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Quantifying deficits in the perception of fear and anger in morphed facial expressions after bilateral amygdala damage

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Abstract

Amygdala damage has been associated with impairments in perceiving facial expressions of fear. However, deficits in perceiving other emotions, such as anger, and deficits in perceiving emotion blends have not been definitively established. One possibility is that methods used to index expression perception are susceptible to heuristic use, which may obscure impairments. To examine this, we adapted a task used to examine categorical perception of morphed facial expressions [Etcoff, N. L., & Magee, J. J. (1992). Categorical perception of facial expressions. *Cognition*, *44*(3), 227–240]. In one version of the task, expressions were categorized with unlimited time constraints. In the other, expressions were presented with limited exposure durations to tap more automatic aspects of processing. Three morph progressions were employed: neutral to anger, neutral to fear, and fear to anger. Both tasks were administered to a participant with bilateral amygdala damage (S.P.), age- and education-matched controls, and young controls. The second task was also administered to unilateral temporal lobectomy patients. In the first version, S.P. showed impairments relative to normal controls on the neutral-to-anger and fear-to-anger morphs, but not on the neutral-to-fear morph. However, reaction times suggested that speed-accuracy tradeoffs could account for results. In the second version, S.P. showed impairments on all morph types relative to all other subject groups. A third experiment showed that this deficit did not extend to the perception of morphed identities. These results imply that when heuristics use is discouraged on tasks utilizing subtle emotion transitions, deficits in the perception of anger and anger/fear blends, as well as fear, are evident with bilateral amygdala damage.

Keywords: Face perception; Facial affect; Face morph; Valence; Neuropsychology

Neurological studies implicate the amygdala in processing facial expressions of emotion. Initial studies of a patient with bilateral amygdala damage found impaired perception of specific facial expressions of emotion, namely fear, while other aspects of face processing were intact (Adolphs, Tranel, Damasio, & Damasio, 1994, 1995). Subsequent studies have confirmed deficits in processing the facial expression of fear (e.g. Adolphs, Tranel et al., 1999; Anderson, Spencer, Fulbright, & Phelps, 2000; Calder et al., 1996; Young, Aggleton, Hellawell, Johnson, & Broks, 1995; Young, Hellawell, Van de Wal, & Johnson, 1996). These results converge with fMRI studies of healthy participants, which implicate the amygdala in the perception of fear (e.g. Morris et al., 1998; Whalen et al., 1998, 2001; reviewed in Vuilleumier & Pourtois, in press). Together, these findings support the critical role of the amygdala in perceiving fearful facial expressions.

Despite these findings, several issues regarding the role of the amygdala in the perception of facial expressions remain unresolved. First, perceptual processing of fearful expressions is intact in some patients with bilateral amygdala damage (e.g. Adolphs, Tranel et al., 1999; Hamann & Adolphs, 1999; Hamann et al., 1996). Second, patients with bilateral amygdala lesions can show impairments in the perception of other emotional expressions. However, these are not consistent across patients (e.g., Adolphs, Tranel et al., 1999; Calder et al., 1996). Third, deficits in the perception of emotional expressions can vary across testing sessions within a given patient. For example, patient S.P., who has bilateral amygdala damage due to epilepsy (Phelps et al., 1998), completed similar facial expression rating tasks on two occasions, where the only difference between the two tasks was the number of stimulus repetitions (Adolphs, Tranel et al., 1999; Anderson & Phelps, 2000). On the first occasion, S.P.'s ratings were impaired for fear, disgust, sadness and

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anger (Adolphs, Tranel et al., 1999). On the second occasion, S.P. showed impairments in rating fear, disgust, sadness, and happiness (Anderson & Phelps, 2000).

In a prototypical face rating study, subjects rate the intensity of individual basic emotions in faces posing various facial expressions. One criticism of these and other studies of amygdala-damaged patients is that the rating tasks used to assess facial expression processing may be insensitive to subtle deficits (see Calder et al., 1996; Sato et al., 2002). Instead, other measures of expression perception were proposed, such as a two-alternative forced choice task (2-AFC) used in the study of categorical perception (e.g. Etcoff & Magee, 1992). In a typical categorical perception experiment, the stimuli consist of morphed facial expressions that are generated by blending pictures of the same model posing different facial expressions in equal increments. Normal participants perceive these continua as falling into different emotion regions with a sharp boundary between them. In other words, the faces at the extreme ends of a continuum are consistently identified as the predominant emotion in the morph. However, at some point, usually in the middle of a morph continuum, there is an abrupt category shift where responding changes sharply from endorsing the emotion on one end of the continuum to the emotion on the other end of the continuum. This shift occurs across the categorical boundary. The morph level representing the boundary is known as the *point of subjective equality* (PSE), which is the level where subjects are most likely to be guessing. This task is thought to be more sensitive because morphed facial expressions create subtle differences in facial expression, and the response shifts across the categorical boundary can be analyzed.

Calder et al. (1996) adapted this 2-AFC task to examine the perception of facial expression in two patients with bilateral amygdala damage. Compared to control subjects who tended to identify morphed expressions categorically, these patients did not show distinct categorical perception (i.e., the category shift where responding shifted from endorsing one emotion to the other was not as abrupt as controls). This was most apparent in the identification of fear but did extend to other negative emotions, although these deficits were not consistent between the two subjects. A similar design was also used to study another patient with amygdala damage, H.Y. (Sato et al., 2002). Relative to controls, H.Y. had a positive bias in judging the facial expressions of anger and fear that were morphed with happiness. In other words, H.Y. needed more anger and fear in a face in order to categorize it as angry or fearful. In addition, H.Y.'s response curves did not show abrupt category shifts for the anger and fear morphs. These findings suggest that amygdala damage impairs the perception of prototypical expressions of fear and that this impairment could extend to other negative, highly arousing emotions.

One limitation of existing 2-AFC experiments is that results have been described qualitatively; the response curves generated by participants have not been subjected to quantitative analysis. The data from two-alternative forced choice experiments are well-suited to quantitative analysis via signal detection theory. Importantly, signal detection methods can be used to determine whether the abruptness of the shift at the categorical boundary is different for amygdala-damaged patients relative to controls. Analysis of the slope of the response curve around the response shift or categorical boundary allows one to determine whether the perception of facial expression is compromised following bilateral amygdala damage (Teunisse & de Gelder, 2001).

Another limitation of existing 2-AFC studies is that they did not examine sensitivity to differences in emotional intensity (i.e., emotional expressions morphed with neutral ones). Therefore, it is not known whether amygdala damage impairs the detection of subtle changes in the intensity of an emotional expression. Unlike the stimuli used in a typical ratings task, which depict prototypical emotions at maximum intensity, the stimuli created by morphing neutral and emotional faces have subtle gradations of facial emotion expression. Hence, 2-AFC tasks using morphed faces may be more sensitive than ratings tasks using prototypical expressions at detecting deficits in emotion processing.

Another question that remains is whether individuals with amygdala damage show impairments in perceiving blends of facial expression. Adolphs et al. (1994) originally suggested this idea based on their observation that relative to controls, patient S.M. did not rate facial expression categories as similar to one another. Multi-dimensional scaling of her emotion ratings revealed a clustering of facial expressions whereas the ratings of controls were more continuous. However, this observation was not consistent across testing sessions (Adolphs et al., 1994) and was not replicated in two additional patients (Hamann & Adolphs, 1999).

Using the 2-AFC task, the perception of emotion blends was directly examined. Calder et al. (1996) ran a subset of emotion morphs consisting of those emotions that are commonly confused with one another, and Sato et al. (2002) examined morphs between oppositely valenced expressions. Both provide some evidence of impairments in judging emotion blends, although the data were not subjected to quantitative analyses. An unresolved issue is whether amygdala-lesioned patients would be impaired on fear-to-anger morphs. Calder et al. (1996) examined the morphing of fearful to angry expressions, and found that one patient consistently identified faces as fearful regardless of the amount of facial anger, while the other patient's response curve was similar to that of controls but was more variable. If amygdala damage impairs identifying of fear and anger, then performance on fear/anger emotion blends should be particularly difficult.

A critical feature of neurologic studies examining facial affect perception is that faces are presented until a response is made, allowing subjects an abundant amount of time to examine facial features. Amygdala-damaged patients may use compensatory cognitive mechanisms to aid them with facial expression identification. One candidate could be feature analysis, where decisions regarding facial expression are based on the displacement of facial features. For example, decisions regarding the facial expression of fear could be based on the detection of features that are prototypical of this emotion such as widened eyes, eyebrows that are drawn inward and upward, and open mouths with the lips pulled back to expose the teeth. The variable use of compensatory strategies or heuristics could give rise to the inconsistencies in behavioral measures of facial expression processing seen both within and between patients. Examination of reaction time could shed light on this issue, but has yet to be done in patient studies of facial expression processing. Because heuristics tend to be time-consuming, speed-accuracy tradeoffs could account for the mixed results found in previous studies of the amygdala and facial expressions of emotion.

The present study investigated the categorical perception of fear, anger, and their blends in patient S.P., an individual with bilateral amygdala damage, who was tested previously using the prototypical face rating task employed by Adolphs and coworkers (Adolphs, Tranel et al., 1999; Anderson & Phelps, 2000). As mentioned earlier, S.P. showed deficits in rating fearful expressions across two separate testing sessions, but her results were inconsistent with regard to anger. Because of this, we examined fearful and angry face morphs, which are both negative and arousing stimuli (Adolphs, Russell, & Tranel, 1999). Three morph progressions were used: neutral to fear, neutral to anger, and fear to anger. The first two of these examine sensitivity to changes in intensity, whereas the third progression was employed to investigate emotion blends.

The data were analyzed with signal detection methods (MacMillan & Creelman, 1991) to quantitatively establish whether S.P.'s performance on the two-alternative forced-choice tasks was different from controls. Specifically, we were interested in determining if S.P.'s sensitivity around the categorical boundary, or the degree of her response shift at the boundary, was significantly different from those of controls. Using these analysis methods, the present study can extend previous results that used qualitative measures of categorical perception in emotion morphs and introduce analyses that, while well suited for 2-AFC tasks, have not been previously applied to experiments in neuropsychological populations.

Two versions of the emotion morph experiment were conducted. In Experiment 1, participants had unlimited exposure to the morphs, whereas in Experiment 2, exposure time was limited. Limited exposure durations should discourage the use of cognitive strategies and hence emphasize more rapid and obligatory processing of faces. Because the amygdala is thought to be involved at early stages of face processing (Morris et al., 1998; Whalen et al., 1998), the version of the task employing finite exposure to faces (Experiment 2) should be a more sensitive index of the role of this structure in processing facial expression. In addition, reaction time data were examined to determine whether speed-accuracy tradeoffs could account for any differences in S.P.'s performance across the two experiments. We reasoned that anomalous or inconsistent performance would be accompanied by longer reaction times, suggesting that cognitive strategies were being used to aid decision-making. Experiment 3 was analogous to Experiment 2 but used morphed changes in facial identity with neutral expression. This experiment was conducted to determine the specificity of any observed impairments to the processing of facial emotion per se, using a task with similar perceptual difficulty. Unilateral temporal lobectomy patients were run on Experiments 2 and 3 to determine whether bilateral damage to the amygdala was necessary to observe changes in performance under limited exposure durations. We predicted that S.P. would show deficits on the expression morph tasks, particularly when exposure was limited, but she would not be impaired on the identity morph task.

1. Experiment 1

1.1. Method

1.1.1. Stimulus development

Emotional facial expressions that have been found to be panculturally representative of the basic emotions of fear and anger were taken from the Ekman pictures of facial affect (Ekman & Friesen, 1976; Matsumoto & Ekman, 1988). Prototypical expressions of fear and anger were morphed together, and also with neutral expressions of the same actor to create the experimental stimuli. Hence, three different morph progressions were created: neutral to anger, neutral to fear, and fear to anger. The same 10 actors were used to construct the different morph types.

The morphs were created using the methods outlined in LaBar, Crupain, Voyvodic, and McCarthy (2003) using MorphMan 2000 software (STOIK, Moscow, Russia). To exclude extraneous cues such as hair, ears, and neckline, faces were initially cropped with an ovoid mask. Images were normalized for contrast and luminance and presented against a grey background. All expressions were posed in full frontal orientations without changes in head orientation either across or within morphs. Approximately 150 fiducial markers were placed on each source image and individually matched via computer mouse to corresponding points on the target image. The eyes, mouth, the corrugator and obicularis oculi muscles and other facial areas deemed important for conveying changes in facial expression (see Bassili, 1979; Ekman & Friesen, 1978) were densely sampled. Source and target faces were used to create continua of emotional facial expressions. Between each source and target emotion, 8 intermediate images with 11.11% increments were created, yielding a total of 10 images in each continuum numbered from 1 to 10. For example, for the neutral-to-anger continuum, morph increment 1 was 100% neutral, increment 2 was 88.88% neutral and 11.11% angry, increment 3 was 77.77% neutral and 22.22% angry, and so on, until face 10, which depicted 100% anger. Thus, a total of 300 images were used in this experiment (3 emotion morph types × 10 models × 10 morph increments). Examples of each of the three emotion continua are shown in Fig. 1.

1.1.2. Subjects

We studied S.P., a 58-year-old woman with bilateral amygdala damage associated with epilepsy. S.P. first showed signs of neurological insult at approximately 3–4 years of age. She was later diagnosed with epilepsy. Medically intractable complex seizures of right medial temporal lobe origin began to occur with greater frequency during adulthood. Hence, at age 48 she underwent right anteromedial temporal lobe resection, which included removal of the right amygdala. MR images prior to surgery also revealed a focal lesion in the left amygdala.

S.P. completed high school and has taken some college courses. She presents a normal neuropsychological profile, including normal performance on the Wechsler Adult Intelligence Scale-Revised (Verbal IQ of 104, Performance IQ of 107, Full Scale IQ of 106). S.P. is able to discriminate between unfamiliar faces as indexed by the Benton test of facial discrimination (Benton, Hamsher, desVarney, & Spreen, 1994). She can discriminate the age and gender of unfamiliar faces. Therefore, S.P. can successfully interpret multiple sources of non-emotional facial information. With regard to her processing of other, non-facial emotional information, S.P. shows deficits on fear conditioning and recognition memory for arousing stimuli (Phelps et al., 1998). In contrast, her ability to judge emotion from voices is intact (Anderson & Phelps, 1998). In addition, her descriptions of her subjective emotional experiences do not differ from those of controls (Anderson & Phelps, 2002). Detailed information regarding S.P.'s lesions and neuropsychological status is available in Phelps et al. (1998).

We also tested 9 age- and education-matched controls, and 20 young controls. The age- and education-matched control group consisted of 9 females ranging from 53 to 66 years of age (mean 57.9 years) who had between 12 and 17 years of education and did not have a history of neurologic or psychiatric illness. Young controls consisted of 6 males and 14 females ranging from 18 to 28 years of age (mean 20.6 years), who had between 12 and 18 years of education with no

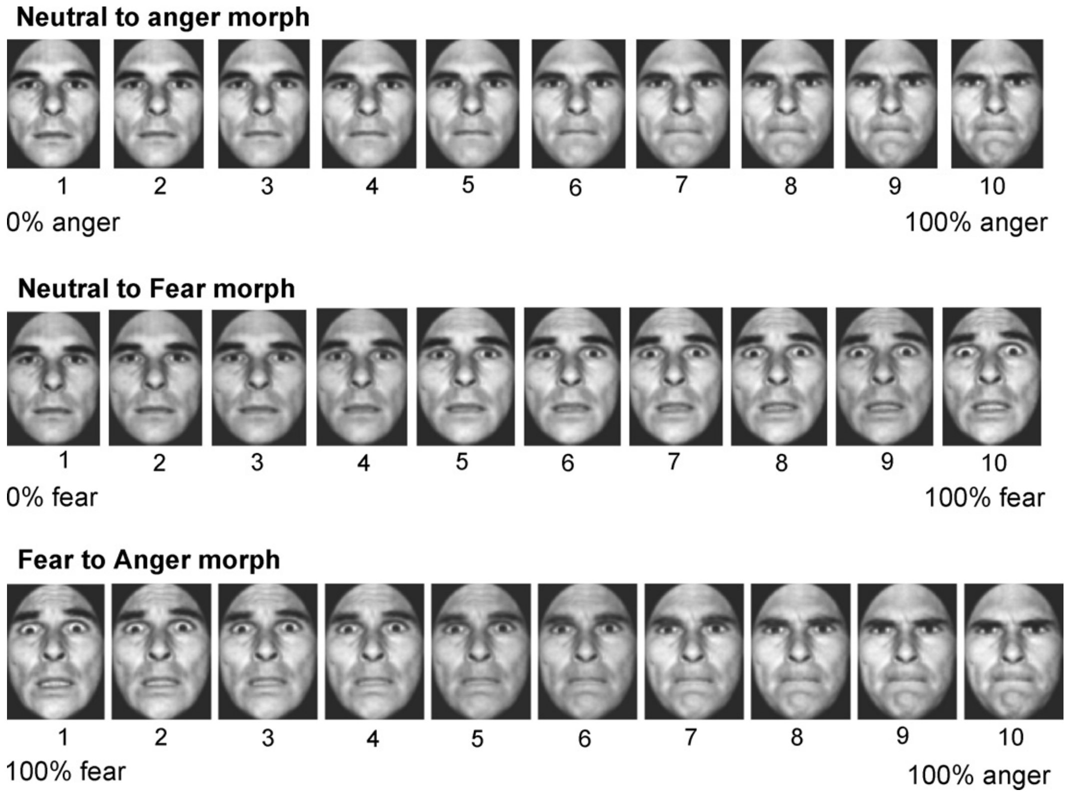

Fig. 1. Examples of the three emotion morph continua used in this experiment: (A) neutral to anger, (B) neutral to fear and (C) fear to anger.

history of neurologic or psychiatric illness. Procedures for human subjects were approved by the Institutional Review Board at Duke University.

1.1.3. Design and procedure

The 300 morphed faces were used in three, two-alternative forced-choice identification tasks, one for each emotional morph type. In each task, faces were presented one at a time and participants were asked to respond as quickly and accurately as possible. Each trial consisted of a fixation for 1000 ms, followed by an individual emotion morph which was presented simultaneously with a response selection screen. The face and response selection screen were displayed until the participant made a response and was followed by a 1000 ms inter-stimulus interval. Fixation was a scrambled face with an overlapping, centrally-positioned fixation cross. The response selection screen consisted of two-alternative facial expression descriptors that differed for each of the three tasks. For example, in the neutral-to-anger morph task, participants were required to indicate whether the face was neutral or angry. Each of the three tasks was administered three times to every participant in the following order: neutral to anger, neutral to fear, and fear to anger. This was done so that each participant would receive the tasks in the same order as S.P. After completing each morph type once, the tasks were re-administered in the same order. There was no time limit for responding and no feedback was given.

1.2. Results

Identification results are summarized in Fig. 2. Simple inspection of these graphs indicated that S.P.'s identification data was qualitatively different from that of controls for the neutral-to-anger and fear-to-anger continua. In order to quantify these differences, the data was analysed with signal detection methods.

First, corrected d' scores for 2-AFC tasks (MacMillan & Creelman, 1991) were computed for each morph increment. The point of maximum confusion was identified by finding the morph increment for each participant that was associated with the lowest sensitivity as assessed by d'. This identified the increment where subjects were most likely to be guessing, which is considered to the PSE between expressions (Currie, 1998). Stable PSE estimates could not be computed for each individual stimulus actor due to a limited number of trials. Instead, PSE estimates were based upon pooling the data across all actors in a given morph continuum. Assuming that the PSE lies near the categorical boundary, cumulative d' (MacMillan & Creelman, 1991) was computed for the two increments before the PSE, the PSE and two increments after the PSE. This yields a function that is measure of the change in sensitivity at the categorical boundary. Increments around the PSE were chosen as a dependent measure for two reasons: first, differences in sensitivity to changes at the categorical boundary (i.e., the abruptness of the response shift) can be used to determine impairments in processing facial expression (Teunisse & de Gelder, 2001); second, ceiling effects due to perfect performance at the extremes of each continua resulted in inflated d' values at these increments. The cumulative d' functions for the three groups on the three morphs are shown on the left side of Fig. 3. The slope of this function was then computed for each participant. This value indexes the sensitivity of the participant to small changes in facial expression where identification is the most difficult.

Averaged slope values for the control groups were compared to S.P. using one-sample *t*-tests with S.P.'s value as the critical value. The slope values for each group and each morph are shown on the right of Fig. 3. For the neutral-to-anger continuum, S.P.'s

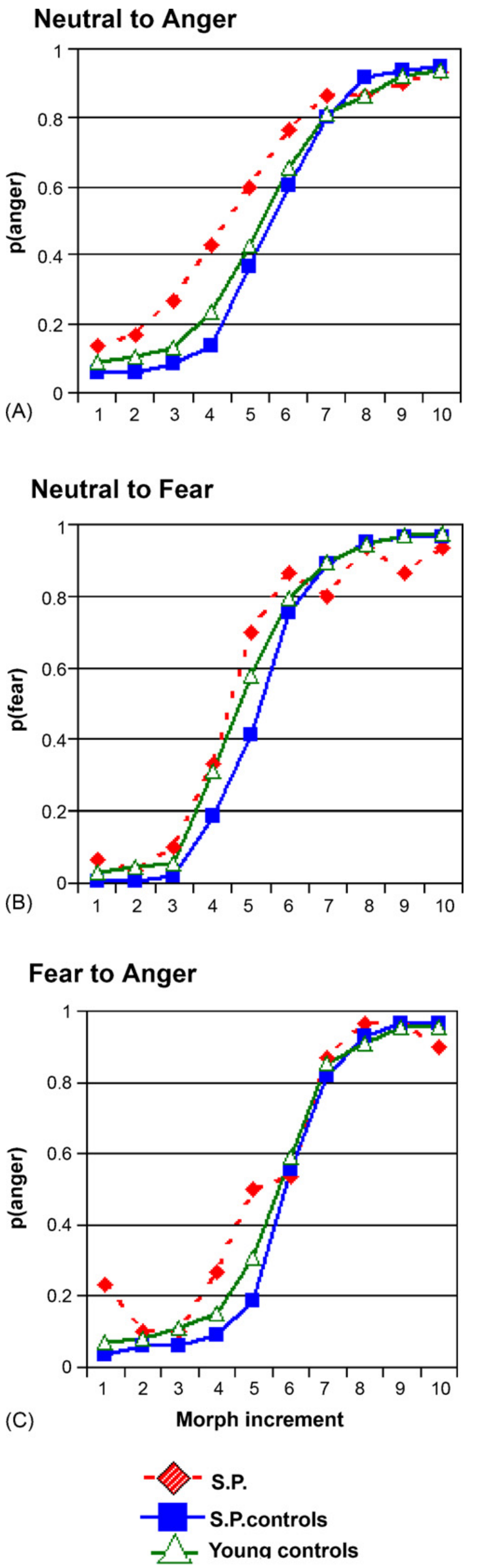

Fig. 2. Identification of emotion in morphed images for the three morph types in Experiment 1. The mean percentage of times that (A) participants identified the images in the neutral-to-anger continuum as angry, (B) participants identified the images in the neutral-to-fear continuum as fearful, (C) participants identified the images in the fear-to-anger continuum as angry.

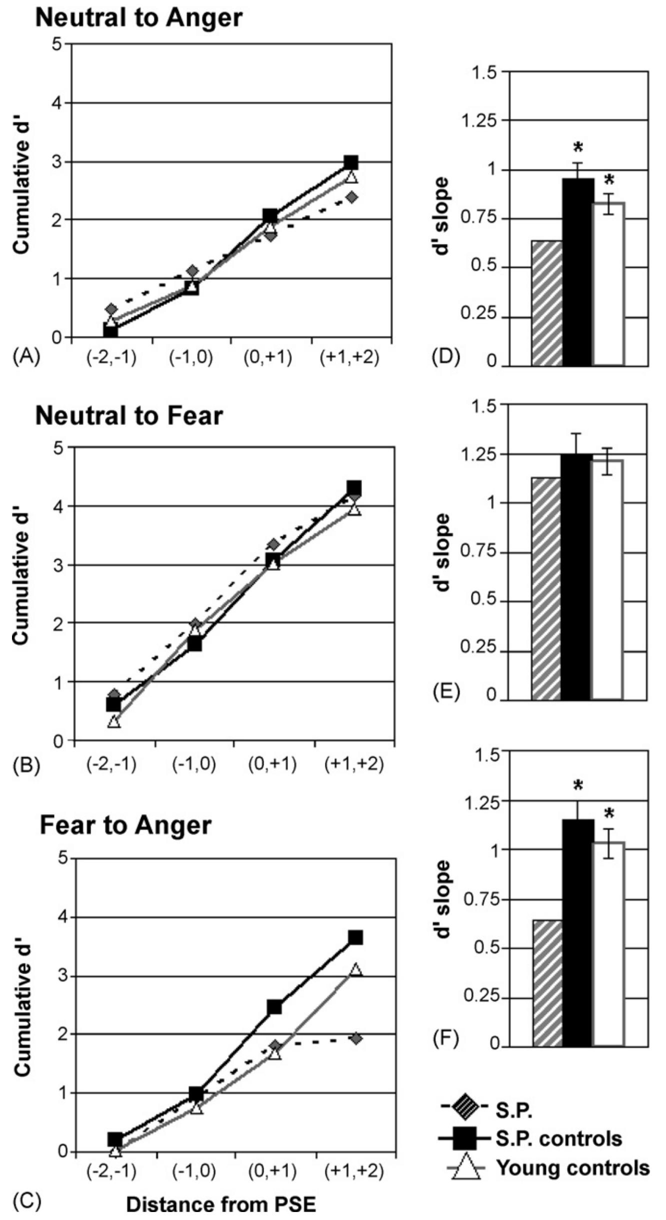

Fig. 3. Cumulative d' functions around the PSE and slopes of these functions for the three morph types in Experiment 1. Cumulative d' functions for (A) the neurral-to-anger morph, (B) the neutral-to-fear morph, and (C) the fear-to-anger morph. The slope of these functions for (D) the neutral-to-anger morph, (E) the neutral-to-fear morph, and (F) the fear-to-anger morph. Asterisk (*) indicates $p < 0.05$ relative to S.P.

slope was significantly lower than that for age-matched controls (.64 versus .95, respectively, $t(8) = 3.7$, $p < 0.01$) and young controls (.64 versus .82, $t(19) = 3.5$, $p < 0.01$). These results indicate that S.P. was significantly less sensitive to increases in facial anger at the categorical boundary. Differences in slope were also evidenced in the fear-to-anger continuum. S.P.'s slope was significantly lower than that for age-matched controls (.64 versus 1.15, respectively, $t(8) = 5.0$, $p < 0.01$) and young controls (.64 versus 1.03, $t(19) = 5.0$, $p < 0.01$). There were no differences between S.P. and either control group for the neutral-to-fear continuum (all p's > 0.05). To summarize, the slope data indicated that at the categorical boundary, S.P. was significantly less sensitive to changes in anger intensity in a face and changes from fear-to-anger, but not to changes in the intensity of fear. In other words, her response shift at the categorical boundary was not as abrupt as the shifts for controls for the neutral-to-anger and fear-to-anger morphs. There were no differences between the slopes of the two control groups on any of the morph progressions (all F's < 2, p's > 0.05).

To determine if she was adopting a heuristic such as feature analysis to aid her in identifying morphed expressions, we also compared S.P.'s reaction times to those of controls with the rationale that heuristic use would be time-consuming. Reaction times for the three identification tasks are summarized in Fig. 4. Inspection of these graphs indicated that S.P.'s reaction times were markedly different from those of controls for all continua. S.P. looked longer at faces across all morph increments and took longer to make decisions about facial expression than controls. For the neutral-to-anger continuum, S.P. was significantly slower than age-matched controls (1146 ms versus 905 ms, respectively, $t(8) = -2.90$, $p < 0.05$) and young controls (1146 ms versus 794 ms, $t(19) = -12.23$, $p < 0.01$). Differences in reaction time were also evidenced in the neutral-to-fear continuum: S.P. was significantly slower than both age-matched controls (1176 ms versus 860 ms, respectively, $t(8) = -3.82$, $p < 0.01$) and young controls (1176 ms versus 732 ms, $t(19) = -18.89$, $p < 0.01$). Finally, S.P. was slower than both her age- and education-matched controls (1839 ms versus 1148 ms, $t(8) = -5.49$, $p < 0.01$) and young controls (1839 ms versus 928 ms, $t(19) = -23.42$, $p < 0.01$) on the fear-to-anger continuum.

1.3. Discussion

When participants are given unlimited exposure to faces, analysis of slope suggested that S.P. was less sensitive to changes in anger intensity at the categorical boundary for the neutral-to-anger and fear-to-anger continua, and her response shifts for these morphs were more shallow. In contrast, S.P.'s performance on the neutral-to-fear continuum did not differ from that of controls. This result was unexpected since S.P. showed deficits in rating the intensity of fearful faces in previous studies (Adolphs, Tranel et al., 1999; Anderson & Phelps, 2000). However, the ratings task used in those studies was different from the current one (verbal labeling of the degree of emotion in prototypical expressions versus 2-AFC recognition of emotion in morphed increments).

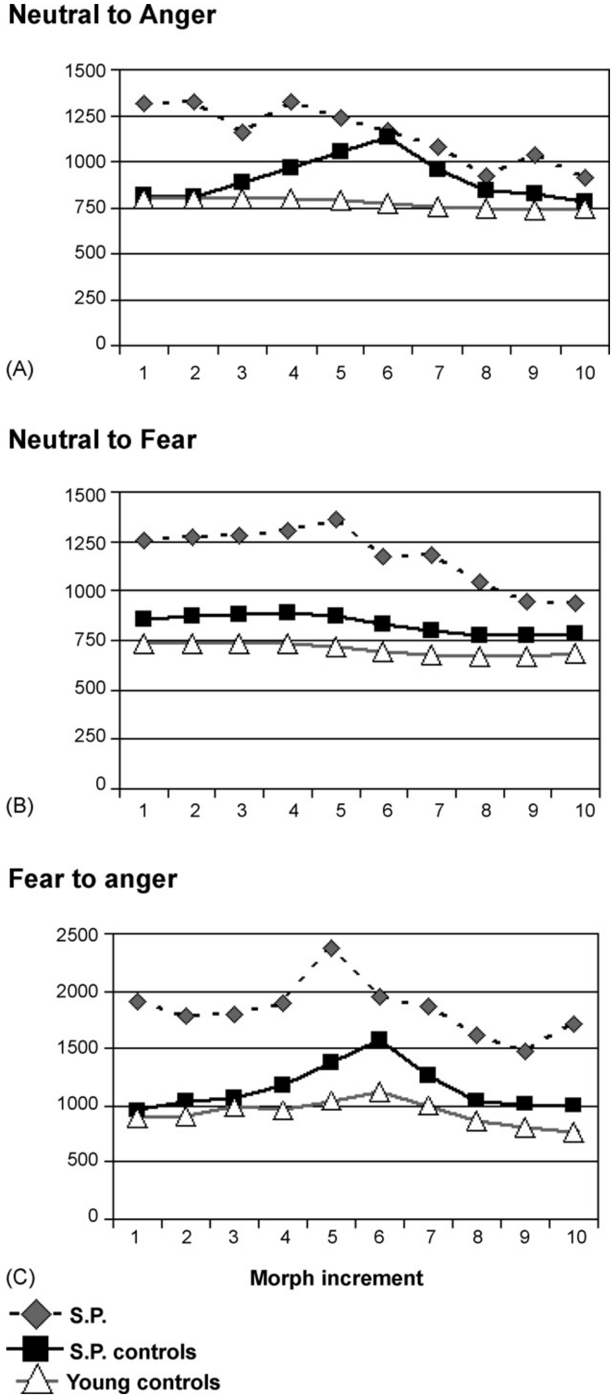

Fig. 4. Median reaction times for (A) the neutral-to-anger continuum, (B) the neutral-to-fear continuum and (C) the fear-to-anger continuum.

One explanation for these results is that S.P. was using some heuristic such as feature analysis to help her make decisions about emotional facial expressions, especially for the fearful expressions. Heuristic use tends to be time-consuming, and S.P.'s median reaction times were suggestive of such processing. If S.P. was using a particular facial feature or set of facial features such as eye or mouth aperture to guide her decision-making, her identification performance could appear normal. To test this hypothesis, we reduced the duration of exposure to faces in the tasks used in Experiment 1 in an attempt to discourage or reduce the use of heuristics. In addition, we included a new cohort of subjects with unilateral medial temporal lobe (MTL) damage in order to investigate if processing impairments would also be evident with unilateral amygdala damage.

2. Experiment 2

2.1. Method

2.1.1. Subjects

We studied S.P., 15 age- and education-matched controls, and 30 young adult controls. S.P. was tested approximately 28 weeks (7 months) after the adminis-

Table 1
Demographics and IQ data for unilateral temporal lobectomy (MTL) patients

Group	Age	Education	Gender	FSIQ
Right MTL [$N = 7$]	33.2 ± 9.0	16.2 ± 3.1	3 females/4 males	100.4 ± 9.3
Left MTL [$N = 6$]	36.5 ± 10.4	15.2 ± 2.3	3 females/3 males	104.8 ± 11.1

Means and standard deviations are shown for age and education (in years) and full scale IQ as measured by the Wechsler Adult Intelligence Scale-Revised.

tration of tasks for Experiment 1. The age- and education-matched control group consisted of 6 males and 9 females ranging from 50 to 66 years of age (mean 55.9 years), who had between 12 and 20 years of education and did not have a history of neurologic or psychiatric illness. A subset of 7 of these controls had also been run in Experiment 1 approximately 6 months prior to Experiment 2. Young controls consisted of 9 males and 21 females ranging from 18 to 22 years of age (mean 18.8 years), with no history of neurologic or psychiatric illness, none of whom participated in Experiment 1. The order of presentation of the three continua was identical to Experiment 1.

Six patients with right medial temporal lobe damage and 7 patients with left MTL damage also participated in this experiment. All unilateral patients had undergone neurosurgical resection for treatment of medically refractory epilepsy 2–8 years prior to participation in this study. The exact extent of the resection varied from patient to patient according to the location of the seizure focus; however, in all patients the amygdala and adjacent medial temporal lobe structures including the hippocampus and uncus were removed unilaterally, whereas tissue from areas outside the temporal lobe was spared. The extent of temporal neocortical excision ranged from 3.5 to 6.5 cm. Demographic and IQ data for all MTL subjects is shown in Table 1. Procedures for human subjects were approved by the Institutional Review Boards at Duke University and New York University.

2.1.2. *Stimulus materials and design*

The stimuli and design of Experiment 2 were identical to those used in Experiment 1 with one exception: individual emotion morphs were presented for 505 ms and then replaced by a response selection screen, which was displayed until the participant made a response.

2.2. *Results*

Identification results are summarized in Fig. 5. Simple inspection of these graphs indicated that S.P.'s identification data were qualitatively different from that of controls, including the group with unilateral MTL damage, for all three continua.

Similar to Experiment 1, the PSE was identified by finding the morph increment for each participant that was associated with the lowest sensitivity as assessed by d'. Next, cumulative d' was computed for the two increments before the PSE, the PSE and two increments after the PSE. The cumulative d' functions for the four groups on the three morphs are shown on the left side of Fig. 6. The slope of this function was then computed for each participant. The slope values for each group and each morph are shown on the right of Fig. 6. Averaged slope values for the control and unilateral MTL groups were compared to S.P. using one-sample t-tests with S.P.'s value as the critical value. Slope values for the right MTL and left MTL patients were compared and found to be equal; hence, the values for the two groups were combined.

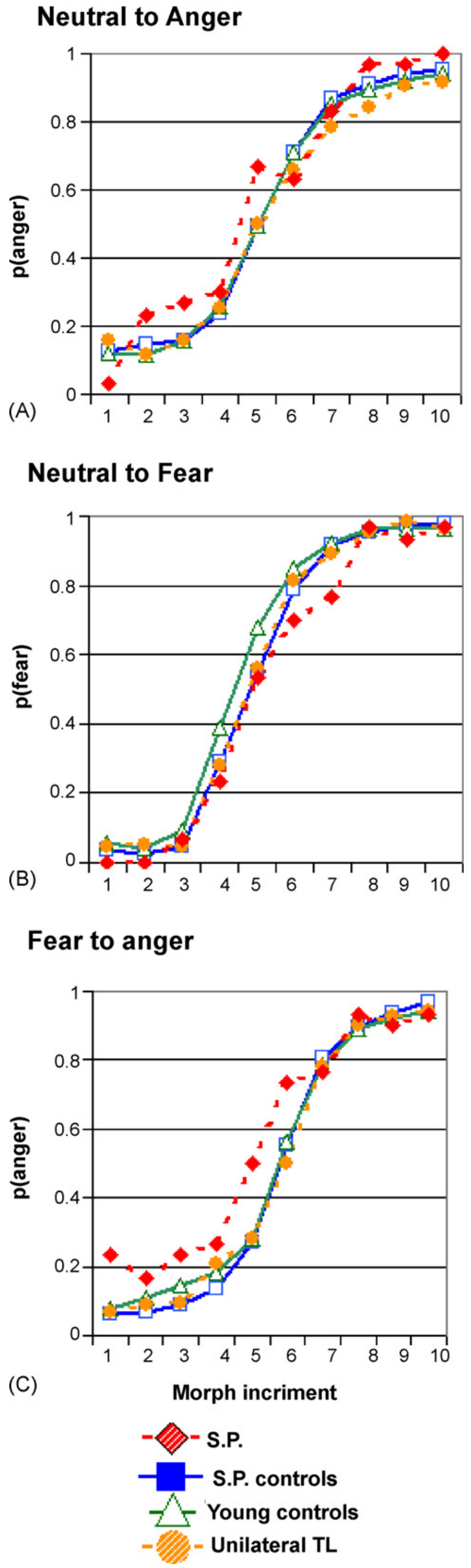

Fig. 5. Identification of emotion in morphed images for the three morph types in Experiment 2. The mean percentage of times that (A) participants identified the images in the neutral-to-anger continuum as angry, (B) participants identified the images in the neutral-to-fear continuum as fearful, (C) participants identified the images in the fear-to-anger continuum as angry.

For the neutral-to-anger continuum, S.P.'s slope was significantly lower than that for age-matched controls (.45 versus .84, respectively, $t(14) = 5.0$, $p < 0.01$), young controls (.45

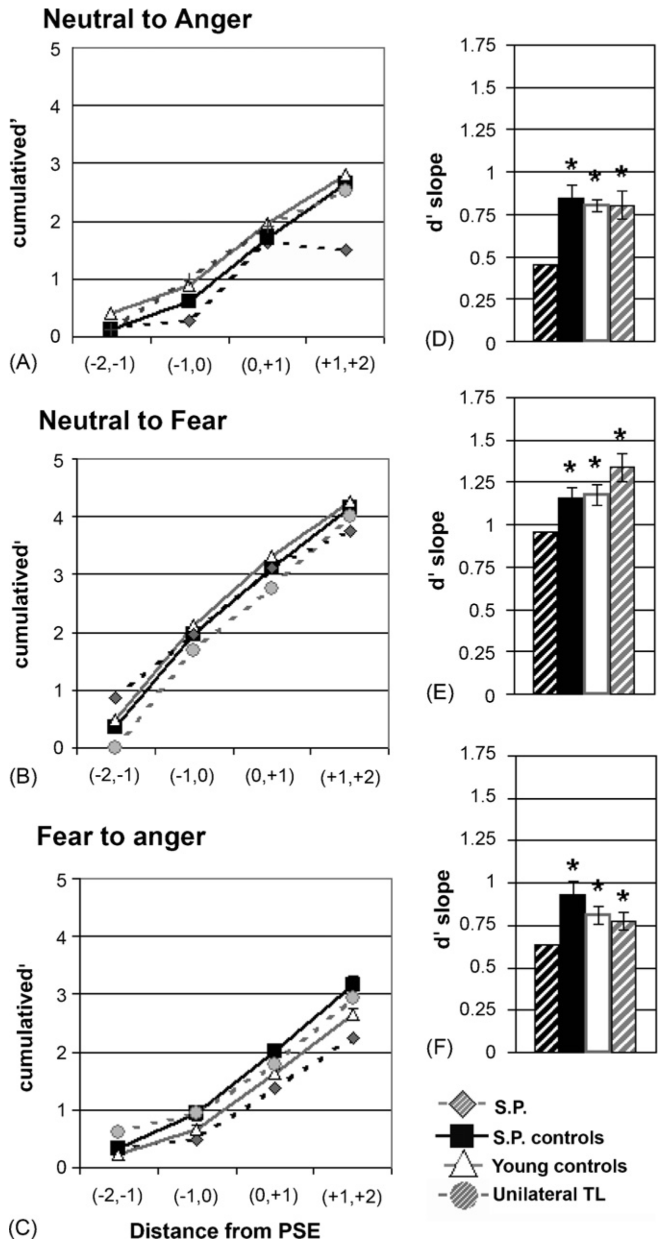

Fig. 6. Cumulative d' functions around the PSE and slopes of these functions for the three morph types in Experiment 2. Cumulative d' functions for (A) the neutral-to-anger morph, (B) the neutral-to-fear morph, and (C) the fear-to-anger morph. The slope of these functions for (D) the neutral-to-anger morph, (E) the neutral-to-fear morph, and (F) the fear-to-anger morph. Asterisk (*) indicates $p < 0.05$ relative to S.P.

Table 2
Median reaction times for Experiments 1 and 2

	Experiment 1		Experiment 2	
	Mean	S.E.M.	Mean	S.E.M.
Neutral to anger				
S.P.	1146		803	
S.P. controls	905	83	463	49
Young controls	794	29	357	28
Neutral to fear				
S.P.	1175		881	
S.P. controls	860	83	429	41
Young controls	732	24	330	25
Fear to anger				
S.P.	1839		1164	
S.P. controls	1148	126	629	41
Young controls	928	39	474	33

versus .80, $t(29) = 9.8$, $p < 0.01$), and unilateral MTL patients (.45 versus .80, $t(12) = 4.2$, $p < 0.01$). These results indicate that S.P. was significantly less sensitive to increases in facial anger across the categorical boundary of this continuum. For the neutral-to-fear continuum, S.P.'s slope was significantly lower than that for age-matched controls (.96 versus 1.16, respectively, $t(14) = 3.1$, $p < 0.01$), young controls (.96 versus 1.18, $t(29) = 3.7$, $p < 0.01$) and unilateral MTL patients (.96 versus 1.3, $t(12) = 4.6$, $p < 0.01$). Differences in slope were also evidenced in the fear-to-anger continuum. S.P.'s slope was significantly lower than that for age-matched controls (.64 versus .93, respectively, $t(14) = 3.7$, $p < 0.01$), young controls (.64 versus .81, $t(29) = 3.6$, $p < 0.01$), and unilateral MTL patients (.64 versus .78, $t(12) = 2.6$, $p < 0.05$). To summarize, the slope data indicated that S.P. was significantly less sensitive to changes in emotion at the categorical boundary across all three continua. There were no differences between the slopes of the three experimental groups (young controls, age-matched controls, MTL patients) on any of the morph progressions (all F's < 2, p's > 0.05).

To determine if changing the exposure duration had a direct effect on S.P.'s performance, we compared her median reaction times from Experiments 1 and 2. As can be seen from Table 2, S.P.'s reaction times were faster with limited stimulus exposure. Median reaction times and slopes for the two healthy control groups were also compared across experiments for the three morph types after removing S.P.'s age- and education-matched controls who had participated in both experiments. For both control groups, reaction time was significantly lower in Experiment 2 for all morph types (main effect of experiment for neutral to anger: $F(1,63) = 71.2$, $p < 0.001$; neutral to fear: $F(1,63) = 79.0$, $p < 0.001$; fear to anger: $F(1,63) = 55.8$, $p < 0.001$). Analysis of slope indicated that sensitivity around the categorical boundary was significantly lower only for the fear-to-anger morph, $F(1,63) = 7.2$, $p < 0.01$. These results suggest that reducing stimulus exposure resulted in a reduction in reaction time for morphs of increasing emotional intensity, and a reduction in both reaction time and sensitivity for emotion blends. This latter result may be related to the overall difficulty of the fear-to-anger morph.

Because S.P. and a subset of her matched controls had already participated in Experiment 1, it was important to consider the role of practice effects on task performance. Three points argue against carry-over effects. First, reaction times were also reduced for young controls in Experiment 2, none of whom had participated in Experiment 1 (Table 2). Second, despite faster reaction times, sensitivity at the categorical boundary was either unaffected or was reduced with limited exposure for all groups (Table 3), thus arguing against a benefit of participation in Experiment 1 on task performance. Finally, the performance of the subset of matched controls that did participate in both experi-

Table 3
Slopes of cumulative d' functions for Experiments 1 and 2

	Experiment 1		Experiment 2	
	Mean	S.E.M.	Mean	S.E.M.
Neutral to anger				
S.P.	0.64		0.45	
S.P. controls	0.95	0.09	0.84	0.08
Young controls	0.82	0.05	0.80	0.04
Neutral to fear				
S.P.	1.13		0.96	
S.P. controls	1.24	0.12	1.16	0.07
Young controls	1.21	0.07	1.18	0.06
Fear to anger				
S.P.	0.64		0.64	
S.P. controls	1.15	0.10	0.93	0.08
Young controls	1.03	0.08	0.81	0.05

ments was compared across experiments. Decreasing stimulus exposure from Experiments 1–2 significantly reduced reaction times across all morph types: neutral to anger, 966 ms (Experiment 1) versus 372 ms (Experiment 2), $t(6) = 11.02$, $p < 0.01$; neutral to fear, 918 ms versus 337 ms, $t(6) = 8.14$, $p < 0.01$; fear to anger, 1235 ms versus 521 ms, $t(6) = 6.86$, $p < 0.01$. However, similar to the analyses conducted above, sensitivity at the categorical boundary was unaffected by our manipulation (all t's less than 2, p's > 0.05). Therefore, it seems unlikely that the results obtained in Experiment 2 are attributable to practice effects.

2.3. Discussion

When participants were given limited exposure to faces, analysis of the slope around the categorical boundary indicated shallower slopes for patient S.P. than the other groups for all three morph types. Thus, S.P. was less sensitive to small changes in emotional intensity and emotion blends relative to the other groups, as her response shift at the categorical boundary was not as abrupt. Unilateral MTL patients showed intact performance on all three morph progressions. Comparison of reaction time data suggested that inconsistent results across Experiments 1 and 2 for the neutral-to-fear morphs are due to speed-accuracy tradeoffs in S.P. Limiting stimulus exposure did have an effect on performance and could have reduced the use of heuristics in this task. Taken together, these results indicate that bilateral amygdala damage results in an impairment in categorical perception of both fear and anger present in morphed expressions.

Because S.P. showed deficits on all three morph types when stimulus duration was limited, it is possible that her impairment is not specific to facial expression, but may stem from impairments in the perception of faces in general or more generalized problems with visual stimuli presented with shorter durations. The former scenario is unlikely, given that S.P. scores within the normal range on the Benton test of facial recognition. Nevertheless, we developed an analogous task with similar perceptual difficulty involving morphs of different identities with neutral facial expressions to rule out these possibilities.

3. Experiment 3

3.1. Method

3.1.1. Subjects

Participants included patient S.P., 16 age- and education-matched controls, 25 young adult controls, and 13 unilateral MTL patients. S.P. was tested approximately 17 months after the administration of Experiment 2 (24 months after Experiment 1). The age- and education-matched control group consisted of 6 males and 10 females ranging from 53 to 64 years of age (mean 59.0 years), who had between 12 and 20 years of education and did not have a history of neurologic or psychiatric illness. A subset of 4 of these controls had been run in Experiment 1 approximately 30 months prior, and a subset of 10 had been run in Experiment 2 approximately 23 months prior to Experiment 3. Young controls consisted of 9 males and 16 females ranging from 18 to 21 years of age (mean 18.8 years), with no history of neurologic or psychiatric illness, none of whom participated in Experiments 1 and 2. All unilateral MTL patients had participated in Experiment 2 during the same testing session. Procedures for human subjects were approved by the Institutional Review Boards at Duke University and New York University.

3.1.2. Stimulus materials and design

The identity morphs were created in the same manner as the expression morphs except that rather from morphing from one expression to another using the same actor, an actor with a neutral facial expression was morphed into another actor of the same gender with a neutral facial expression. The faces were of actors with neutral facial expressions taken from the same Ekman picture series. Eighteen actors were used to create 9 different identity morphs, each consisting of 10 faces, which were used in 9, two-alternative forced-choice identification tasks. Ten of the actors had been used to depict the emotion morphs in Experiments 1 and 2 ("old" faces), eight were new. Otherwise, the design of Experiment 3 was identical to that of Experiment 2 – individual identity morphs were presented for 505 ms and then replaced by a response selection screen, which was displayed until the participant made a response.

3.2. Results

Identification results are summarized in Fig. 7. Visual inspection of Fig. 7A indicated that S.P.'s data were not qualitatively different from that of controls. Similar to the previous experiments, the PSE was identified by finding the morph increment for each participant that was associated with the lowest sensitivity as assessed by d'. Next, cumulative d' was computed for the two increments before the PSE, the PSE and two increments after the PSE. The cumulative d' functions for the four groups on the three morphs are shown in Fig. 7B. The slopes of these functions were then computed for each participant (Fig. 7C). Slope values for the right and left MTL patients were did not differ significantly; hence, the values for the two groups were combined. Averaged slope values for the control and unilateral MTL groups were compared to S.P. using one-sample t-tests with S.P.'s value as the critical value. S.P.'s slope did not differ from that of the unilateral MTL patients (.83 versus .86, respectively, $p > 0.05$) and S.P.'s age- and education-matched controls (.83 versus .89, $p > 0.05$), but did differ from young controls (.83 versus 1.10, $t(24) = 4.0$, $p < 0.01$). Between-groups analysis revealed a main effect of group, $F(2,51) = 3.70$, $p < 0.05$. Post hoc analysis using Tukey's HSD indicated that this result was due to the young controls having higher slopes than the unilateral MTL patients (1.10 versus .86, respectively) and S.P.'s matched controls (1.10 versus .89), indicating a effect of aging on task performance.

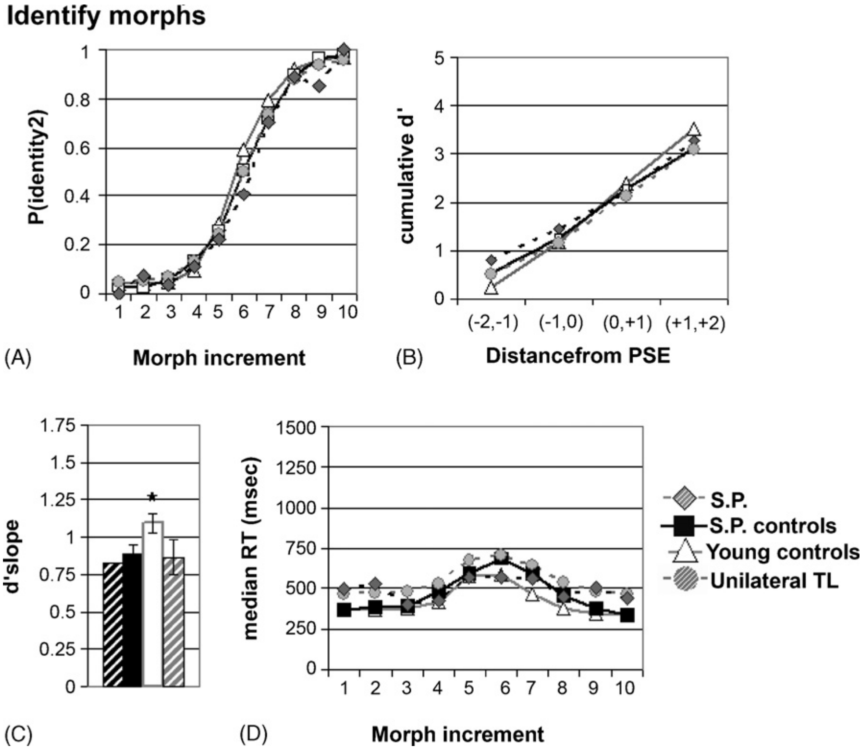

Fig. 7. Identification of identity in morphed images in Experiment 1. (A) The mean percentage of times that participants identified the images in the identity 1 to identity 2 continuum as identity 2, (B) cumulative d' functions for all groups, (C) the slope of these functions, and (D) median reaction times. Asterisk (*) indicates $p < 0.05$ relative to S.P., S.P. controls and unilateral MTL patients.

3.3. Discussion

Examination of S.P.'s slope revealed that her sensitivity to changes in facial identity around the PSE was equal to that of the unilateral MTL patients and age- and education-matched controls. This result shows that S.P.'s deficits are specific to emotional expression morphs and do not extend to morphs of facial identity. d' scores in controls were similar across Experiments 2 and 3, suggesting that the emotion and identity morph tasks were equivalent in perceptual difficulty. A remarkable difference between S.P.'s performance on the emotion versus identity morphs is evident in her reaction times. Unlike the emotion morphs, her median reaction times for the identity morphs did not differ appreciably from the other control groups (Fig. 7D). It is interesting to note that her median reaction time for the identity morphs was more than 300 ms faster than for the emotion morphs in Experiment 2 (Table 2). Thus, her intact performance on this task is not attributable to a speed-accuracy tradeoff and is unlikely to due to her relative familiarity with the Ekman stimulus set. These observations provide further evidence that S.P.'s impairments are limited to the perception of facial expression.

4. General discussion

Our results provide evidence that the amygdala's role in processing facial emotion extends beyond the perception of fearful expressions. We investigated facial expression processing in a patient with bilateral amygdala damage using 2-AFC tasks and analyses based on signal detection theory. In Experiment 1, we examined the identification of the morphed facial expressions of anger and fear allowing unlimited examination of facial expressions. Slope analysis indicated that S.P. was less sensitive to small changes in anger intensity across the categorical boundary for the neutral-to-anger and fear-to-anger morphs. In contrast, S.P. did not show impairments in the neutral-to-fear morphs, which was surprising given her performance in previous studies of fearful expression, albeit using a different task and stimulus materials (Adolphs, Tranel et al., 1999; Anderson & Phelps, 2000). Reaction times indicated prolonged decision-making on the part of S.P., suggesting that she may have been using some heuristic such as featural displacement to guide her decision-making when exposure duration was unlimited.

In Experiment 2, the exposure duration of each face was reduced to encourage more automatic processing of facial expression and to minimize reliance on cognitive heuristics. Altering the exposure time of faces had an effect on results from otherwise identical tasks. Relative to healthy controls and unilateral temporal lobectomy patients, S.P. showed impairments in perceiving changes in intensity of both anger and fear, and also in judging blends of fear and anger. Most notably, S.P. did not show normal sensitivity to changes in facial expression in that her response shifts across the categorical boundary were not as sharp as those of the control and unilateral MTL patient groups. Experiment 3 provided evidence that S.P.'s deficits in facial affect processing under time constraints did not extend to categorical perception of morphed changes in facial identity. Because patients with unilateral damage performed normally under time constraints in both the facial affect and identity tasks, bilateral damage to the amygdala may be critical to show this dissociation. Our finding that the unilateral MTL group (both the right and left MTL groups) performed normally relative to controls is inconsistent from Anderson et al. (2000) who demonstrated that right MTL patients showed impairments in rating the intensity of withdrawal-related emotions. The reason for this divergence is unclear; however, two explanations are possible. First, there are task differences between the two studies. Whereas Anderson et al. (2000) used intensity ratings of canonical facial expressions, our study employed 2-AFC discriminations of morphed facial expressions. Alternatively, the divergence could be due to differences in the degree or extent of MTL damage in the patient groups across the two studies.

The different results from the first two experiments on the neutral-to-fear morphs is most likely due to the fact that limited face presentation does not promote strategic, cognitively mediated processing. This possibility is supported by the reduction in S.P.'s reaction times from the first to the second experiment, as well as a reduction in sensitivity to changes in emotion blends across the two versions of the task. The first version of the task would be more amenable to heuristics/strategic processing, whereas strategic processing should be reduced in the second version. As a result, processing should be faster, but possibly less accurate when stimulus duration is limited. The role of the amygdala in rapid, obligatory aspects of face processing has been shown in fMRI studies using masked, rapidly presented facial expressions (e.g., Whalen et al., 1998).

Heuristic use may account for the mixed results regarding the specificity of impairments in both these and other tasks used to index the perception of facial expression. For example, most of the tasks used to assess facial expression processing allow participants an unlimited amount of time to examine faces. In this situation, identifying a face as fearful may merely involve examining eye or mouth aperture and have less to do with perceiving the face as scared per se. Similarly, an angry face may be identified by furrowed brows. Heuristic use may account for S.P.'s inconsistent performance on the face rating tasks over testing sessions (Adolphs, Tranel et al., 1999; Anderson & Phelps, 2000). S.P. is highly familiar with the Ekman faces, and her ability to pose facial expressions of emotions appears to be intact (Anderson & Phelps, 2000), indicating that she is aware of the featural changes that signal different facial expressions. Therefore, she may use this knowledge to help her make judgments about facial expressions under unlimited time constraints. Future research should employ more rapid stimulus presentation than that used in these experiments and examine additional patients with bilateral damage to definitively establish the role of the amygdala in the automatic, obligatory processing of facial expressions. As the present study indicates, the collection of reaction time data should help in the interpretation of results both within and across patients.

The finding that S.P. was impaired at identifying angry faces in both intensity morphs and emotion blends implicates the amygdala in the perception of anger, a finding also supported by Sato et al. (2002). Other studies of amygdala-lesioned patients found deficits in rating and identifying angry faces (Adolphs, Tranel et al., 1999; Calder et al., 1996), although results were inconsistent. These inconsistencies could be due to the tasks used to assess the perception of anger, which may not have been sensitive enough to consistently detect this deficit. The finding that S.P. showed impaired identification of anger is consistent with some recent neuroimaging studies that have reported amygdala activation to angry faces in healthy participants (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Kesler-West et al., 2001; LaBar et al., 2003; Whalen et al., 2001; Yang et al., 2002; but see Blair, Morris, Frith, Perrett, & Dolan, 1999). Together, these findings suggest that the amygdala's role in perceiving facial expressions of emotion may extend to other negative and arousing emotions, and is not merely limited to fear. Future research should extend the findings of this study to other emotional expressions since it is possible that S.P.'s deficits might be due to the relative difficulty of discriminating fearful and angry facial expressions (e.g., Rapcsak et al., 2000). A recent study by Adolphs and Tranel (2004) has demonstrated that patients with bilateral amygdala damage were impaired at rating neutral-to-sad morphs, but not neutral-to-happy morphs, implicating the amygdala in the perception of sadness. However, this result contradicts that of Sato et al. (2002), who found that H.Y. did not appear to be impaired in a 2-AFC task with happiness and sadness.

The present study also directly examined the possibility that amygdala damage is associated with impairments in perceiving blends of emotion (Adolphs et al., 1994). Although examined by Calder et al. (1996) and Sato et al. (2002), our study presents the first quantitative description of this phenomenon using 2-AFC tasks. S.P. showed impairments on both the unlimited and limited presentation versions of this task. In addition, she reported that this identification task was the most difficult of the three morph types. This comment is supported by the observation that S.P.'s reaction times were longest for the fear-to-anger morphs. One possible explanation for S.P.'s performance on this particular morph type is that blends of facial expression are biologically relevant but ambiguous stimuli. According to Whalen (1998), a possible function of the amygdala is as part of a vigilance system that is evoked by ambiguous but relevant learning situations. Emotion blends can have more than one interpretation; therefore, the amygdala should be more engaged by an emotion blend than a prototypical emotion in order to acquire the additional information necessary for the stimulus to be understood. If this is the case, then it is possible that S.P.'s performance on this task is impaired because she is lacking an integral part of this vigilance system. Further study should examine whether S.P. and other amygdala-lesioned patients have difficulties with all emotion blends or only blends involving fear or anger. Given that the fear-to-anger morphs were the most difficult to discriminate for all groups, it is possible that S.P.'s deficits might be due to the relative difficulty of discriminating emotion blends and may not be specific to blends of fear and anger (see Rapcsak et al., 2000 for a discussion of this issue).

A limitation of our study was the use of only one task to assess categorical perception: the 2-AFC paradigm. This paradigm can be used to examine the abrupt category shift where responding changes sharply from endorsing the emotion on one end of the continuum to the emotion on the other end of the continuum.

Therefore, although our results indicate that S.P.'s perception of fear and anger is impaired, it would be premature to conclude that S.P. does not perceive facial expressions of emotion in a categorical manner. We can only conclude that her response shift to changes in emotion or changes in emotional intensity is not as abrupt as those of controls and unilateral MTL patients. This is especially true in the case of the neutral-to-emotion morphs, as it is not clear whether 'neutral' constitutes a category of facial expression or merely the absence of expression. In order to more definitively conclude that her categorical perception of facial expressions is impaired, discrimination tasks (ABX tasks: Etcoff & Magee, 1992; Teunisse & de Gelder, 2001) should be administered.

In conclusion, by demonstrating that the identification of facial expressions can be affected by the length of time that a face is viewed, the present study provides evidence that the use of cognitive heuristics or strategies is an important factor when studying emotion on the face. Discouraging the use of heuristics can help clarify the role of the amygdala in the perception of facial expression because it reduces reliance on processes that are cortically-mediated, allowing for more sensitive tests of amygdala function. Applying quantitative signal detection analyses to speeded 2-AFC tests of morphed expressions reveals new insights into the role of the amygdala in emotional processing and permits an assessment of the contribution of speed-accuracy tradeoffs to task performance. The development of an analogous test involving morphed changes in facial identity enabled us to show a dissociation between performance across facial affect and identity tasks that are directly comparable. Our findings support a growing body of literature that suggests the amygdala's role in facial expression processing is not circumscribed solely to the perception of fear.

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