	1.4
BDC mean	happy	1.6	2.3	1.8	2.1	1.3	1.8	2.4
	sad	1.9	1.1	1.7	2.7	1.6	3.3	1.7

Mean consistency is shown for all those stimuli in an emotion category. Label consistency was calculated as the number of times a subject changed a label for a stimulus in that emotion category. Rating consistencies to the six labels was calculated as the absolute value of the difference in ratings given on the two testing occasions.

subjects with bilateral amygdala damage to label sad morphs, despite their impaired ability to assign differential ratings to them.

DISCUSSION

We used a sensitive task that permitted us to plot emotion rating and labeling as a function of increasing structural change in the morph stimulus. At least two points are worth emphasizing here: Our stimuli should be more sensitive to possible impairment than prototypical emotional expressions, and they should also be more typical of emotions encountered in everyday life. That is, the prototypical expressions often used in studies are in fact not typical or modal stimuli with respect to real life (Horstmann, 2002). Given the data we obtained, it would seem preferable in future studies to use morphs of emotional expressions rather than only the prototypes, as has typically been done. Furthermore, we used the two different tasks that have been most commonly used to assess judgment of emotions from facial expressions. In addition to these within-subject factors of emotion intensity and task condition, we had a between-subjects factor of lesion group, comparing performances given by subjects with bilateral amygdala damage to those with unilateral amygdala damage, brain damage sparing the amygdala, and normal controls.

We found that subjects with bilateral amygdala damage stood out as a group showing impaired performances. Their impairments were specific to judging sadness rather than happiness, and to performing the rating task rather than the labeling task. Moreover, the impairment could not be attributed to the smaller sample size of the group with bilateral amygdala damage, nor simply to more inconsistent performance. The data thus support the idea that bilateral damage to the amygdala impairs processing of sadness from facial expressions, and that the rating task is more sensitive to detect this impairment than the labeling task. A further finding was that subjects with right temporal lobectomy performed somewhat worse than subjects with left temporal lobectomy (cf. Figures 4 and 5), consistent with prior reports (Adolphs et al., 2001; Anderson et al., 2000). One surprising aspect of this latter pattern was that subjects with left temporal lobectomy in fact appeared to be ''more'' sensitive to sad faces than even normal controls (Figures 3 and 5).

There are two major caveats in the interpretation of the data. First, four out of the five subjects with bilateral amygdala damage had bilateral medial temporal lobe damage that included the amygdala plus surrounding structures and white matter. In support of the idea that the findings from this group are representative of bilateral amygdala damage, we found the same pattern of impairment in the subject (SM046) with selective bilateral amygdala damage, and we found no such impairment in several brain-damaged control subjects who had large lesions. A second caveat concerns the issue of task difficulty. Could the findings be explained by positing that rating sad morphs is generally more difficult than rating happy morphs? We contend that this is implausible, simply from an examination of the performances of control subjects in Figures 2 and 3. Normal and brain-damaged controls both assigned intensity ratings to the weakest happy morphs that were no greater than those assigned to the weakest sad morphs, confirming the design of our stimuli which attempted to generate roughly equally weak stimuli (our morphing method ensured that this was the case in terms of the discriminability of the morphed emotion from a neutral face when shown side by side; the ratings shown in Figures 2 and 3 show that this is also the case when subjects rate each individual morph on

the intended emotion). Controls also gave intensity ratings to the unintended emotions that were as great for happiness as they were for sadness. When we compare the two left plots (normal and brain-damaged controls) for happiness (Figure 2) and sadness (Figure 3), it appears that, if anything, happiness was generally harder for controls to recognize than sadness. Yet the data from the subjects with bilateral amygdala damage provide a striking contrast: Their ratings of sadness are lower and less specific than their ratings of happiness. Furthermore, if their impairment was due to nonspecific difficulty, then it should be noticeably more severe for the fainter sad morphs than for the stronger sad morphs: but this does not appear to be the case. When closely examining the patterns of data, then, the possibility that the impaired sadness ratings given by subjects with bilateral amygdala damage could be attributed to nonspecific difficulty is not supported. Notwithstanding these considerations, it will be important in future studies to verify this impression by obtaining additional measures that assess task difficulty, such as reaction times to the stimuli.

How can we make sense of the errors made by subjects with bilateral amygdala damage? Across the different emotion morphs, an overall pattern of impairment emerged in subjects with bilateral amygdala damage: They apparently confused emotions that are configurally (Dailey, Cottrell, Padgett, & Adolphs, 2002) and semantically (Adolphs et al., 1994; Russell, 1980) closely related. Thus, happiness is confused to some extent with surprise, and sadness with disgust. Both of these confusions are also occasionally made by normal subjects, but bilateral amygdala damage appears to result in more intrusions of unintended emotions, as well as lower intensity ratings on the intended emotion, which together produced less specificity. Intrusions of incorrect emotions have also been noted in other studies that have analyzed data from subjects with bilateral amygdala damage (Sato et al., 2002; Schmolck & Squire, 2001).

It is interesting that we found no impairment on the same stimuli when using the labeling task. One possible explanation might be that the labeling task was always administered after the rating task, when subjects would have had more experience with the stimuli. An argument against this possibility is that we did not find any improvement in rating task performances in those subjects who were administered multiple rating tasks. Another interpretation is that the rating task can detect impairments that the labeling task cannot. For instance, a subject may be unable to assign normal ratings to expressions of sadness, when rating across multiple emotions, but may nonetheless be able to figure out that the label ''sad'' is more appropriate than any other label. These findings emphasize the importance of using multiple tasks in providing a thorough assessment of emotion processing abilities.

The impaired judgment of sadness following bilateral amygdala damage extends the amygdala's role beyond processing of fear; the relatively intact judgment of happiness restricts it to negatively valenced emotions. While the findings to date do not yet provide a complete account of precisely which emotions depend on the amygdala, they support the idea that several emotions of negative valence have such a dependency. Furthermore, the present findings still leave open the possibility that fear processing is even more dependent on the amygdala than is sadness processing. A goal for the future will be a specification of what factor it is that is shared in common by all those emotions (and, for that matter, other social information) whose processing depends on the amygdala. Additional studies with stimuli such as the ones used here, with a variety of tasks, and using both lesion and functional imaging methods, will be needed to address this topic.

METHODS

Subjects

We tested 26 normal subjects with no history of neurological or psychiatric disease, 16 subjects with unilateral left amygdala damage, 11 with unilateral right amygdala damage, 5 with complete bilateral amygdala damage, and 12 brain-damaged controls with lesions that spared the amygdala. All subjects were selected from the Department of Neurology's Patient Registry, and had been fully characterized both in terms of their background neuropsychology as well as location and extent of lesion. All subjects with unilateral amygdala damage had undergone neurosurgical resection for the treatment of temporal lobe epilepsy. All brain-damaged controls had lesions due to stroke. Subjects with bilateral amygdala damage included one subject with selective bilateral amygdala damage due to Urbach–Wiethe disease (SM046), and four with complete but nonselective amygdala damage due to encephalitis. Neuropsychological and demographic background data are given in Table 1. Most critically, the impaired performances of subjects with bilateral amygdala damage described below could not be attributed to any basic visuoperceptual impairment: Their performance IQ, ability to discriminate faces (from the Benton Faces task), and other measures of visuoperceptual ability did not differ from those of the other subject groups.

All subjects gave informed written consent to participate in the studies, in accordance with the Declaration of Helsinki and as approved by the institutional review board of the University of Iowa.

Stimuli

We chose morphs of a single individual's face (PE) from the Ekman and Friesen stimulus set. We generated linear morphs between a neutral expression and a

happy or sad prototypical expression, as described in detail previously (Jansari, Tranel, & Adolphs, 2000). We generated a series of 19 morphs, progressing from the neutral face to the emotional face (i.e., the first 9 were more similar to neutral, while the last 9 were more similar to the emotion, and the 10th was exactly intermediate). Figure 1 shows examples of the stimuli we used.

In a prior experiment (Jansari et al., 2000), an independent set of 28 normal subjects (different from the 26 used in the present study) had provided data on the discriminability of these morphs from a neutral face. We chose our stimuli such that their discriminability from neutral ranged between 80% and 100%, thus focusing on stimuli that were just sufficiently different from neutral that they could be reliably discriminated most of the time by normal subjects. We chose five morphs each of a happy face (morphs 2, 3, 4, 5, 6 from the initial series of 19), and of a sad face (morphs 5, 6, 7, 8, 9). The lower morph numbers for happiness reflect the fact that a prototypical happy face is configurally more distant from a neutral face than are prototypical sad faces, due primarily to the large change in mouth configuration (the smile), which makes them easier to discriminate. In addition to these faint emotion morphs, we showed subjects three neutral faces, for a total of 13 stimuli.

Experimental Task

Rating Task

Subjects were shown the stimuli one at a time with notime limit, and asked to provide a rating on a scale of 1–10 for each of the basic emotions. Stimuli were presented in randomized order, and the entire series was rated on one emotion at a time before proceeding to the next emotion; thus the entire stimulus set was seen six times in order to rate them on the six basic emotions (happy, afraid, surprised, angry, disgusted, sad) (Schmolck & Squire, 2001; Adolphs et al., 1995; Adolphs, Tranel, et al., 1999). We calculated, for each subject and each stimulus, the difference between ratings given to that stimulus for an emotion morph stimulus compared with that subject's mean rating of the three neutral stimuli. Thus, Figures 2 and 3 show how much more (or less) intense subjects judged the morphs to exhibit specific emotions than neutral faces. This scoring procedure corrected for any baseline biases that subjects might have had in assigning emotion ratings, by subtracting the emotional intensity they attribute to an entirely neutral expression.

Labeling Task

Upon completion of the rating task, subjects were presented with a list of the six emotion labels and given a six-alternative forced-choice task in which they had to choose the label best describing the stimuli (Schmolck & Squire, 2001; Broks et al., 1998; Calder et al., 1996). Accuracy scores were calculated as means of the binary correctness scores (0 = incorrect, 1 = correct). The labeling task was always given after the ratings task, as the categorical response it required could potentially bias the more unconstrained ratings that subjects could give on the ratings task.

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