

Anteromedial Temporal Lobe Damage Blocks Startle Modulation by Fear and Disgust

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The acoustic startle reflex (ASR) is potentiated during negative emotion, but attenuated during positive emotional experience. The modulation of the ASR by fear depends critically on the amygdala. The authors investigated ASR modulation to fearful, disgusting, pleasant, and neutral stimuli in 12 patients with unilateral damage to the anteromedial temporal lobe including the amygdala (6 left, 6 right), 1 patient with bilateral temporal lobe damage including the amygdala, and 12 comparison participants. Both groups with unilateral damage, as well as the subject with bilateral damage, showed a complete lack of ASR potentiation to both fear and disgust stimuli. The findings suggest that potentiation of the ASR by disgust and fear depends on the integrity of the anteromedial temporal lobe.

As a model of emotional processing, the modulation of the acoustic startle reflex by emotional experience is a robust, often-replicated finding (Bradley, Codispoti, Cuthbert, & Lang, 2001; Koch & Schnitzler, 1997; Lang, Bradley, & Cuthbert, 1990). The paradigms used to illustrate this modulation range from those applicable to both animals and humans, such as fear conditioning protocols (Brown, Kalish, & Farber, 1951; Grillon & Davis, 1995), to those uniquely used with human participants, such as the modulation of startle by emotional imagery (Vrana & Lang, 1990) or affective foreground stimuli such as pictures (Vrana, Spence, & Lang, 1988) or sounds (Bradley & Lang, 2000). The general finding from these studies is that the experience of negative emotion enhances, whereas positive emotion reduces, the magnitude of the startle reflex. This pattern of results, along with the feasibility of testing these paradigms across species, has made startle modulation protocols a popular and informative technique within affective science.

The role of the amygdala in the modulation of the startle reflex has been studied extensively in animal models (Davis, 1992; Hitchcock & Davis, 1986; Koch & Schnitzler, 1997; Rosen & Davis, 1988) and in a few studies in humans (Angrilli et al., 1996; Funayama, Grillon, Davis, & Phelps, 2001). Animal research shows that stimulation of the amygdala enhances the startle reflex (Rosen & Davis, 1988), whereas lesion of the central nucleus of the amygdala reduces the magnitude of fear potentiation of the reflex (Hitchcock & Davis, 1991). The amygdala is not necessary for the expression of the reflex, which is controlled at the brain-stem level (Yeomans & Frankland, 1995), nor is it necessary for pleasure-attenuated startle (Koch, Schmid, & Schnitzler, 1996).

This pleasure-attenuation effect, assessed by startle measurement during conditioned food-reward trials is, however, dependent on the integrity of the nucleus accumbens. Angrilli and colleagues (1996) demonstrated a lack of potentiation of the startle response measured from both the left and the right orbicularis oculi muscles to unpleasant pictures in 1 patient with a right amygdala lesion. Testing patients with left- or right-sided temporal lobectomy including amygdala damage, Funayama and colleagues (2001) demonstrated a differential, lateralized pattern of startle modulation: Right temporal lobectomy patients did not show the expected pattern of startle modulation to picture stimuli (pleasant < neutral < unpleasant), whereas left temporal lobectomy patients did show this pattern.

The specificity of startle modulation by individual emotional categories has been studied in several experiments. Examining the startle response to fearful, disgusting, neutral, and pleasant stimuli, Balaban and Taussig (1994) demonstrated that the startle response was most potentiated by fearful stimuli, whereas responses to disgusting stimuli were not significantly larger than responses to neutral stimuli. Similarly, Bradley et al. (2001) showed that the startle reflex was most potentiated by pictures depicting animal or human attack (which could be categorized as fearful), whereas startle responses were smaller, although still potentiated above those to neutral stimuli, to pictures depicting mutilations or contamination (which could be categorized as disgusting). A more recent study, however, has shown that presentation of disgusting pictures results in the largest startle response, over and above responses to fearful pictures (Yartz & Hawk, 2002). This finding, however, held only for women, whereas men showed no difference between startle response to fear and disgust pictures. Overall, these studies suggest that although the potentiation of startle to negative emotional stimuli is a robust finding, the specificity of this potentiation to specific categories of negative emotion is an unresolved issue.

In accord with findings of differential startle magnitude to fear and disgust stimuli, many studies have documented different neural areas involved in fear versus disgust processing. Specifically, this work has supported a role for the amygdala in the processing of fearful information, whereas the anterior insula and basal gan-

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This work was supported by National Institute of Neurological Disorders and Stroke Program Project Grant P01 NS19632. We thank Terry Blumenthal for assistance with startle data processing and E. Sumie Funayama for information relating to the stimuli and specifics of her research.

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Table 1
Demographic, Neuropsychological, and Neuroanatomical Data

Measure	Patient 1673	NC (<i>n</i> = 12)	LTL (<i>n</i> = 6)	RTL (<i>n</i> = 6)	Statistic	<i>p</i>
Demographics						
Age	73	31 ± 2.6	37 ± 4.1	33 ± 3.7	<i>F</i> = 0.9	> .40
Gender	M	4 F, 8 M	3 F, 2 M	2 F, 4 M	$\chi^2 = 1.2$	> .50
Education	13	16.3 ± 0.8	13.6 ± 0.9	13.3 ± 1.0	<i>F</i> = 5.8	.01
Patient's age at seizure onset ^a	—	—	10.8 ± 6.9	15.0 ± 2.7	<i>t</i> < 1	> .50
Neuropsychology						
VIQ	103	—	92.0 ± 5.1	98.5 ± 6.4	<i>t</i> < 1	> .30
PIQ	91	—	100.6 ± 3.8	108.0 ± 5.9	<i>t</i> = 1.0	> .40
Benton Faces	40	—	45.5 ± 1.3	44.8 ± 1.6	<i>t</i> < 1	> .20
BDI	17	—	11.6 ± 2.2	3.8 ± 1.9	<i>t</i> = 2.7	.025
Neuroanatomy						
Amygdala volume						
Left	0	—	702 ± 149	2,276 ± 78	<i>t</i> = 6.8	.0001
Right	0	—	1,687 ± 60	1,173 ± 238	<i>t</i> = 1.8	.051
Hippocampal volume						
Left	0	—	1,270 ± 237	3,982 ± 252	<i>t</i> = 7.8	.0001
Right	0	—	3,937 ± 361	1,830 ± 229	<i>t</i> = 4.9	.001

Note. Means and standard errors are reported. Dashes indicate that data were not gathered. NC = normal control participants; LTL = left temporal lobectomy patients; RTL = right temporal lobectomy patients; M = male; F = female; VIQ = Wechsler Adult Intelligence Scale—Revised (WAIS-R) Verbal IQ Scale; PIQ = WAIS-III Performance IQ Scale; Benton Faces = Benton Facial Recognition Test; BDI = Beck Depression Inventory.

^a in years (*n* = 10).

glia are implicated in the response to disgusting stimuli (for review, see Adolphs, 2002). Studies using both functional neuroimaging (Blair, Morris, Frith, Perrett, & Dolan, 1999; Morris et al., 1996) and patients with amygdala lesions (Adolphs, Tranel, Damasio, & Damasio, 1994, 1995) have implicated the amygdala in the processing of facial expressions of fear. In contrast, studies of disgust processing have shown activity in the anterior insular cortex, but not the amygdala (Calder, Keane, Manes, Antoun, & Young, 2000; Calder, Lawrence, & Young, 2001; Phillips et al., 1997). These studies suggest that different neural substrates may mediate the experience of fear and disgust, even though both states are globally experienced as unpleasant.

This study addressed two unanswered questions: (a) What is the effect of amygdala lesions on modulation of the acoustic startle reflex by different emotions of negative valence, specifically fear and disgust? and (b) Does the amygdala play a role in the modulation of startle by pleasant emotions, or is its role restricted to unpleasant emotions? We addressed these questions by examining modulation of startle to stimuli from three different emotion categories—pleasant, disgust, and fear—in patients with unilateral damage to the amygdala and in 1 patient with bilateral amygdala damage. Previous work has been equivocal with respect to cerebral asymmetry and startle modulation. In light of this, we examined laterality of the startle reflex as an open question, in terms of both amygdala damage and recording site (left vs. right orbicularis oculi).

Method

Participants

Participants were 12 patients who had undergone temporal lobectomy for the treatment of medically intractable epilepsy (6 right [RTL] and 6 left [LTL]; see Table 1 for demographic and neuropsychological data) and 12

healthy comparison participants (8 male, 4 female). We additionally tested 3 patients with bilateral amygdala damage: Patients 046, 1951, and 1673. Only one of these patients (1673) showed reliable startle reflexes to the stimuli (measurable reflexes for at least 50% of all stimuli), and so data from the other 2 patients are not reported.¹ Patient 1673 acquired brain damage as a result of encephalitis, which resulted in bilateral damage to the medial temporal lobes, including complete lesions of the amygdalae and hippocampi, as well as partial damage to surrounding cortices. All patients were selected from the Patient Registry of the Division of Cognitive Neuroscience at the University of Iowa. All participants were right-handed. All patients were individually administered a 2–3-hr neuropsychological battery that included measures of intellect, anterograde verbal and visual memory, visuoperception, language, and executive functioning. Key indices from this battery are presented in Table 1. All participants gave informed consent to participate in these studies, which were approved by the Human Subjects Committee of the University of Iowa.

Magnetic resonance images were obtained from all patients in a 1.5-T scanner (4096 Plus; General Electric, Waukesha, WI). The scanning protocol used in this study is identical to that used in J. S. Allen, Damasio, and Grabowski (2002). All brains were reconstructed in three dimensions in Brainvox (Frank, Damasio, & Grabowski, 1997), an interactive family of programs designed to reconstruct, segment, and measure brains from magnetic resonance-acquired images. All regions were traced by hand on contiguous coronal slices of the brain.

The remaining volumes of the amygdala and hippocampus were traced in both hemispheres of each patient. Whole brain volumes were also determined. Criteria for the boundaries of both the amygdala and hip-

¹ The finding that only 1 out of 3 patients with amygdala damage show reliable startle reflexes is interesting in itself. One patient, 046, has Urbach–Wiethe disease, which leaves hyaline deposits in the skin that could affect EMG recordings. Patient 1951 had encephalitis, and his brain damage is the most extensive of the 3 patients. Both patients reported feeling startled to the noise bursts, but their EMG responses were not consistent.

pocampus were derived from the atlas of Duvernoy (1988). By a method similar to that of Convit et al. (1999; see also Szabo, Xiong, Lancaster, Rainey, & Fox, 2001), point sets tracing the boundaries of the amygdala and hippocampus were first made in the parasagittal and axial planes; these point sets were then projected to the coronal slices to guide tracing of the regions of interest.

Materials and Design

Sixty pictures were selected from the International Affective Picture System (Lang, Bradley, & Cuthbert, 1999). Pictures were chosen to represent four affective categories: pleasant, neutral, fear, and disgust. Digitized versions of the pictures were displayed on a computer screen 0.5 m in front of the participant. Each participant viewed the picture set in a different, random order. Picture presentation was controlled by PsyScope 1.2.5 software (Cohen, MacWhinney, Flatt, & Provost, 1993). Each picture was presented for 6 s, with an interstimulus interval of between 7 and 9 s, randomly distributed among all pictures. The acoustic startle probe was a 50-ms burst of white noise with an instantaneous rise time and a magnitude of 98 dB. The probe was generated with a Biopac MP150 stimulator and delivered via Sennheiser headphones (Model HDA 200). Startle probes were delivered during 75% of the picture presentations, evenly distributed across pleasant, neutral, fear, and disgust picture categories (12 startle probes presented within each category). Startle probes were presented between 2,500 and 5,000 ms after picture onset.

Electromyographic (EMG) activity from the orbicularis oculi was collected with two In Vivo Metrics (Healdsburg, CA) recording electrodes placed directly below both the right and the left eye using the placement recommended by Fridlund and Cacioppo (1986). Electrode impedances were less than 10,000 Ω . Raw signals were recorded with Biopac EMG150 amplifiers passing 30–500 Hz, with a gain multiplication of 5000, and all EMG data were sampled with a Biopac MP150 interface at a rate of 1000 Hz. The MP150 recorded the EMG signal, which was then half-wave rectified and integrated, with a 10-ms time constant.

Procedure

The participant was seated in a small laboratory room. After the participant had filled a consent form, the electrodes were placed on the participant. Prior to presentation of the affective picture sets, each participant viewed four neutral pictures and received four startle probes, to orient them to the procedure. Prior to the presentation of the experimental stimuli, participants were instructed that they would see a series of pictures varying in emotional content and were asked to “devote all their attention to each picture for the entire time it is onscreen, and to try to ignore the sounds from the headphones.”

After the completion of startle response measurement, pictures were rated on scales of pleasure, arousal, fear, and disgust. For each picture, participants were asked to rate it on the following 9-point scales: *pleasant–unpleasant*, *calming–arousing*, *not fearful–very fearful*, and *not disgusting–very disgusting*. One participant from the RTL group was unable to complete the stimulus ratings.

Data Reduction and Analysis

The following procedure was used to reduce EMG responses to startle probes to eyeblink reflex magnitudes: Peak detection was performed on the integrated EMG response to each probe (between 20 and 120 ms after the white noise burst). Eyeblink reflex magnitudes were calculated by subtracting the amount of integrated EMG activity at reflex onset from the peak amplitude (maximum activity between 20 and 120 ms after probe onset). Each individual startle response was viewed by an experimenter. A total of 7.9% of all eyeblink reflexes were excluded from further analyses because of excessive noise or because the onset of the reflex began less

than 20 ms following the startle probe. Tests for outliers revealed 1 LTL patient to show average startle reflex that was an extreme outlier (Z score = 3.03; greater than other participants' responses), therefore this patient's data were removed from the startle analyses.²

The primary independent variables were group (control, LTL, and RTL), eye (left or right), and stimulus category (pleasant, neutral, fear, disgust). The dependent variables were the eyeblink EMG magnitude and ratings of the stimuli.

The analyses were conducted with a 3 Group \times 2 Eye \times 4 Category repeated measures analysis of variance (ANOVA), with group as a between-subjects variable and eye and category as within-subjects variables. Planned polynomial contrasts were conducted to test the pattern of response to the picture categories. Follow-up 2 Eye \times 4 Category analyses were conducted within each group in order to determine each group's pattern of response across stimulus categories. Stimulus ratings were analyzed with a 3 Group \times 4 Category repeated measures ANOVA. All analyses on within-subjects variables used the mixed-model univariate ANOVA, as opposed to the multivariate approach, because of the relatively small sample size, as suggested by Maxwell and Delaney (1990). The Greenhouse–Geisser epsilon correction procedure (Geisser & Greenhouse, 1959) was used in order to control for the inflated Type I error rate associated with the mixed-model univariate ANOVA when the sphericity assumption is not met (see Vasey & Thayer, 1987). A measure of effect size (eta-squared) is included for each ANOVA analysis. An initial evaluation showed no significant effects of gender on startle magnitude, $F(1, 18) < 1$, $p > .8$, nor did gender interact with group; all analyses are thus collapsed over the variable of gender.

The volume of both right and left amygdalae and right and left hippocampi were combined for separate measures of total amygdala and total hippocampal volumes for use in the correlation analyses. Correlation analyses between the volume of neural structures and startle responses were conducted by using Pearson's correlation coefficient.

Results

Stimulus Ratings

Table 2 presents means and standard errors of the mean for the ratings of all stimulus categories. Ratings of stimuli generally confirmed the a priori classifications of stimuli. Pleasant pictures were rated as more positive than the other categories on ratings of valence, $F(3, 60) = 77.3$, $p < .01$, $\eta^2 = .79$. The groups showed different patterns of valence ratings, as evidenced by a Group \times Category interaction, $F(6, 60) = 3.4$, $p = .02$, $\eta^2 = .25$. There was no overall group difference in valence ratings, however, $F(2, 20) < 1$, $p > .70$, $\eta^2 = .02$. There was additionally a main effect of category for arousal ratings, with disgust, fear, and pleasant pictures being rated as more arousing than the neutral pictures, $F(3, 60) = 33.9$, $p < .01$, $\eta^2 = .80$. The groups showed different patterns of arousal ratings across the picture categories: Group \times Category interaction, $F(6, 60) = 2.7$, $p = .04$, $\eta^2 = .28$. There was no overall group difference in valence ratings, however, $F(2, 20) < 1$, $p > .40$, $\eta^2 = .08$.

Fear pictures were rated as more fearful than the other picture categories ($ps < .01$, $\eta^2 = .95$). There was a significant group difference in fear ratings, $F(2, 20) = 4.0$, $p < .04$, $\eta^2 = .29$, with the LTL group rating the pictures significantly more fearful than

² This patient showed no difference from the others in terms of demographics or neuropsychology but showed heightened responsivity to the startle probes in terms of both EMG responses and self-report after completion of the study.

Table 2
Mean (± SEM) Affective Ratings Across Picture Categories and Groups

Rating type	Picture category			
	Pleasant	Neutral	Fear	Disgust
Valence				
Control	6.7 ± 0.5	4.2 ± 0.4	2.0 ± 0.3	1.6 ± 0.2
LTL	6.8 ± 0.8	5.0 ± 0.6	1.3 ± 0.2	1.3 ± 0.1
RTL	5.7 ± 0.3	4.0 ± 0.7	3.5 ± 0.8	2.5 ± 0.8
Arousal				
Control	6.2 ± 0.5	2.6 ± 0.3	6.6 ± 0.4	6.5 ± 0.5
LTL	5.3 ± 0.7	3.6 ± 0.4	6.5 ± 0.9	6.3 ± 0.9
RTL	3.0 ± 0.9	2.1 ± 0.6	6.2 ± 1.1	6.9 ± 1.4
Fear				
Control	2.2 ± 0.2	1.3 ± 0.1	6.3 ± 0.5	4.3 ± 0.5
LTL	3.3 ± 0.4	2.8 ± 0.5	8.0 ± 0.4	5.8 ± 0.5
RTL	2.8 ± 0.4	2.3 ± 0.6	7.1 ± 0.8	6.0 ± 1.1
Disgust				
Control	1.3 ± 0.1	1.2 ± 0.1	4.0 ± 0.5	7.2 ± 0.5
LTL	2.8 ± 0.8	2.6 ± 0.6	7.4 ± 0.7	7.7 ± 0.3
RTL	2.5 ± 0.8	3.1 ± 0.9	4.5 ± 0.7	6.9 ± 1.0

Note. LTL = left temporal lobectomy group; RTL = right temporal lobectomy group.

the controls ($p = .04$). There was no Group × Category interaction, however. Disgust pictures were rated as more disgusting than the other picture categories ($ps < .01$, $\eta^2 = .87$). There was a main effect of group in disgust ratings, $F(2, 20) = 7.1$, $p = .01$, $\eta^2 = .41$, with the LTL group rating the pictures as more disgusting than the healthy controls ($p = .01$). The groups also showed a different pattern of disgust ratings across stimulus categories: Group × Category interaction, $F(6, 60) = 2.7$, $p = .04$, $\eta^2 = .30$.

Startle Reflex Magnitude

Table 3 presents means and standard errors of the mean for startle magnitude across the three groups, for each picture category, across both eyes. The groups showed different patterns of

Table 3
Mean (± SEM) Left- and Right-Eye Startle Reflex Magnitudes Across Participant Groups and Stimulus Categories

Eye and group	Picture category			
	Pleasant	Neutral	Fear	Disgust
Left eye				
Control	31.7 ± 4.9	36.6 ± 6.0	41.0 ± 6.1	42.8 ± 6.1
LTL	33.7 ± 7.0	35.2 ± 6.2	31.5 ± 5.4	32.3 ± 5.3
RTL	29.9 ± 5.8	38.2 ± 4.7	34.2 ± 4.1	32.5 ± 4.4
1673	37.7	41.4	31.6	39.5
Right eye				
Control	42.4 ± 4.9	49.1 ± 5.3	53.0 ± 5.3	55.5 ± 5.9
LTL	32.0 ± 3.2	32.9 ± 6.7	31.2 ± 4.0	29.4 ± 3.7
RTL	43.0 ± 9.7	45.6 ± 9.0	45.8 ± 10.8	43.7 ± 10.0
1673	28.8	31.6	24.6	29.2

Note. LTL = left temporal lobectomy group; RTL = right temporal lobectomy group; 1673 = patient with bilateral medial temporal lobe damage.

response to the stimulus categories as assessed by a significant Group × Category linear interaction effect, $F(2, 20) = 4.0$, $p < .04$, $\eta^2 = .28$ (see Figures 1 and 2). Within-group analyses showed that only the control group showed a linear pattern of response: (pleasant < neutral < fear < disgust), $F(3, 33) = 5.0$, $p = .01$, $\eta^2 = .31$, whereas the temporal lobectomy groups did not show this pattern: RTL, $F(3, 15) = 2.2$, $p = .18$, $\eta^2 = .31$; LTL, $F(3, 12) < 1$, $p > .5$, $\eta^2 = .12$. In the control group, responses to the pleasant stimuli were smaller than responses to either the fear or the disgust stimuli ($p = .023$ and $p = .014$, respectively), but there was no significant difference between responses to disgust versus fear pictures ($p > .50$). In the RTL group, responses to pleasant stimuli were smaller than those to fearful stimuli ($p = .029$). There were no other pairwise differences between categories in either temporal lobectomy group. The groups did not differ in overall startle magnitude, $F(2, 20) = 1.3$, $p > .30$, $\eta^2 = .11$. Although responses from the right eye tended to be larger than responses from the left eye, this effect was not significant, $F(1, 60) = 2.8$, $p = .11$, $\eta^2 = .12$. The variable of eye did not interact with any of the other variables; however, the control group showed a trend toward greater startle responses from the right eye, $F(1, 33) = 4.8$, $p = .051$, $\eta^2 = .30$. This trend was not found for either temporal lobectomy group ($Fs < 1.3$, $ps > .30$, $\eta^2 < .32$).

Because of the differences in group size between the comparison and temporal lobectomy groups, we conducted an analysis of the emotional modulation of the startle reflex in 6 randomly selected control participants to determine whether this number was sufficient to show the expected pattern of emotional modulation. This analysis revealed a significant effect of emotion in these 6 comparison participants, $F(3, 18) = 9.1$, $p < .01$, $\eta^2 = .60$, suggesting that the sample sizes of the temporal lobectomy groups was sufficient to detect an effect of emotion on startle magnitude in these participants.

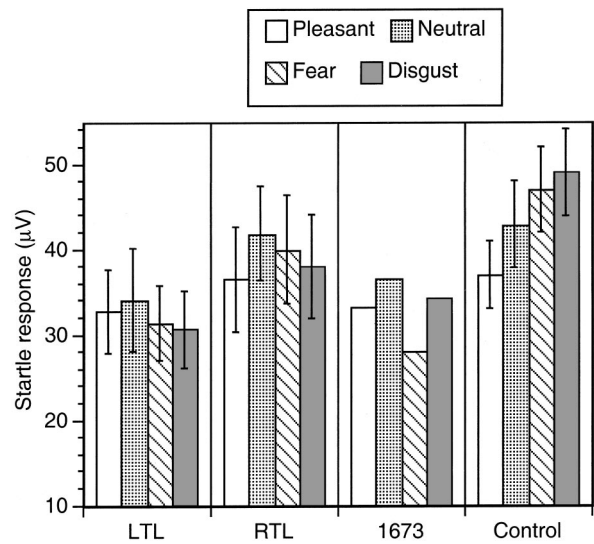


Figure 1. Mean (± SEM) startle responses (in microvolts) averaged across both eyes. LTL = left temporal lobectomy group ($n = 5$); RTL = right temporal lobectomy group ($n = 6$); 1673 = patient with bilateral amygdala damage; Control = healthy control participants ($n = 12$).

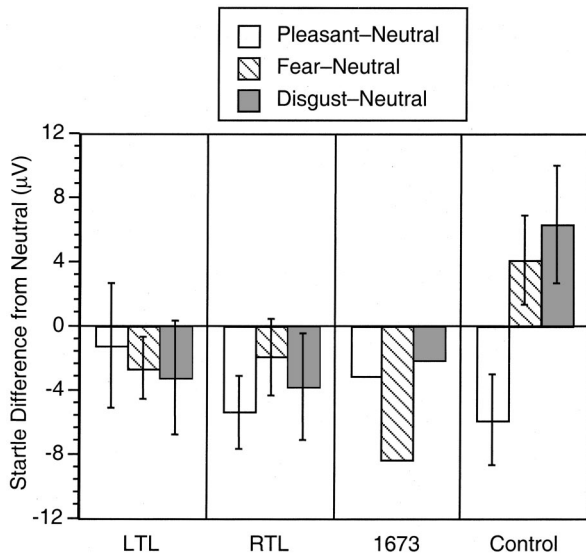


Figure 2. Mean (\pm SEM) differences in startle magnitude between affective categories and neutral, averaged across both eyes. LTL = left temporal lobectomy group ($n = 5$); RTL = right temporal lobectomy group ($n = 6$); 1673 = patient with bilateral amygdala damage; Control = healthy control participants ($n = 12$).

Patient 1673 did not show emotional modulation of the startle reflex recorded from either the left or the right orbicularis oculi recording site, for any of the emotion categories (see Table 3 and Figure 2 for mean responses from this patient). His data are not included in any of the statistical analyses presented here.

In order to compare these results to previous work examining emotion-modulated startle using the three valence categories of pleasant, neutral, and unpleasant, we combined the responses to the fear and disgust stimuli in order to form an unpleasant picture category. A 3 Group \times 3 Valence Category ANOVA showed that the groups differ in their pattern of response to the valence categories, $F(2, 20) = 3.6$, $p < .05$, $\eta^2 = .26$ (Group \times Category linear interaction effect). As in the four category analyses, the control group showed a significant linear effect of stimulus category, $F(2, 22) = 6.1$, $p = .01$, $\eta^2 = .36$, with the pattern pleasant $<$ neutral $<$ unpleasant. Neither the RTL group, $F(2, 10) = 3.5$, $p = .11$, $\eta^2 = .41$, nor the LTL group, $F(2, 8) < 1$, $p > .5$, $\eta^2 = .12$, showed a significant effect of stimulus category.

Differences in startle response pattern across groups in this study could be driven by the magnitude of response from only a few individuals (e.g., a few of the controls could have shown large differences between pleasant and unpleasant stimuli, whereas the temporal lobectomy patients may not have shown this magnitude of difference). Alternatively, it could be that most of the control participants showed the expected pattern but the temporal lobectomy patients did not. We tested these possibilities by assessing the number of participants within each group that showed the following patterns: pleasant $<$ neutral $<$ unpleasant, and separately, pleasant $<$ unpleasant (regardless of responses to neutral). The percentages showing the pleasant $<$ neutral $<$ unpleasant pattern in the control, RTL, and LTL groups were 42%, 20%, and 0%, respectively. This pattern was not statistically significant, $\chi^2(2, N = 23) = 3.6$, $p = .17$. Analysis of the pattern pleasant $<$

unpleasant, however, indicated a significant difference across groups: control, 83%; RTL, 67%; LTL, 20%, $\chi^2(2, N = 23) = 6.2$, $p = .04$.

Correlations Between Ratings and Startle Responses

We conducted correlations between the average affective ratings of the stimuli and the average startle response to the stimuli within each group. Results show that only in the control group were there significant relationships between stimulus ratings and startle responses. Ratings of fear, disgust, and pleasantness were significantly associated with startle responses in the control group ($r_s = .28$, $.41$, and $-.35$; $p_s < .05$, respectively). Ratings of arousal did not show a significant linear correlation ($r = .15$, $p > .10$) with startle magnitude. Neither temporal lobectomy group showed these patterns of association either with normative ratings of the stimuli or with their own within-group ratings ($r_s < .16$, $p_s > .15$).

Correlations Between Neuroanatomy and Startle Responses

Correlations were conducted between volumes of amygdala and hippocampus and startle responses from temporal lobectomy patients. There were no significant correlations between the volume of remaining amygdalae or hippocampi and either startle level ($r_s < .30$, $p_s > .40$) or potentiation to unpleasant picture categories ($r_s < .20$, $p_s > .70$).

Discussion

We investigated the effect of unilateral anteromedial temporal lobe damage including the amygdala on the modulation of the acoustic startle reflex by pleasant, neutral, fear, and disgust stimuli measured bilaterally from the orbicularis oculi muscles. First, we showed that both LTL and RTL patients failed to show the normal potentiation of the startle reflex by either fear or disgust stimuli. Second, the patients with right-sided damage also showed a significant pleasure-attenuated startle, whereas the left-sided group did not show this pattern. A single patient with complete bilateral amygdala damage similarly showed no potentiation to fear or disgust stimuli but did show an attenuated response to pleasant stimuli compared with neutral stimuli.

Results from this study are consistent with animal research showing that the amygdala is necessary for the modulation of the startle reflex by fear (Davis, 1992; Hitchcock & Davis, 1986; Rosen & Davis, 1988), but not by pleasant stimuli (Koch et al., 1996). All patients in our study had varying degrees of damage to either the left or right amygdala, which may result in an alteration of top-down influences on the startle reflex circuit. These findings are consistent with previous studies examining the startle reflex in patients with right amygdala damage (Angrilli et al., 1996; Funayama et al., 2001); both of those studies showed that damage to the right amygdala, caused by either a tumor (Angrilli et al., 1996) or unilateral temporal lobectomy as in our study (Funayama et al., 2001), resulted in a block of the normal potentiation of the startle reflex by unpleasant visual stimuli. Recordings from both the left and the right orbicularis oculi from those with right amygdala damage show significantly reduced startle reactivity to pleasant stimuli compared with responses to fearful stimuli.

However, results from the LTL group in our study are inconsistent with the results of Funayama et al. (2001), who instead found a normal pattern of emotional startle modulation (unpleasant > neutral > pleasant) in an LTL group. This discrepancy between the two studies is surprising because the protocols used were similar (e.g., both used affective stimuli drawn from the same source, both used the same number of startle probes per stimulus category, and both used patients who had unilateral amygdala damage resulting from the same etiology). There are, however, several differences between the studies that might account for this discrepancy in findings. One is that the two groups of patients from the different studies may have had varying degrees of brain damage. Funayama and colleagues report that in their patients, "the extent of the lesion is standard and does not vary greatly between subjects, regardless of side of lesion," and they describe their patients as having removal of "70–80% of the amygdala and all of the hippocampus" (Funayama et al., 2001, p. 727). The surgical procedures for all the patients in the study by Funayama and colleagues were conducted by the same surgeon (E. S. Funayama, personal communication, March 2003), whereas patients in our study received surgical treatment from one of several different surgeons. Consequently, patients in our study had variable degrees of medial temporal lobe damage, ranging from 30% to 91% amygdala volume reduction in the damaged hemisphere compared with the intact hemisphere (see Table 1 for neuroanatomical volumes from each patient group). One would predict that variability in amygdala volume might be reflected in startle magnitude, but correlation analyses from our study found no significant relationship between amygdala volume and startle level or potentiation, perhaps as a result of presurgical amygdala pathology or insufficient variance in amygdala damage for such a correlation to achieve significance.

Another difference between the two studies is that the stimuli used by Funayama and colleagues (2001) were all images depicting people, whereas those used in our study were not. In order to directly compare results from the current study to those from Funayama et al., we examined startle responses to a subset of the stimuli that included images of people.³ Results from this analysis were entirely consistent with those from our prior analysis (no emotional modulation of startle in LTL group) and different from those of Funayama et al. (2001). It is thus unlikely that the inclusion of people in the stimuli can explain the discrepant results. Finally, patients in the LTL group had higher scores on the Beck Depression Inventory (BDI) than those in the RTL group in the current study (see Table 1). Although no measure of depression was reported by Funayama et al., previous research by other investigators has shown altered emotional modulation of startle in depressed patients (N. B. Allen, Trinder, & Brennan, 1999). Although none of our patients fell within the range of clinical depression, the greater reported depression in the LTL group may nonetheless have contributed to differences in startle modulation. Finally, although the LTL group in the Funayama et al. study showed a normal pattern of emotional modulation of startle to picture stimuli, these same patients showed an abnormal startle response to instructed fear, indicating that in at least one measure of startle modulation, these patients were abnormal. Any of the above considerations, alone or in combination, may account for the differences between our findings and those of Funayama et al.

(2001), an issue that, in the end, can only be resolved with further independent studies.

Fear Versus Disgust

Consistent with previous research using emotional modulation of the startle reflex, control participants in the current study showed a linear pattern of startle magnitude increasing from pleasant to unpleasant stimuli. The unpleasant stimulus category in the current investigation consisted of equal numbers of fearful and disgusting picture stimuli. The control participants showed a larger response to disgust than to fear pictures, although this difference was not statistically significant. Neither the LTL nor RTL groups showed potentiated startle responses to fear or disgust stimuli. This finding is counter to predictions derived from research which suggests that the amygdala is preferentially involved in the processing of fear stimuli (for a review, see Adolphs, 2002), whereas other neural areas such as the insular cortex play a role in the processing of disgust (Calder et al., 2000, 2001; Phillips et al., 1997). All of the patients had damage to the anteromedial temporal lobes, including the amygdala, but none of them had damage to insular cortex or basal ganglia. Both animal and human research has suggested that the insula processes affective information prior to at least one level of amygdala processing (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Shi & Davis, 1999). Results from these patients do not allow for a determination of the role of insula–amygdala communication in emotional startle modulation, however. The current results suggest that the emotional modulation of the startle reflex by the amygdala encompasses both fearful and disgusting stimuli, and potentially pleasant stimuli as well.

In spite of the lack of startle potentiation to fear or disgust pictures by either patient group, the temporal lobectomy groups showed similar patterns of stimulus ratings compared with the control group. Although the patterns of ratings were similar across groups, differences were evident for fear and disgust ratings; the LTL group rated the pictures as higher in fear and disgust than the other groups. It seems unlikely that the somewhat higher ratings given by the temporal lobectomy patients could explain their abnormal emotion modulation of startle, as the former were abnormally elevated whereas the latter were abnormally reduced. Previous work has shown that amygdala damage does not affect processing of stimulus valence but does attenuate arousal ratings of face stimuli (Adolphs, Russell, & Tranel, 1999). This is in line with work from animals and functional neuroimaging in humans

³ These stimuli included 7 from the pleasant category and 18 from the unpleasant category (comprising both fearful and disgusting stimuli). Only 3 pictures from the neutral category used in our investigation included depictions of people, and so these were not included in the follow-up analysis. This resulted in a 2 Valence (pleasant with people vs. unpleasant with people) \times 3 Group analysis. There was no significant effect of valence or group, nor was there an interaction between group and valence ($ps > .10$), likely due to low statistical power arising from the smaller number of stimuli in this analysis. Examination of mean differences across groups, however, demonstrated that the control group showed greater responses to the unpleasant stimuli than to the pleasant stimuli (unpleasant–pleasant \pm standard error: 8.6 ± 5.0), whereas neither temporal lobectomy group showed the same magnitude of difference between the two stimulus sets (2.0 ± 2.2 for LTL and 3.2 ± 1.7 for RTL groups).

suggesting a more prominent role for the amygdala in the processing of arousal/intensity of stimuli than in processing valence (Anderson, Christoff, Stappen, et al., 2003; Cahill, 2000; Hamann, Ely, Hoffman, & Kilts, 2002; Small et al., 2003). This disconnection between ratings and startle modulation is interesting and points to future research designed to elucidate the mechanisms of the amygdala's influence on different emotional behaviors.

Pleasure-Attenuated Startle

Results of this study lend partial support to previous findings from animal research demonstrating that the amygdala is not necessary for the attenuation of the startle reflex by pleasant emotional experience (Koch et al., 1996). Koch and colleagues (1996) showed that lesion of the nucleus accumbens, but not the amygdala, resulted in abolished pleasure attenuation of the startle reflex without affecting the overall magnitude of the reflex. These authors suggest that this effect is due to a disruption in the mesolimbic dopamine pathway, which includes the nucleus accumbens (Koch & Schnitzler, 1997). Although only the RTL group in the current study showed a significant attenuation of the startle reflex while viewing pleasant stimuli, on average, the left-sided group and the bilateral patient showed a lower magnitude of response to the pleasant stimuli compared with neutral stimuli. This is in stark contrast to the complete lack of potentiation to the unpleasant stimuli, both fearful and disgusting, by all patients with amygdala damage. Future research could address the neural substrates of pleasure-attenuated startle in humans by testing patients with lesions to the ventral striatum, including the nucleus accumbens.

Issues of Laterality

Several studies have addressed the lateralization of the startle reflex and its modulation by top-down factors such as attention and emotion. Hackley and Graham (1987) showed greater responses from the right orbicularis oculi than from the left to binaural startle probes, whereas startle reflexes to monaural probes were greater on the ipsilateral recording side. Bradley, Cuthbert, and Lang (1991) demonstrated that left-sided, but not right-sided, monaural presentation of the startle probe resulted in the expected linear modulation of the reflex by affective pictures (pleasant < neutral < unpleasant; Bradley et al., 1991). Using the threat-of-shock paradigm, Grillon and Davis (1995) demonstrated that right-sided, but not left-sided, monaural startle probe presentation led to a pronounced potentiation of startle. These findings suggest a lateralization of startle modulation that is task-dependent (picture viewing vs. threat of shock). They are also consistent with the work of Funayama and colleagues (2001), who showed that LTL patients showed normal startle modulation to pictures, but not threat of shock, and that patients with RTL showed normal startle modulation to threat of shock, but not pictures.

Considerable research on the neural organization of emotion has suggested a cerebral asymmetry of emotional processes. Different models have arisen from this research, one of which suggests that emotion is lateralized to the right hemisphere (Borod, 1993); one which holds that positive emotions are distributed to the left hemisphere, whereas negative emotions are relegated to the right hemisphere (Davidson & Irwin, 1999); and another which suggests

that individual emotions are processed by discrete neural substrates (Adolphs et al., 1995; Blair et al., 1999; Ekman, 1992). These models have each found empirical support in one form or another, although with the enhanced spatial resolution of structural and functional neuroimaging, more recent work has focused on delineating discrete neural substrates of individual emotions (for review, see Adolphs, 2002).

Several studies have examined the potential lateralization of the neural correlates of both the startle reflex itself as well as its affective modulation. Considerable neuroanatomical research has elucidated the circuitry of the startle reflex (Davis, Gendelman, Tischler, & Gendelman, 1982; Koch & Schnitzler, 1997; Yeomans & Frankland, 1995). Davis and colleagues demonstrated that the startle circuitry of the rat consists of an ipsilateral pathway from the auditory nerve to the ventral cochlear nucleus, which crosses the brainstem to the contralateral nucleus reticularis pontis caudalis (RPC; Davis et al., 1982). The top-down influence of the amygdala on the startle circuit consists of a predominantly ipsilateral connection between the central nucleus of the amygdala to the RPC via the caudal amygdalofugal pathway (Rosen, Hitchcock, Sananes, Miserendino, & Davis, 1991). Lesions anywhere along this circuit block fear-potentiated startle in the rat (Hitchcock & Davis, 1991). The RPC sends output to the ipsilateral facial nucleus, which contains the motoneurons that innervate the orbicularis oculi muscle (Meloni & Davis, 1992). The actual connections of the human startle circuitry have not been characterized, but the cross-species similarity in the reflex circuitry suggests that connections in the human should be similar to those documented in other species such as the rat or cat (Yeomans & Frankland, 1995).

On the basis of this ipsilateral connection from the amygdala to the RPC to the facial nucleus, one might expect an attenuated emotional modulation of startle measured from the recording site ipsilateral to the lesion. This pattern was not found, however. This may be due to the predominantly contralateral projections of the auditory system. Previous research examining the asymmetry of startle reactivity has shown lateralized effects only using monaural stimulation (Bradley et al., 1991; Grillon & Davis, 1995), although Hackley and Graham (1987) showed larger right-sided eyeblink reflexes during binaural stimulation. These findings suggest that with binaural auditory stimulation, as used in the current study, the intact contralateral connections from the auditory connections through the amygdala to the output circuitry may contribute to the overall level of the bilateral eyeblink reflexes. The lack of startle reflex potentiation to unpleasant stimuli from both left and right recording sites in these patients suggests that perhaps the integrity of both right and left anteromedial temporal lobe is necessary for the normal modulation of the response. Indeed, Patient 1673, with bilateral medial temporal lobe damage, showed a similar lack of startle potentiation to unpleasant stimuli from both the left and right orbicularis oculi. Future work could further address this by using both monaural and binaural stimulation in an emotion-modulated startle paradigm with temporal lobectomy patients.

Summary

Results from this study further support the hypothesis that the anteromedial temporal lobe is a key component in the modulation of the startle reflex by negative emotion, in humans as in other animals. Damage to either the right or left anteromedial temporal

lobe region, including the amygdala, is sufficient to abolish the normal modulation of the acoustic startle reflex by either fear or disgust pictures. Although the amygdala has been most associated with the emotion of fear, these results illustrate that amygdala damage alters the response to disgust stimuli as well. A specific role of the amygdala for pleasure-attenuated startle cannot be suggested with these data, as all patients showed a (nonsignificant) reduction in startle magnitude to the pleasant stimuli. These data support animal research that suggests a role for the nucleus accumbens, but not the amygdala, in pleasure-attenuated startle. These patterns were found in the measurement of the reflex from both left and right orbicularis oculi recording sites and suggests that unilateral amygdala damage affects the modulation of the startle reflex bilaterally.

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Received July 22, 2003

Revision received October 14, 2003

Accepted October 20, 2003 ■