Research Article

EXPRESSION WITHOUT RECOGNITION: Contributions of the Human Amygdala to Emotional Communication

Adam K. Anderson and Elizabeth A. Phelps
Yale University

Abstract—*A growing body of evidence from humans and other animals suggests the amygdala may be a critical neural substrate for emotional processing. In particular, recent studies have shown that damage to the human amygdala impairs the normal appraisal of social signals of emotion, primarily those of fear. However, effective social communication depends on both the ability to receive (emotional appraisal) and the ability to send (emotional expression) signals of emotional state. Although the role of the amygdala in the appraisal of emotion is well established, its importance for the production of emotional expressions is unknown. We report a case study of a patient with bilateral amygdaloid damage who, despite a severe deficit in interpreting facial expressions of emotion including fear, exhibits an intact ability to express this and other basic emotions. This dissociation suggests that a single neural module does not support all aspects of the social communication of emotional state.*

Internal affective states are often associated with the production of observable emotion-specific facial (Ekman, 1992) and vocal (Scherer, 1986) expressions. These substantially invariant signals allow for effective nonverbal social communication of emotional state. Social organisms are often dependent on the correct appraisal of these signals to mobilize appropriate actions to biologically significant events. For example, in nonhuman primates, it has been shown that the observation of social signals of fear early in development is critical for the acquisition of normal affective reactions to dangerous environmental stimuli (e.g., Mineka, Davidson, Cook, & Keir, 1984). In light of its biological importance, social-emotional communication has been proposed as representing a distinct capacity supported by a defined neural substrate (Borod, 1993; Bowers, Bauer, & Heilman, 1993; Kling & Brothers, 1992; Rosvold, Mirsky, & Pribram, 1954).

Recent progress in specifying the neural substrates of human emotion has emphasized the involvement of the amygdaloid complex, a relatively small cluster of nuclei located within the anterior temporal lobes (e.g., Aggleton, 1992; LeDoux, 1996). Numerous sources of evidence from both human and nonhuman animals suggest that the amygdala is involved in such varied emotional functions as the acquisition of conditioned-fear responses (e.g., Bechara et al., 1995; LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; for review, see LeDoux, 1996), the emotional modulation of memory (LaBar & Phelps, 1998; for review, see Cahill & McGaugh, 1998), and the evaluation of stimuli with affective significance (e.g., Blanchard & Blanchard, 1972; Irwin et al., 1996), including social expressions of emotion (Adolphs, Tranel, Damasio, & Damasio, 1994; Breiter et al., 1996; Broks et al., 1998; Calder et al., 1996; Morris et al., 1996; Young, Hellawell, Van De Wal, & Johnson, 1996). Accordingly, the amygdala has been widely viewed as the best candidate for a neural substrate dedicated to emotional functioning.

Address correspondence to Adam K. Anderson, Department of Psychology, Yale University, P.0. Box 208205, New Haven, CT 06520-8205; e-mail: adam.k.anderson@yale.edu.

Evidence supporting the amygdala's involvement in social communication has come from studies of lesions of the amygdala in nonhuman primates. Such lesions have been shown to cause a lowering of social rank (Rosvold et al., 1954), which can result in isolation and eventual early mortality in the wild (Kling & Brothers, 1992). There is now substantial evidence implicating the amygdala in the normal evaluation of social signals in humans as well. Lesions of the amygdala in humans impair the evaluation of critical nonverbal social signals such as direction of eye gaze (Young et al., 1996) and the ability to distinguish between threatening and docile-looking faces (Adolphs, Tranel, & Damasio, 1998). The majority of evidence has demonstrated that the human amygdala is more important for the appreciation of social signals related to danger than for the appreciation of any other stimulus class (Adolphs et al., 1994, 1998; Breiter et al., 1996; Broks et al., 1998; Calder et al., 1996; Morris et al., 1996; Scott et al., 1997). In particular, damage to the amygdala yields differentially severe impairments in the evaluation of expressions of fear (Adolphs et al., 1994; Broks et al., 1998; Calder et al., 1996). This evidence suggests the human amygdala may represent a critical neural substrate for the appraisal of social signals to biologically significant events.

However, the specification of the human amygdala's role in the social communication of emotion is incomplete. Although multiple sources of evidence support the conclusion that the amygdala is important for the evaluation of emotional social signals, particularly those of fear, the extent of the amygdala's larger contribution to emotion and its social communication remains unclear. The effective social communication of emotion requires the capacity to both encode (send) and decode (receive) emotional signals. If the amygdala supports all aspects of emotional signaling in humans, then it should be important for the propagation of social signals as well. Accordingly, damage to the amygdala should result in similar impairments in the ability to express and to evaluate facial expressions of emotion. We tested this hypothesis in a patient with bilateral amygdala damage (patient S.P.), by examining conjointly her ability to evaluate and to express fear, and five other basic facial signals of emotion.

METHOD

Participants

We studied S.P., a 54-year-old woman whose first signs of neurological insult occurred early in development, at approximately 3 to 4 years of age. S.P. was later diagnosed with epilepsy. She was considered for surgical treatment when her medically intractable complex partial seizures of right medial temporal lobe origin began to occur with greater frequency during middle age. At the age of 48, S.P.

had her right amygdala removed secondary to an anteromedial temporal lobe resection. In addition, prior to her right temporal lobe resection, a lesion in the left amygdaloid region was observed. Two biopsies in this region revealed reactive gliosis extending throughout her left amygdala. More detailed information on S.P.'s neuropsychological status and illustrations of the extent of her lesions are available in Phelps et al. (1998).

S.P. received a high school education, has taken college courses, and presents a normal neuropsychological profile, including normal IQ (Verbal IQ of 104, Performance IQ of 107, and Full-Scale IQ of 106 on the Wechsler Adult Intelligence Scale–Revised). S.P.'s visual-perceptual functioning was found to be largely unimpaired. Her discrimination of the identity of unfamiliar faces, as assessed by the Benton test of facial discrimination (Benton, Hamsher, des Varney, & Spreen, 1994), was intact. In addition, S.P. was asked to judge whether a face exemplar was male or female and to make old/young judgments regarding the age of faces. She revealed a largely intact ability to discriminate both the gender (40/40 = 100%) and the age (28/32 = 87.5%) of unfamiliar faces. These findings suggest S.P. was able to interpret multiple sources of nonemotional information contained in faces.

We compared S.P.'s performance with the performance of 20 control subjects of similar age and education on three measures of emotional functioning: facial affect evaluation, lexical affect identification, and facial affect generation. Informed consent was obtained from all participants prior to their participation.

Materials and Procedure

Facial affect evaluation

For this task, S.P. and control subjects rated how appropriately a verbal emotion term matched a presented facial expression. Six emotion terms were used in the experiment (*afraid*, *angry*, *disgusted*, *happy*, *sad*, and *surprised*), and the facial stimuli consisted of prototypical exemplars for these emotions, plus neutral expressions. Each facial emotion category had six independent exemplars of that emotion (three male, three female), for a total of 42 facial stimuli. Facial affect stimuli were a selected subset from the *Pictures of Facial Affect* series (Ekman & Friesen, 1976). From the provided norms, the average percentage agreement for the six exemplars chosen to represent each emotion in this experiment was 90.8% for afraid, 92.5% for angry, 97.5% for disgusted, 99.8% for happy, 88.5% for sad, and 96% for surprised facial expressions.

The experimental procedure was based on that of Adolphs et al. (1994). Upon presentation of a facial exemplar, participants were to evaluate the facial expression with regard to a previously presented emotion term. For example, when presented with the term "happy," subjects were asked to respond to the question "How happy does this person look?" on a scale from 1 to 6 (1 = *not at all*, 6 = *very much*). Each face was seen once with each emotion term. Emotion terms were blocked so that a subject was given the same emotion term for all 42 faces before the switch to a new emotion term. The order of blocks was randomized across participants. Neither S.P. nor control subjects had been exposed to any of these stimuli prior to testing.

Lexical affect identification

For this task, S.P. and control subjects were asked to indicate which emotion term best matched an emotional situation described in a written sentence. Ten sentences were administered for each of the six emotion types used in the facial affect evaluation task (anger, disgust, fear, happiness, sadness, and surprise). Participants were asked to read each sentence independently and pick from the six emotion terms the one that was most appropriate for the described situation.

Facial affect generation

For this task, S.P. and control subjects were asked to pose six emotions they were previously asked to evaluate. Participants were positioned in the view of a computer-controlled digital camera that acquired 8-bit images at a rate of 30 per second. A window of live footage of the subject's actions was presented on the computer screen. On a given trial, each subject was presented with one of six facial expression terms (*afraid*, *angry*, *disgusted*, *happy*, *sad*, and *surprised*), with a neutral expression administered first as a baseline. The participant was requested to first think of an event that would make him or her feel the named emotion and then show what the appropriate facial expression for that emotion would look like. Each emotion was administered twice in succession, with filming lasting 10 s per trial. The order of emotion terms was random across participants. Control subjects performed the facial generation task approximately 1.5 hr following completion of the facial evaluation task. S.P. generated her expressions 1 month following completion of the facial evaluation task.

Scoring of the generated affective expressions was accomplished using four condition-blind judges. For each subject, the first condition-blind observer was asked to select a single clip from each of the two films taken of each expression type, resulting in 12 clips (6 expressions × 2 runs), plus a neutral expression. Each clip was chosen to represent the point of "peak" expressiveness for the given emotion type during the 10 s of filming. The three remaining judges were presented with these isolated film clips plus the neutral expression for comparison. Each judge was asked to rate the appropriateness of each expression for its target emotion on a scale from 1, *not at all*, to 6, *very much*. All judges were first given prototypical exemplars of each emotion type from the *Pictures of Facial Affect* series (Ekman & Friesen, 1976) to use as a basis for their ratings. The reliability of the ratings was then determined by computing the average correlation between the ratings of the three judges (average Pearson's $r = .76$). The aggregate reliability of the composite ratings across the three judges was computed with the Spearman-Brown equation ($r = .91$). With this sufficient interjudge agreement, we collapsed the ratings across judges and submitted the average ratings for S.P. and control subjects to analysis.

RESULTS

Facial Affect Evaluation

We first considered the ratings of the facial expressions prototypical for each emotion term and found that S.P. was severely impaired in her appraisal of fear, yielding a mean rating of 2.67 out of 6 ($z = 3.3$, $p < .05$). However, her impairments were not restricted to fear. S.P. revealed diminished sensitivity to expressions of disgust ($M = 2.17$, $z = 6.9$, $p < .05$), sadness ($M = 3.17$, $z = 2.8$, $p < .05$), and, to a lesser extent, happiness ($M = 4.33$, $z = 3.5$, $p < .05$), as well. Her ratings of expressions of surprise and anger were unimpaired.

Although we cannot ascertain whether these deficits in evaluating expressions in addition to fear are due to damage to S.P.'s amygdala directly, or to her additional right-hemisphere cortical lesions, evidence suggests that selective amygdalar lesions result primarily in impairments in fear (Adolphs et al., 1994; Calder et al., 1996). Patients with more encompassing lesions to the amygdala and other medial temporal lobe structures have also shown less selective deficits in recognition of facial expressions (Anderson, LaBar, & Phelps, 1996; Schmolck & Squire, 1999). Across patients, however, damage to the amygdala is most associated with impairments in the recognition of fear (Broks et al., 1998). Further, S.P. exhibited a pattern of impairment in the evaluation of expressions other than fear that is largely consistent with her extra-amygdalar damage in the right anteromedial temporal lobe (Anderson et al., 1996). Thus, we conservatively assert that S.P.'s deficits in recognizing expressions of fear are associated with lesions of her amygdala.

To further establish the extent of S.P.'s impairment in the evaluation of fearful facial expressions, we next analyzed her evaluation of fearful content across expressions prototypical of various emotions. Figure 1 illustrates that unlike control subjects, S.P. did not discriminate fear from expressions prototypical of other affective states. In fact, she perceived expressions of sadness as more representative of fear than prototypical expressions of fear (ratings of 3.17 for sad faces vs. 2.67 for fearful faces). Similarly, although the control subjects' ratings were much higher for fearful expressions (4.77) than for neutral expressions (1.67), S.P. barely discriminated fearful from neutral expressions (ratings of 2.67 and 2.17, respectively). A comparison of facial expression evaluation in S.P. and other patients with bilateral amygdala damage is available in Adolphs, Tranel, et al. (1999).

Lexical Affect Identification

S.P.'s deficit in evaluating facial expressions of fear, however, was not due to an inability to interpret the meaning of the emotion terms used in the experiment. When asked to assign the appropriate emotion label to descriptions of emotional situations, S.P. performed within the normal range on all emotions: Out of 10 sentences for each emotion, she chose the correct label 9 times for fear (vs. 9.0 ± 2.4 for control subjects), 7 times for anger (vs. 9.2 ± 2.7), 8 times for disgust (vs. 9.2 ± 1.7), 9 times for happiness (vs. 9.6 ± 1.4), 10 times for sadness (vs. 8.4 ± 3.3), and 5 times for surprise (vs. 8.7 ± 2.6). Thus, S.P. revealed relatively intact lexical knowledge of various emotional states.

Facial Affect Generation

As illustrated in Figure 2, the average ratings of the three judges revealed that S.P.'s production of facial expressions was equal to, or better than, the mean performance of control subjects for all expression types. There were no significant differences between S.P. and control subjects on any expression type (z scores ranged from −0.01 for happy to −1.47 for angry, all ps > .14). S.P.'s expressions were

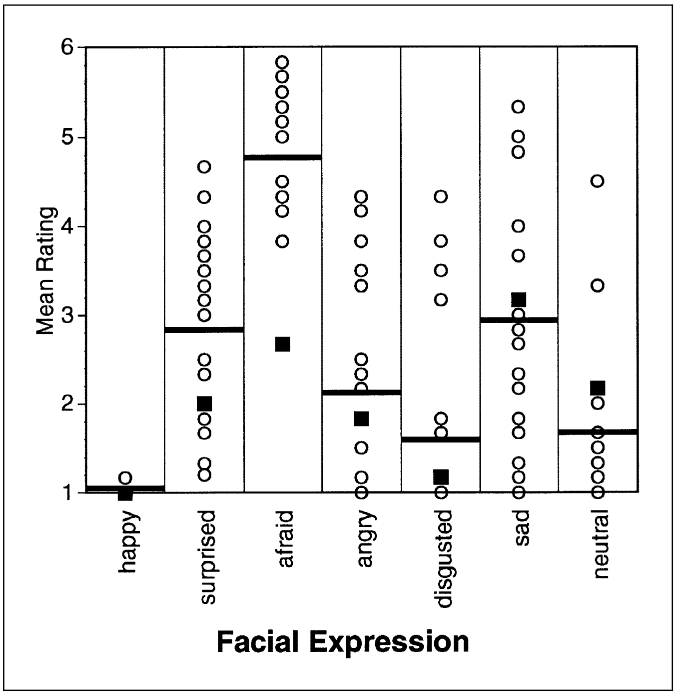

Fig. 1. S.P.'s and control subjects' ratings of fear for expressions prototypical of six emotion types plus neutral expressions. The ratings indicate how much S.P. and control subjects viewed each type of facial expression as representative of fear, on a scale from 1 (*not at all*) to 6 (*very much*). Data for control subjects are represented by open circles (overlapping data points are not represented), and S.P.'s ratings are represented by filled squares. The heavy horizontal bars indicate means for the control subjects.

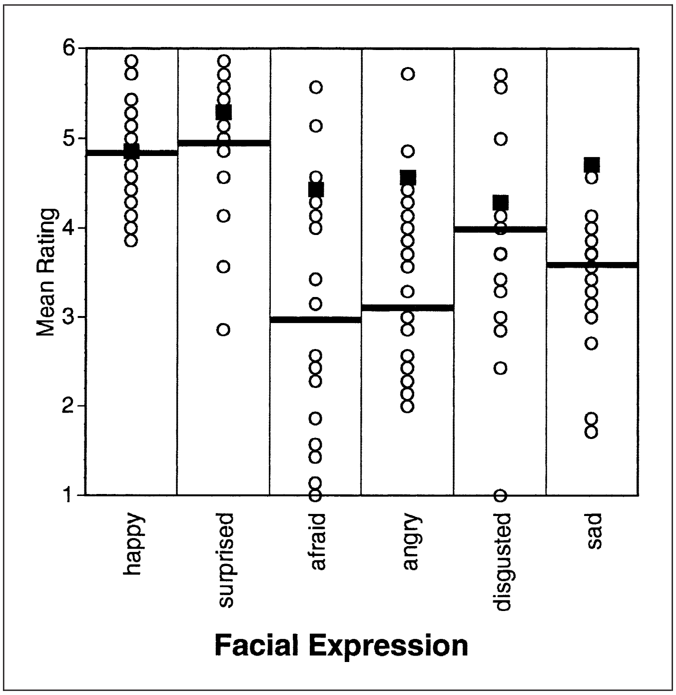

Fig. 2. Condition-blind judges' ratings of the appropriateness of S.P.'s and control subjects' facial expressions. The ratings indicate how much the judges viewed each subject's facial expressions as representative of the target emotion, on a scale from 1 (*not at all*) to 6 (*very much*). Data for control subjects are represented by open circles (overlapping data points are not represented), and S.P.'s ratings are represented by filled squares. The heavy horizontal bars indicate means for the control subjects.

generally as accurate as the upper range of control performance, ranging from the 50th percentile for happy expressions to the upper 90th percentile for sad expressions.

In particular, although S.P. provided little evidence that she could identify expressions of fear, she was remarkably capable of displaying fear. The judges' ratings revealed that S.P.'s fearful expressions were in the normal range (4.43 vs. 2.96 for control subjects, $z = -1.1$, $p > .30$) and were as accurate as the upper range of control subjects' fearful expressions, falling in the top 85th percentile. As illustrated in Figure 3, standardized difference scores between S.P. and control subjects reveal that although S.P. was severely impaired in her ratings of fearful faces, judges rated her fearful expressions as intact. This dissociation is best illustrated in Figure 4a. The picture on the left is a prototypical exemplar of fear from the *Pictures of Facial Affect* series (Ekman & Friesen, 1976). S.P. did not endorse this face as fearful in the evaluation task, giving it a rating of 2 on the fear scale (in comparison, control subjects gave it a rating of 5.0, $z = 1.97$, $p < .05$). S.P.'s graphic portrayal of fear is shown on the right in Figure 4a. Figure 4b shows examples of S.P.'s generated expressions to each of the six basic emotion types. As these illustrations demonstrate, in contrast to her impaired performance in the evaluation of facial emotion, S.P. is largely able to convey emotion with her own face.

DISCUSSION

Evidence of S.P.'s impaired ability to evaluate facial expressions is consistent with the human amygdala's proposed role in the appraisal of social displays of emotion (Adolphs et al., 1994; Breiter et al., 1996; Broks et al., 1998; Calder et al., 1996; Morris et al., 1996). Our

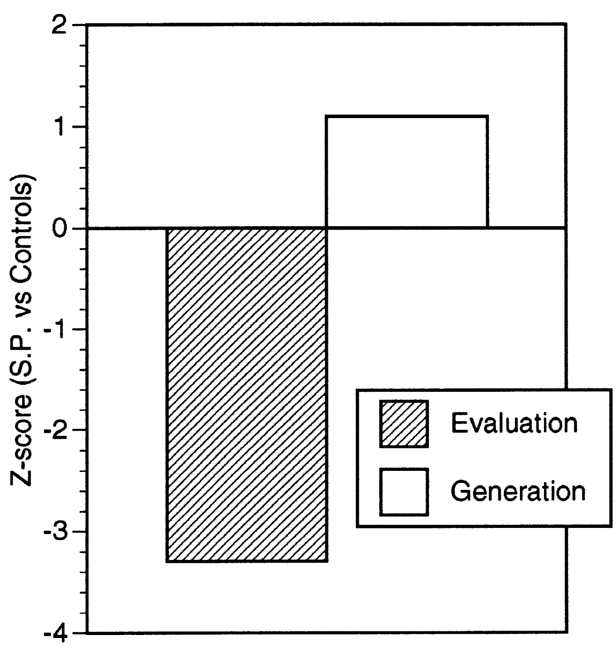

Fig. 3. Standardized difference scores (S.P.'s minus control subjects' means) for performance on the evaluation and the generation of facial expressions of fear.

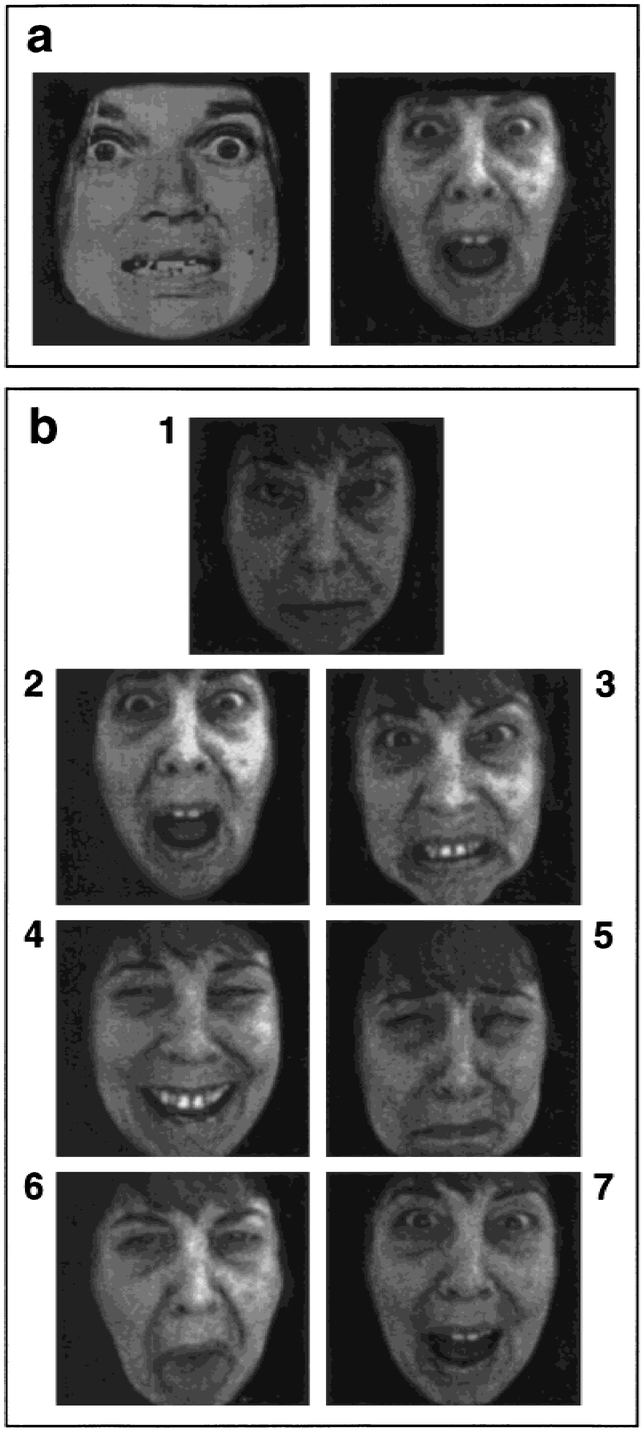

Fig. 4. S.P.'s generation of facial expressions. In (a), the face on the left is an example of a fearful expression that S.P. did not endorse as fearful; the face on the right is an example of S.P.'s own facial expression of fear, rated to be an accurate depiction of fear by condition-blind judges. The faces in (b) are examples of S.P.'s facial expressions of neutral content (1), fear (2), anger (3), happiness (4), sadness (5), disgust (6), and surprise (7).

results agree with those of previous studies in that we found that damage to the amygdala impairs the normal appraisal of fearful facial displays (Adolphs et al., 1994; Broks et al., 1998; Calder et al., 1996), but we also found that S.P.'s impairments in the appraisal of facial emotion were not restricted to fear. Considering her extra-amygdalar damage, it is not possible to ascertain whether these additional impairments are due to damage to the amygdala specifically, or to her additional right-hemisphere anteromedial temporal lobe resection (Anderson et al., 1996). Nonetheless, our findings suggest that the extent of her bilateral amygdalar damage is sufficient to reveal impairments in evaluating expressions of fear, as found in prior studies (Adolphs et al., 1994; Broks et al., 1998; Calder et al., 1996).

In contrast, we provide evidence that lesions of the amygdala and surrounding right-hemisphere anteromedial cortex do not compromise the ability to express fear and other basic emotions. S.P.'s inability to correctly appraise the emotional meaning contained in faces, despite her accurate portrayal of these same emotions, provides evidence that these two functions are dissociable (Borod, Koff, Lorch, & Nicholas, 1986; Ross, 1981). Much as verbal language is divided into comprehension and production processes in the brain (e.g., Geschwind, 1970), the evaluation and generation of nonverbal emotional signals appear to be largely distinct capacities, dependent on different brain regions (e.g., Ross, 1981). This finding provides further evidence that, like cognition, emotion has a modular organization. Emotions are not unitary constructs supported by a single neural locus, but can be decomposed into specialized subcomponents. Accordingly, the observed selectivity of impairment for the particular mode of communication (evaluation vs. generation) demonstrates that the human amygdala supports only the encoding of affect, and therefore does not play a larger role in the social communication of emotional state.

Facial expressions are often an observable concomitant of internal affective states. Our finding of spared affective facial behavior may then be viewed as contradicting evidence of the amygdala's role in the generation of affective experience (for review, see Davidson & Irwin, 1999). However, our results cannot address directly the amygdala's involvement in the evocation of central affective states and their influence on resultant spontaneous facial expressions. Electrophysiological measures suggest that spontaneous facial expressions accompanying changes in affective state involve the recruitment of anterior brain regions (Davidson, Ekman, Saron, Senulis, & Friesen, 1990) that may include the amygdala. Rather than implicating the amygdala, however, such findings more likely reveal that regions within the frontal lobes, such as the ventromedial or orbitofrontal sectors, are critical for the generation of affective experience (Davidson & Irwin, 1999) and associated facial expressions (Weddell, Miller, & Trevarthen, 1990). We conclude that the amygdala is not necessary for the appropriate facial display of fear and other emotions, but may nevertheless be involved in their amplification in genuine emotion-eliciting contexts.

There may be some concerns regarding the basis of S.P.'s intact facial expressions. For example, the ordering of the tasks allowed for S.P. and control subjects to view facial expressions before being asked to generate them. Could this initial viewing possibly have helped S.P. to generate facial expressions? This is unlikely for two reasons. In S.P.'s case, the delay between the evaluation and generation tasks was sufficiently long (i.e., 1 month) to make this explanation improbable. Further, S.P. offered little evidence that she could easily discriminate expressions of fear, for example, from those that were simply neutral. Therefore, her impaired perceptions were not likely to have aided her ability to generate accurate facial expressions. In addition, both S.P. and control subjects were requested to first think of an event appropriate for the target emotion to be displayed. The importance of this instruction, and whether genuine affective states were induced in S.P. and control subjects, is unknown. Nevertheless, if S.P. were impaired in the ability to achieve the target affective state relative to control subjects, we expect this would have resulted in muted facial expressiveness, which was not apparent in S.P.'s performance. In fact, although her performance did not differ significantly from that of control subjects, judges rated her expressions to be generally more accurate.

WHAT IS THE HUMAN AMYGDALA'S ROLE IN SOCIAL COMMUNICATION?

The amygdala's selective contribution to the appraisal but not the expression of emotion may be revealing about the amygdala's precise role in humans. One well-established function of the amygdala is its contribution to emotional learning and memory (Cahill & McGaugh, 1998; LeDoux, 1996). We propose that the facial display of emotion is not mediated by the amygdala because it is not an acquired capacity. The production of nonverbal expressions of emotion is thought to be largely innate (Darwin, 1872/1998), as suggested by demonstrations that the congenitally blind and deaf display a variety of facial and vocal emotions (Eibl-Eibesfeldt, 1973). Although there is evidence to suggest that young infants can visually discriminate some emotions (Nelson & De Haan, 1997), competence in evaluating facial expressions continues to develop well past infancy (Kolb, Wilson, & Taylor, 1992; Nelson & De Haan, 1997). The amygdala may therefore be important for the acquisition of the significance of facial expressions. Consistent with this notion, some studies suggest that damage to the amygdala early in development is an important prerequisite for the impaired evaluation of facial expressions (Adolphs et al., 1994; Anderson et al., 1996; Hamann et al., 1996; but see Broks et al., 1998).

This interpretation, however, is restricted to the domain of nonverbal expressions of emotion. We found that S.P. revealed intact knowledge related to fear and other emotions she found difficult to interpret from faces. She revealed no deficit in matching emotion terms appropriately to descriptions of emotional situations. This result is consistent with findings from other studies of patients with amygdala lesions revealing largely spared emotional knowledge (Adolphs, Tranel, Damasio, & Damasio, 1995; Broks et al., 1998; but see Adolphs, Russell, & Tranel, 1999). Intact comprehension of emotion-inducing situations, at least as tested here, is mediated through lexical knowledge. Thus, as previously argued (Adolphs et al., 1995), the amygdala may be more important for the analysis of nonverbal than verbal expressions of emotion (Adolphs et al., 1994, 1998; Young et al., 1996). Accordingly, although situation-emotion schema may be learned, they may be largely mediated through verbal knowledge, and hence are likely supported by other neural systems outside the amygdala.

The amygdala may also be involved in the acquisition of emotional responses through nonverbal social communication. For example, it has been shown in nonhuman primates that the social display of fear is an important pathway for learning about the emotional significance of potentially harmful stimuli (e.g., Mineka et al., 1984). Thus, fearful facial expressions may be important for learning to fear previously neutral environmental stimuli. According to this perspective, the amygdala's contributions to the appraisal of social signals may be related to the role such expressions play in the acquisition of stimulus significance. Therefore, the preserved expression but impaired appraisal of facial expressions may reflect the amygdala's larger and more fundamental role in emotional learning and memory (Cahill & McGaugh, 1998; Phelps & Anderson, 1997).

Acknowledgments—A portion of this work was presented at the 27th Society for Neuroscience Conference, New Orleans, LA, October 1997. We would like to thank S.P. for her generous participation in this research and her permission to publish her facial expressions. This work was supported by National Institute of Mental Health Grant 50812 to E.A.P.

REFERENCES

Adolphs, R., Russell, J.A, & Tranel, D. (1999). A role for the human amygdala in recognizing emotional arousal from unpleasant stimuli. *Psychological Science*, *10*, 167–171.

Adolphs, R., Tranel, D., & Damasio, A.R. (1998). The human amygdala in social judgment. *Nature*, *393*, 470–474.

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, *372*, 669–672.

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1995). Fear and the human amygdala. *Journal of Neuroscience*, *15*, 5879–5891.

Adolphs, R., Tranel, D., Hamann, S., Young, A.W., Calder, A.J., Phelps, E.A., Anderson, A., Lee, G.P., & Damasio, A.R. (1999). Recognition of facial emotion in nine individuals with bilateral amygdala damage. *Neuropsychologia*, *37*, 1111–1117.

Aggleton, J.P. (1992). *The amygdala: Neurobiological aspects of emotion, memory, and mental dysfunction*. New York: Wiley-Liss.

Anderson, A.K., LaBar, K.S., & Phelps, E.A. (1996). Facial affect processing abilities following unilateral temporal lobectomy. *Society for Neuroscience Abstracts*, *22*, 1866.

Bechara, A., Tranel, D., Damasio, H., Adolphs, R., Rockland, C., & Damasio, A.R. (1995). Double dissociation of conditioning and declarative knowledge relative to the amygdala and hippocampus in humans. *Science*, *269*, 1115–1118.

Benton, A.L., Hamsher, K., des Varney, N.R., & Spreen, O. (1994). *Contributions to neuropsychological assessment: A clinical manual*. New York: Oxford University Press.

Blanchard, D.C., & Blanchard, R.J. (1972). Innate and conditioned reactions to threat in rats with amygdaloid lesions. *Journal of Comparative and Physiological Psychology*, *81*, 281–290.

Borod, J.C. (1993). Cerebral mechanisms underlying facial, prosodic, and lexical emotional expression: A review of neuropsychological studies and methodological issues. *Neuropsychology*, *7*, 445–463.

Borod, J.C., Koff, E., Lorch, M.P., & Nicholas, M. (1986). The expression and perception of facial emotion in brain-damaged patients. *Neuropsychologia*, *24*, 169–180.

Bowers, D., Bauer, R.M., & Heilman, K. (1993). The nonverbal affect lexicon: Theoretical perspectives from neuropsychological studies of affect perception. *Neuropsychology*, *7*, 433–444.

Breiter, H.C., Etcoff, N.L., Whalen, P.J., Kennedy, W.A., Rauch, S.L., Buckner, R.L., Strauss, M.M., Hyman, S., & Rosen, B. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron*, *17*, 875–887.

Broks, P., Young, A.W., Maratos, E.J., Coffey, P.J., Calder, A.J., Isaac, C.L., Mayes, A.R., Hodges, J.R., Montaldi, D., Cezayirli, E., Roberts, N., & Hadley, D. (1998). Face processing impairments after encephalitis: Amygdala damage and recognition of fear. *Neuropsychologia*, *36*, 59–70.

Cahill, L., & McGaugh, J.L. (1998). Mechanisms of emotional arousal and lasting declarative memory. *Trends in Neurosciences*, *21*, 294–299.

Calder, A.J., Young, A.W., Rowland, D., Perrett, D., Hodges, J.R., & Etcoff, N.L. (1996). Facial emotion recognition after bilateral amygdala damage: Differentially severe impairment of fear. *Cognitive Neuropsychology*, *13*, 699–745.

Darwin, C. (1998). *The expression of the emotions in man and animals*. New York: Oxford University Press. (Original work published 1872)

Davidson, R.J., Ekman, P., Saron, C., Senulis, J., & Friesen, W.V. (1990). Approach/withdrawal and cerebral asymmetry: Emotional expression and brain physiology. *Journal of Personality and Social Psychology*, *58*, 330–341.

Davidson, R.J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences*, *3*, 11–12.

Eibl-Eibesfeldt, I. (1973). The expressive behavior of the deaf-and-blind-born. In M. von Cranbach & I. Vine (Eds.), *Social communication and movement* (pp. 163–167). New York: Academic Press.

Ekman, P. (1992). An argument for basic emotions. *Cognition and Emotion*, *6*, 169–200.

Ekman, P., & Friesen, W.V. (1976). *Pictures of facial affect*. Palo Alto, CA: Consulting Psychologists Press.

Geschwind, N. (1970). The organization of language and the brain. *Science*, *170*, 940–944.

Hamann, S.B., Stefanacci, L., Squire, L.R., Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1996). Recognizing facial emotion. *Nature*, *379*, 497.

Irwin, W., Davidson, R.J., Lowe, M.J., Moch, B.J., Sorenson, J.A., & Turski, P.A. (1996). Human amygdala activation detected with echo-planar functional magnetic resonance imaging. *NeuroReport*, *7*, 1765–1769.

Kling, A.S., & Brothers, L.A. (1992). The amygdala and social behavior. In J.P. Aggleton (Ed.), *The amygdala* (pp. 353–378). New York: Wiley Press.

Kolb, B., Wilson, B., & Taylor, L. (1992). Developmental changes in the recognition and comprehension of facial expression: Implications for frontal lobe function. *Brain & Cognition*, *20*, 74–84.

LaBar, K.S., Gatenby, C., Gore, J.C., LeDoux, J.E., & Phelps, E.A. (1998). Human amygdala activation during conditioned fear acquisition and extinction: A mixed-trial fMRI study. *Neuron*, *20*, 937–945.

LaBar, K.S., & Phelps, E.A. (1998). Arousal-mediated memory consolidation: Role of the medial temporal lobe in humans. *Psychological Science*, *9*, 490–493.

LeDoux, J.E. (1996). *The emotional brain*. New York: Simon & Schuster.

Mineka, S., Davidson, M., Cook, M., & Keir, R. (1984). Observational conditioning of snake fear in rhesus monkeys. *Journal of Abnormal Psychology*, *93*, 355–372.

Morris, J.S., Frith, C.D., Perrett, D.I., Rowland, D., Young, A.W., Calder, A.J., & Dolan, R.J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, *383*, 812–815.

Nelson, C.A., & De Haan, M. (1997). A neurobehavioral approach to the recognition of facial expressions in infancy. In J.A. Russell & J.M. Fernandez-Dols (Eds.), *The psychology of facial expression* (pp. 176–204). Cambridge, England: Cambridge University Press.

Phelps, E.A., & Anderson, A.K. (1997). Emotional memory: What does the amygdala do? *Current Biology*, *7*, R311–R314.

Phelps, E.A., LaBar, K.S., Anderson, A.K., O'Connor, K.J., Fulbright, R.K., & Spencer, D.D. (1998). Specifying the contributions of the human amygdala to emotional memory: A case study. *Neurocase*, *4*, 527–540.

Ross, E.D. (1981). The aprosodias: Functional-anatomical organization of the affective components of language in the right hemisphere. *Archives of Neurology*, *38*, 581–589.

Rosvold, H.E., Mirsky, A.F., & Pribram, K.H. (1954). Influence of amygdalectomy on social behavior in monkeys. *Journal of Comparative and Physiological Psychology*, *47*, 173–178.

Scherer, K.R. (1986). Vocal affect expression: A review and a model for future research. *Psychological Bulletin*, *99*, 145–165.

Schmolck, H., & Squire, L.R. (1999). Impaired differentiation of facial emotion in patients with complete bilateral amygdala lesions. *Society for Neuroscience Abstracts*, *25*, 2150.

Scott, S.K., Young, A.W., Calder, A.J., Hellawell, D.J., Aggleton, J.P., & Johnson, M. (1997). Impaired auditory recognition of fear and anger following bilateral amygdala lesions. *Nature*, *385*, 254–257.

Weddell, R.A., Miller, J.D., & Trevarthen, C. (1990). Voluntary emotional facial expressions in patients with focal cerebral lesions. *Neuropsychologia*, *28*, 49–60.

Young, A.W., Hellawell, D.J., Van De Wal, C., & Johnson, M. (1996). Facial expression processing after amygdalotomy. *Neuropsychologia*, *34*, 31–39.

(RECEIVED 3/16/99; ACCEPTED 7/12/99)