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Sequential ordering of morphed faces and facial expressions following temporal lobe damage

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Abstract

A card ordering task was developed to evaluate the role of the temporal lobe in perceiving subtle featural displacements of faces that contribute to judgments of facial expression and identity. Individuals with varying degrees of temporal lobe damage and healthy controls were required to manually sort cards depicting morphs of facial expressions or facial identities so that the cards were sequentially ordered from one morph endpoint to another. Four morph progressions were used—three emotion morphs (neutral-to-anger, neutral-to-fear, and fear-to-anger) and an identity morph. Five exemplars were given per morph type. Debriefing verified that participants were using feature-level cues to sort the cards. A patient with bilateral amygdala damage due to epilepsy did not differ in her sorting abilities from unilateral temporal lobectomy patients or controls. In contrast, a post-encephalitic patient with widespread left temporal lobe damage showed impairments that were most marked on the fear-to-anger and identity sorts. These results show that amygdala-damaged individuals can use information contained in facial expressions to solve tasks that rely on feature-level analysis, which recruits processing in other temporal lobe regions involved in making fine featural distinctions.

Keywords: Amygdala; Emotion; Facial affect; Face morph; Brain lesions

The idea that the amygdala plays a critical role in processing facial expression was advanced by Adolphs, Tranel, Damasio, and Damasio (1994), who described a patient with rare selective bilateral amygdala damage (S.M.) characterized by impairments in rating the intensity of facial expressions, especially the expression of fear. This finding was replicated in other patients with bilateral amygdala damage (e.g. Adolphs et al., 1999; Calder et al., 1996; Young, Aggleton, Hellawell, Johnson, & Broks, 1995; Young, Hellawell, Van De Wal, & Johnson, 1996) and has also been supported by neuroimaging studies showing amygdala activation to fearful faces in healthy adults (e.g. Morris et al., 1998; Whalen et al., 1998, 2001).

The specificity of the amygdala's involvement in processing fearful facial expressions, however, has remained unclear. Studies of individuals with bilateral amygdala damage have provided some inconsistencies, with different patients showing varying degrees of facial emotion decoding abilities (e.g. Adolphs et al., 1999; Adolphs & Tranel, 2004; Calder et al., 1996; Hamann et al., 1996; Hamann & Adolphs, 1999; Sato et al., 2002). Neuroimaging evidence has also provided mixed results regarding amygdalar involvement in processing expressions other than fear (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Blair, Morris, Frith, Perrett, & Dolan, 1999; Kesler-West et al., 2001; LaBar, Crupain, Voyvodic, & McCarthy, 2003; Whalen et al., 2001; Yang et al., 2002). A recent study by Adolphs et al. (2005) may provide an explanation for some of these inconsistencies. Their patient S.M.'s deficits in processing fearful facial expression appears to stem from the fact that she fails to spontaneously attend to the eye region of faces, which is critical for identifying fear. It is possible that the apparent involvement of the amygdala in evaluating certain facial expressions may be due to its involvement in processing information from the eye region of faces. The degree to which this finding holds for other patients may provide one account for inter-individual variability in the patient findings as well as the specificity of the neuroimaging findings to some categories of emotion over others.

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A related explanation for the variability in the patient findings is that amygdala-damaged patients may use slower, compensatory cognitive mechanisms to aid them with expression identification. This idea was supported by Graham, Devinsky, and LaBar (2006), who found that when heuristics use was discouraged by reducing exposure time to morphed facial expressions, deficits in the perception of anger and anger/fear blends, as well as fear, were evident in a patient with bilateral amygdala damage. However, with unlimited exposure durations, performance significantly improved. According to this conception, the amygdala's role in processing facial expression will vary depending on the demands of the task. The use of strategies to ameliorate deficits in facial expression processing has been found in children with autism (Teunisse & de Gelder, 2001), but the possibility that amygdala-damaged individuals could also be using strategies to differing degrees of success has not received much attention. Adolphs et al. (2005) reported that when patient S.M. was instructed to attend to the eye region of faces, her perception of fearful facial expressions appeared normal. This finding suggests that if individuals with bilateral amygdala damage are told what to look for, they can use this information strategically to help them overcome more automatic processing deficits due to amygdala damage.

Amygdala activation in healthy adults is also sensitive to task demands under some circumstances, especially those that relate to intentional (explicit) versus incidental (implicit) aspects of emotion processing (e.g. Critchley et al., 2000; Whalen et al., 1998). For example, Carlsson et al. (2004) demonstrated that masked phobic stimuli elicit left amygdala activation, whereas awareness of phobic stimuli was associated with bilateral amygdala activation and additional activity in a network of cortical brain regions, including the insula, anterior cingulated, and orbitofrontal cortex. Given that the amygdala is more consistently implicated in rapid, covert processing of faces (e.g. Bishop, Duncan, & Lawrence, 2004; Vuilleumier, Armony, Driver, & Dolan, 2003; Williams, Morris, McGlone, Abbott, & Mattingley, 2004), additional task-related factors may influence its involvement on explicit emotion processing tasks. Explicit emotional judgments tend to recruit additional processing in frontotemporal cortical areas compared to non-emotional judgments (e.g. gender or age judgments) using the same facial expressions (Critchley et al., 2000; Gorno-Tempini et al., 2001; Gur et al., 2002). Therefore, task demands could affect the extent to which the amygdala versus cortical regions are preferentially recruited across different studies (see also Hariri, Bookheimer, & Mazziotta, 2000) and could also account for some of the inconsistencies observed in the current literature regarding the amygdala's role in processing facial expression.

One explicit processing strategy that could aid emotion recognition judgments is feature analysis, where decisions regarding facial emotion are based on a deliberate analysis of the perceptual displacement of specific facial features. In particular, expression processing after amygdala damage could be preserved if the task emphasizes strategic, featural processing, and recruits cortical areas that are involved in making fine-grained distinctions between visual stimuli. The amygdala has been linked to the rapid processing of low frequency components of faces and facial expressions through magnocellular channels, whereas ventral and lateral temporal neocortical areas have been linked to processing high frequency components via parvocellular channels (Vuilleumier et al., 2003). This suggests that two routes exist for information regarding facial expressions of emotion: a rapid, implicit, amygdala-mediated pathway and a more voluntary, strategic, cortically-mediated pathway. Therefore, processing the high frequency information necessary to perform fine featural discriminations should not be dependent upon the amygdala, even if emotional faces are used as stimuli. Instead, more lateral and ventral temporal lobe areas may be important, consistent with their role in using featural information to discriminate objects within a category, as previously shown in monkeys (Freedman, Riesenhuber, Poggio, & Miller, 2003).

In the present study, a sequential ordering task was developed using morphed faces to assess the role of the amygdala and other temporal lobe areas in perceiving the featural displacements that accompany changes in facial emotion and identity. This task involves presenting subjects with cards showing facial expression and identity morphs of varying increments, and requires the subject to order the cards in a logical progression from one morph endpoint to another. Because this task provides all the relevant perceptual cues across the morph increments simultaneously, we reasoned that the execution of this task should promote cortically-mediated strategies such as analysis of featural displacements. Accordingly, ventrolateral temporal lobe areas should be involved in performing this task, whereas medial temporal lobe structures, including the amygdala, should not be critical.

The task was administered to three different patient types that varied in their degree of temporal lobe damage—(1) a group of unilateral medial temporal lobectomy patients (TLBs) who underwent excision of the anteromedial temporal lobe for the surgical treatment of retractable epilepsy, (2) patient S.P., a right temporal lobectomy patient who had sustained additional damage circumscribed to her left amygdala (Phelps et al., 1998), and (3) patient C.B., a post-encephalitic patient with more widespread damage to the left temporal lobe. We hypothesized that patient S.P. and the TLB patients would show relatively intact performance on this task. We previously found that patient S.P. is impaired at two-alternative forced choice recognition of the same morphs, especially under time constraints. Therefore, a demonstration of intact performance in the present study would show a dissociation in performance as a function of task demands using identical stimuli. For patient C.B., three outcomes were considered. First, if the right ventrolateral temporal lobe areas implicated in face processing are primarily responsible for performance on this task (e.g. Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997; McCarthy, 2000), then C.B. should perform normally since her right hemisphere is spared. Alternatively, if left temporal lobe areas implicated in the analysis of surface details (Peper & Irle, 1997) and face parts (Rossion et al., 2000) are critical to this task, then C.B. should have problems across all sorts presented. Finally, as a task that emphasizes both faces and feature analytic strategies, which vary in their respective dependence on the two cerebral hemispheres, this task may recruit right and left temporal lobe areas differentially, according to the difficulty or, perhaps, biological plausibility of the morph sort (e.g. LaBar et al., 2003).

1. Methods

1.1. Stimulus development

Emotional facial expressions 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). Prototypical expressions of fear and anger were morphed together, and anger and fear were also morphed with neutral expressions to create the experimental stimuli. Hence, three different emotional morph progressions were created: neutral-to-anger, neutral-to-fear, and fear-to-anger. Identity was kept constant across the three emotion morphs (i.e. the same actor was used, only the expression changed). The same six actors were used to construct the three different emotion morphs. 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 with a neutral facial expression. The faces were of actors with neutral facial expressions taken from the same Ekman picture series. Ten actors were used to create five different identity morphs.

The morphs were created using the methods outlined in LaBar et al. (2003). Between each source and target emotion, eight 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. Five exemplars of each emotion sort were presented using different actors. All morph sets were printed onto $4'' \times 6''$ index cards that could then be shuffled and manipulated.

1.2. Subjects

We studied S.P., a 58-year-old woman with bilateral amygdala damage associated with epilepsy, who first showed signs of neurological insult at 3–4 years of age and was later diagnosed with epilepsy. During adulthood, medically intractable complex seizures of right medial temporal lobe origin began to occur with greater frequency. At age 48, she underwent right anteromedial temporal lobe resection, including removal of the right amygdala. MR images taken 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, and 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, des Varney, & 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 ratings of the intensity of emotional facial expressions, S.P. has been tested on two occasions (Adolphs et al., 1999; Anderson & Phelps, 2000). On the first occasion, S.P.'s ratings were impaired for fear, disgust, sadness, and anger (Adolphs et al., 1999). On the second occasion, she showed impairments in rating fear, disgust, sadness, and happiness (Anderson & Phelps, 2000). In contrast, her ability to describe her personal emotional experiences does not differ appreciably from controls (Anderson & Phelps, 2002) and her ability to judge emotions from vocalizations is intact (Anderson & Phelps, 1998). Detailed information regarding S.P.'s lesions and neuropsychological status is available in Phelps et al. (1998).

We also tested C.B., a 32-year-old female with an Associate's degree. At age 22, C.B. had a series of severe headaches, during which she displayed abnormal behaviors. These were followed by a series of generalized tonic–clonic seizures, resulting in a diagnosis of herpes simplex encephalitis and subsequent treatment with anticonvulsant medications. MR images taken at age 32 revealed extensive damage to left temporal lobe, including the inferior and middle temporal gyri along their entire rostrocaudal extent, medial temporal–occipital junction, anterior aspect of the superior temporal gyrus, and all structures contained within the anteriomedial temporal lobes (i.e. amygdala, hippocampus, entorhinal/perirhinal cortices) (Fig. 1). Additionally, there is slight damage to the left globus pallidus and inferior portion of the insula, as well as the midline basal forebrain and nucleus accumbens. Her frontal, parietal, and occipital lobes are intact in the left hemisphere, and there is no damage to the right hemisphere.

Neuropsychological evaluation at age 32 indicated that C.B. performed normally on the Mini Mental State Exam (score: 28). Her IQ was low average (verbal IQ of 85, performance IQ of 84, and full scale IQ of 84). Her performance across domains of the WMS-III varied from borderline to extremely low, consistent with the extent of her left temporal lobe damage. She demonstrated some naming deficits (Short Boston Naming score: 12/15). C.B. continues to struggle with episodic memory deficits and has mild language-related impairments, such as aphasia, anomia, and paraphasia. Her face recognition performance as indexed by the Benton face recognition test falls within the normal range (long form score: 42, low average). Prior to this study, C.B.'s facial emotion recognition abilities had not been assessed.

Six patients with right medial temporal lobe damage (three female and three male) and seven patients (three female and four male) with left medial temporal damage comprised the TLB group. They ranged from 24 to 60 years in age (mean = 41.5 years) and had between 12 and 21 years of education (mean = 15.7 years). All TLB patients had average full scale IQs (FSIQ: 89–112, mean FSIQ = 102.3). 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 3.5–6.5 cm.

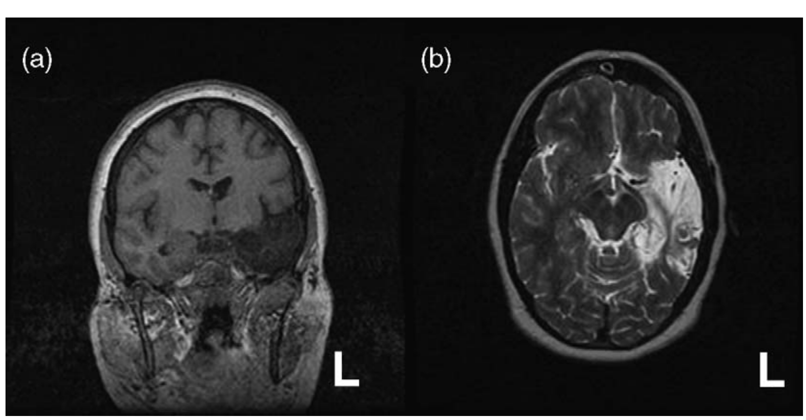

Fig. 1. Structural MRI scans of patient C.B. illustrating extent of left temporal lobe damage. (a) T1-weighted scan in coronal section at the level of the amygdala and (b) FLAIR scan in axial section at the level of the middle temporal gyrus. The left hemisphere (L) is depicted on the right side of the images.

The task was validated with two different control groups: a group of Duke undergraduates and a group of older adults. The young control group served as the control group for patient C.B. and consisted of 8 males and 12 females ranging from 18 to 21 years of age (mean 19.4 years), who had between 12 and 15 years of education with no history of neurologic or psychiatric illness. We also tested 17 age- and education-matched controls for patient S.P., three of whom did not complete the identity sort. This control group consisted of 11 females and 6 males ranging from 50 to 66 years of age (mean 55.9 years) who had between 12 and 17 years of education and did not have a history of neurologic or psychiatric illness. Procedures for human subjects were approved by the Institutional Review Boards at Duke University and New York University. All subjects provided written informed consent to participate and were either paid or received course credit for their participation.

1.3. Design and procedure

The morphed faces were divided into four sorting blocks, one for each morph type. Each block consisted of five sort trials. Practice trials were given for the emotion morphs. The blocks were given in the same order: neutral-to-anger, neutral-to-fear, fear-to-anger, and identity. Block order was fixed so that each participant would receive the tasks in the same order as patients S.P. and C.B. Each trial started in the same manner: the two extreme morph anchors (for example, the 100% neutral, 0% angry, and the 0% neutral, 100% angry stimuli in the neutral-to-anger morph block) were placed as anchors at the ends of a continuum. The intervening eight morph cards were shuffled and placed in random order in front of the participant, who was required to sort the morphs so that they progressed logically from one morph anchor to the other. There was a 60 s time limit for sorting and feedback was available for the practice trial. A schematic depiction of a neutral-to-anger morph sort trial is shown in Fig. 2. If the participant did not finish the sort within 1 min, the sort was terminated and the data for the trial was discarded (this occurred in a negligible number of trials, <1%). The order in which the participant placed the morphs and the sorting duration were recorded for each sort trial. After completing the experiments, subjects were asked to describe what facial information they used to complete the sort trials.

1.4. Data analysis

Concordance was used as an estimate of sorting accuracy and was measured with Kendall's tau, a non-parametric index of the degree of the similarity between two sets of rankings, which is highly sensitive to deviations in ordering (Siegel & Castellan, 1988). As tau values approach 1.0, sorting accuracy increases. To determine if S.P. and C.B.'s performance differed from that of the other groups, they were compared to TLBs, younger controls, and older controls via one sample *t*-tests with their respective means as the critical values. Differences between the concordance values and mean sort times across the two patients (S.P. and C.B.) could not be determined statistically because they are case reports, so they must be inferred from qualitative differences in their statistical profiles. To assess group differences between the TLB patients and controls, the mean sort times and concordance of TLBs and the two control groups were compared via repeated measures ANOVAs with group as a between subjects factor and sort block as a within subjects factor. To protect against type I error, degrees of freedom were corrected with Greenhouse-Geisser epsilon where applicable. Where significant effects were found, post hoc comparisons were conducted with Bonferroni corrections for type I error.

2. Results

Debriefing confirmed that the sorting task involved feature-based analysis; all subjects reported that they focused on how one or two particular facial features changed while sorting, regardless of the morph type. For example, on the neutral-to-fear sort, most subjects (including those with temporal lobe damage) reported using increasing eye or mouth aperture to guide their sort, while on the identity sort, subjects would use features such as presence of freckles or width of the lip, nose or eyebrow. Two performance indices were examined—mean sort time and concordance of each subject's ordering with the correct order. Reaction time and concordance values for the right TLB and left TLB patients were compared and found to be equal; hence, the values for the two groups were combined to form the TLB group.

2.1. Reaction time

Mean sorting times for the different individuals and groups across the four sort types are shown in Fig. 3. Between-groups analysis of the TLB and two control groups did not find any group differences in sorting times, $F < 1$, but did find a difference between the sorting times for the different morph blocks, $F(2, 88) = 13.21$, $p < 0.01$. Post hoc analyses showed that this effect reflects the fact that the identity morphs took longer to sort than the emotion morphs. There were no differences in sorting times for the three emotion morphs types.

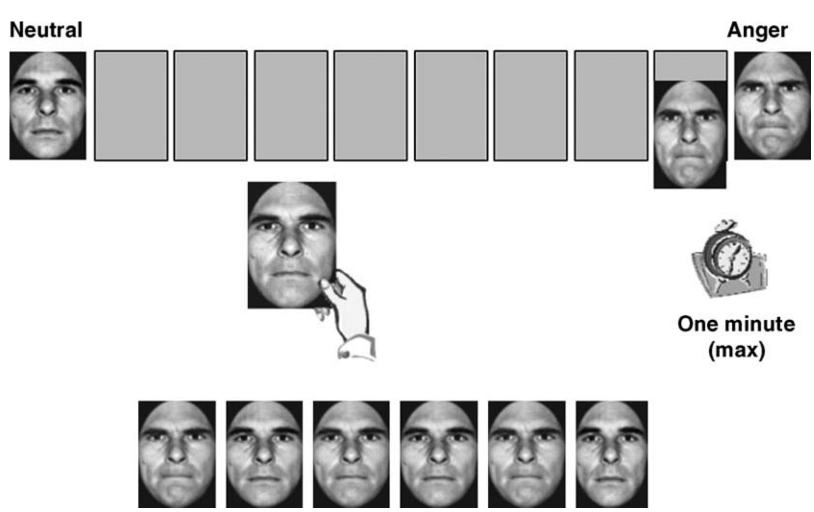

Fig. 2. Example of the stimuli and procedure used in this experiment. One trial from a neutral-to-anger morph progression is depicted.

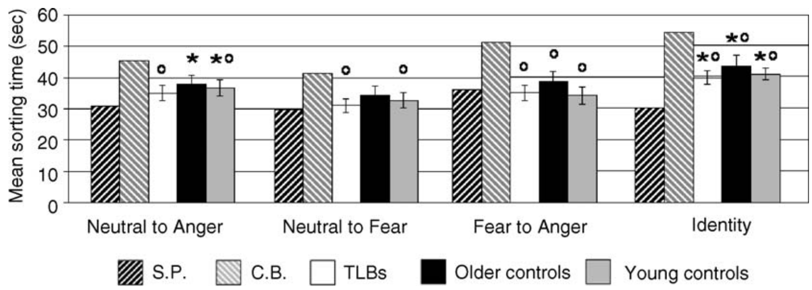

Fig. 3. Mean sorting times for patient S.P., patient C.B., unilateral temporal lobectomy patients (TLB), older controls, and younger controls across the four morph types. Standard error is indicated by error bars where applicable. (*) $p<0.05$ relative to S.P.; (◯) $p<0.05$ relative to C.B.

Comparison of S.P.'s sorting times to those of the TLB group and the two control groups revealed that she performed the neutral-to-anger sorts more quickly than her age-matched controls, $t(16)=2.46$, $p<0.05$, and young controls, $t(19)=2.19$, $p<0.05$. There were no differences in sorting times between S.P. and the other groups on the neutral-to-fear or the fear-to-anger morph sorts. She performed more quickly than all three groups on the identity sort (versus TLBs: $t(12)=4.49$, $p<0.01$; versus young controls: $t(19)=5.52$, $p<0.01$; versus age-matched controls: $t(13)=4.16$, $p<0.01$). In short, S.P.'s reaction times indicated that she did not encounter difficulties with this task.

Comparison of C.B.'s sorting times to those of the TLB group and the two control groups revealed that she performed the neutral-to-anger sorts more slowly than the TLB group, $t(12)=-4.27$, $p<0.01$, and young controls, $t(19)=-3.20$, $p<0.01$. She was also slower than the TLB group and young controls on the neutral-to-fear sorts (versus TLBs: $t(12)=-4.66$, $p<0.01$; versus young controls: $t(19)=-3.57$, $p<0.01$). C.B.'s sort times were slower than those of any of the groups on the fear-to-anger sort (versus TLBs: $t(12)=-6.48$, $p<0.01$; versus young controls: $t(19)=-6.25$, $p<0.01$; versus older controls: $t(16)=-4.48$, $p<0.01$) and the identity sort (versus TLBs: $t(12)=-6.56$, $p<0.01$; versus controls: $t(19)=-6.65$, $p<0.01$; versus older controls: $t(13)=-2.40$, $p<0.05$). Overall, C.B.'s reaction times indicate that she had more difficulty completing this task than other participants, particularly the fear-to-anger and identity blocks.

2.2. Concordance: Kendall's tau

Concordance values for the different individuals and groups across the four sort types are shown in Fig. 4. Between-groups analysis of the TLB group and the two control groups revealed a main effect of group, $F(2, 43)=11.40$, $p<0.01$. Post hoc tests revealed that this main effect reflected a tendency for the young controls to sort more accurately than either the TLB or the older control group, who did not differ from each other. There was also a main effect of morph type, $F(3, 65)=18.73$, $p<0.01$. Post hoc comparisons revealed that this was due to the fact that, overall, performance on the fear-to-anger and identity sorts was lower than performance on the neutral-to-anger and fear-to-anger sorts. These main effects were mediated by a significant group by morph type interaction, $F(3, 65)=3.26$, $p<0.05$. The lower performance on the fear-to-anger and identity morphs was a pattern common to the TLB and older control groups, whereas the performance profile for the young control group showed no difference across morph types.

Comparison of S.P.'s concordance values to those of the TLB group and the two control groups revealed that she performed the neutral-to-anger sorts less accurately than young controls, $t(19)=2.19$, $p<0.05$. This was also the case for the neutral-to-fear, fear-to-anger, and the identity morph sorts (neutral-to-fear: $t(19)=2.63$, $p<0.05$; fear-to-anger: $t(19)=4.50$, $p<0.01$; identity: $t(19)=6.17$, $p<0.01$). There were no differences between the sorting performance of S.P. and the TLB group and her age-matched controls on any of the morph sorts except that she outperformed the TLB group on the identity sort, $t(12)=2.29$, $p<0.05$. In summary, S.P.'s sorting performance did not differ appreciably from any of the groups except the young control group. Importantly, there were no differences between S.P. and her age-matched controls on any of the morph sorts.

Comparison of C.B.'s sorting accuracy to that of the TLB group and the two control groups revealed that she performed the neutral-to-anger sorts less accurately than young

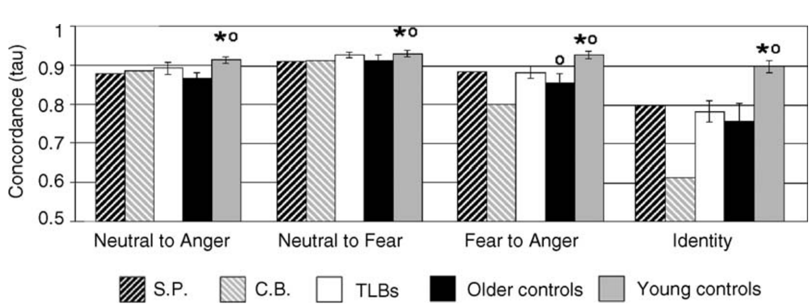

Fig. 4. Mean concordance values (Kendall's tau) for patient S.P., patient C.B., unilateral temporal lobectomy patients (TLB), older controls, and younger controls across the four morph types. Standard error is indicated by error bars where applicable. (*) $p<0.05$ relative to S.P.; (◯) $p<0.05$ relative to C.B.

controls, $t(19) = 3.14$, $p < 0.01$. She also sorted less accurately than young controls on the neutral-to-fear sorts, $t(19) = 2.25$, $p < 0.05$. On the fear-to-anger sorts, C.B.'s performance accuracy was impaired relative to the TLB patients and both control groups (versus TLBs: $t(12) = 5.42$, $p < 0.01$; versus young controls: $t(19) = 12.98$, $p < 0.01$; versus older controls: $t(16) = 2.30$, $p < 0.05$). Compared to all three groups, she also performed more poorly on the identity sort (versus TLBs: $t(12) = 4.51$, $p < 0.01$; versus young controls: $t(19) = 17.67$, $p < 0.01$; versus older controls: $t(13) = 4.51$, $p < 0.01$). In summary, analysis of C.B.'s concordance values produced results that mirrored her sorting times—overall, she had some difficulty on this task, especially on the fear-to-anger and identity morphs.

3. Discussion

Judgments of facial expression and identity depend on multiple sources of information from the face that vary in their reliance on cortical versus subcortical routes of processing. The present study was designed to assess the role of the temporal lobe in the analysis of featural displacements, which accompany subtle changes in emotional expression and identity. Confirming our hypothesis that the card ordering task would encourage cortically-mediated strategic processing, subjects reported using specific morph features to help them perform the task. Across both facial expression and identity morph sorts, normal performance was observed in a patient with bilateral amygdala damage (S.P.) and patients with restricted unilateral anteromedial temporal lobectomy. This result is especially interesting since S.P. performs poorly on some emotion recognition judgments from the same stimulus set (Adolphs et al., 1999; Anderson & Phelps, 2000) and can use heuristic strategies to ameliorate some of her recognition deficits (Graham et al., 2006), which suggests that amygdala involvement in facial expression processing is task-dependent. In contrast to patient S.P., post-encephalitic patient C.B., who sustained more extensive left temporal lobe damage, had difficulty with the sorting task on both the fear-to-anger and identity morphs. This latter finding suggests that posterior left temporal lobe areas are recruited when difficult featural distinctions need to be made between perceptually-similar faces, on the basis of both facial expression and identity. Analysis of reaction time and accuracy suggested that performance in the patients was not associated with speed-accuracy tradeoffs. Overall, the findings support a dissociation between the roles of the amygdala and posterior temporal neocortex in feature-based processing that supports judgments of facial expression and identity. We expand on each of these findings in turn below.

Debriefing confirmed our assumption that the temporal order sorting task encouraged the use of feature-analytic strategies in that subjects reported focusing on specific facial features to complete the task. An interesting observation was that these features tended to be implicitly dynamic for emotion judgments (e.g. increasing eye or mouth aperture), whereas they were static features in the identity judgments (e.g. nose or lip width, freckles). While descriptive, this tendency is congruent with the perspective that emotion judgments are dependent upon the dynamic characteristics of faces, whereas identity judgments rely more on more static facial aspects (e.g. Bruce & Young, 1986).

S.P. was only outperformed on this task by the young controls, an effect that could be attributable to age. Importantly, her performance did not differ from the TLB group or her age- and education-matched control group. Therefore, bilateral amygdala damage does not appear to be associated with deficits on this task. The TLB group also did not differ from other control groups in terms of sorting time or performance. Patient S.P. actually outperformed the TLB patients on the identity sorts, but it is likely that this could be attributed to S.P.'s relative familiarity with the stimulus set. S.P.'s relatively quick sort times, in particular for the identity morphs, may also reflect her familiarity with the Ekman stimuli, to which she has been exposed on several occasions over a period of 10 years.

The results from the TLB patients and patient S.P. confirm that the amygdala is not critically involved in face processing tasks that encourage strategic, feature-based analysis and compliment our previous finding that deficits in the perception of fear and anger in face morphs are more prominent when strategy use is discouraged, for example by limiting exposure duration (Graham et al., 2006). These results also compliment those of Adolphs et al. (2005), who found that when they instructed their patient S.M. to attend to the information in the eye region of faces, she no longer showed deficits in rating the intensity of fearful faces. Together, these findings converge to suggest that when individuals with bilateral amygdala damage are aware of the featural changes that signal different emotions (either by instruction or by having all perceptual information available at the time of test), they may be able to use this information to discriminate the feature changes that signal different emotions, and thus, potentially improve facial emotion recognition. One caveat to this implication is that in the present study, participants were not asked to label or recognize the emotions present (they were provided the emotion labels for the morph endpoints), so the extent to which featural strategies are spontaneously deployed by amygdala-lesioned patients in explicit recognition tasks requires further study (see also Adolphs et al., 2005).

In combination, these results are consistent with the view that the amygdala is involved in more rapid, obligatory aspects of face processing that are less amenable to cognitive control (e.g. Critchley et al., 2000; Gläscher & Adolphs, 2003; Whalen et al., 1998; Williams et al., 2004), and that amygdala-lesioned patients can benefit from cortically-mediated cognitive strategies, including feature analysis, that rely on posterior temporal neocortex. S.P. is able to successfully pose various facial expressions of emotions, implying that she is aware of the featural changes that accompany different emotional displays (Anderson & Phelps, 2000). Therefore, she is apparently able to use this information to help her make judgments about facial expressions when those cues are simultaneously available at test, even for fearful expressions. Under certain task conditions, then, normal performance can be elicited in amygdala-lesioned patients using the same facial expression stimuli, which, under other circumstances, yield performance deficits.

In contrast to S.P., patient C.B. exhibited more dramatic deficits on this task. Her performance on the neutral-to-anger and neutral-to-fear sorts showed evidence of subtle impairments: she sorted more slowly than the TLB and young control groups and had lower accuracy relative to the young control group. Her impairments were more marked on the fear-to-anger and identity sorts, where she had both reaction time and accuracy difficulties relative to all other groups. Between-groups analysis indicated that the control groups and the TLB group performed most poorly on the fear-to-anger and identity sorts and took the longest to sort identity morphs, indicating that these morphs were the most difficult to sort. C.B.'s deficits on the more difficult morph types could be attributed to the extensive damage to ventrolateral regions of her left temporal lobe and gives us insight into the role of left temporal areas in face processing. Importantly, because her deficits were not specific to emotional expression, the results from patient C.B. implicate a more general function of left ventrolateral temporal cortex in feature-based analysis of faces.

The left inferior temporal lobe has been shown to play an integral role in the discrimination of visual patterns (Kawashima et al., 1998). Single cell recordings from the human lateral temporal lobes have demonstrated that both temporal lobes are active during face processing tasks. Whereas activity in the right hemisphere appears to be face-selective, left temporal lobe activity is less specific, occurring to both faces and complex patterns (Lucas, Schoenfield-McNeill, Weber, & Ojemann, 2003). Left temporal lobe areas have been linked to processing the non-emotional surface details of faces (Peper & Irle, 1997) and face parts (Rossion et al., 2000). Because the completion of our task is dependent upon detecting subtle featural changes, this task may recruit processing in the left temporal neocortex, even when this damage is not accompanied by specific face processing deficits (e.g. prosopagnosia).

One possibility is that the fine-grained part-based analysis attributed to left temporal lobe areas (Peper & Irle, 1997; Rossion et al., 2000) provide task-dependent support to the right temporal lobe areas normally recruited during face processing, and this support becomes especially important when the task involves making difficult featural discriminations. Another possibility is that while neutral-to-anger and neutral-to-fear morphs depict biologically plausible motion whose processing has been attributed to superior temporal lobe structures (e.g. Jellema & Perrett, 2003) that are right-lateralized in humans (e.g. Allison, Puce, & McCarthy, 2000; Pelphrey et al., 2003; Pelphrey, Viola, & McCarthy, 2004), the fear-to-anger and identity morphs may be less plausible and require recruitment of other temporal lobe areas whose duties are not circumscribed to face processing, including those in the left hemisphere. These possibilities warrant attention in future research.

In conclusion, the present study demonstrated that individuals with amygdala damage can have intact performance on perceptual tasks employing changes in facial emotion and identity, and qualifies the conditions under which the amygdala and other temporal lobe areas are recruited for processing information in faces. Specifically, the amygdala did not play a critical role in a face task that emphasized feature-analytic strategic processing, suggesting that this structure is not important for making fine featural discriminations. Instead, more ventrolateral temporal areas appear to be important, including left temporal lobe regions that are not selectively associated with facial affect processing. Differential recruitment of these pathways across experimental paradigms may account for inconsistencies in facial affect research regarding the role of the amygdala and underscores the notion that stimuli depicting emotional states rely on multiple processing pathways, including those that do not encode emotional reactions per se. Because our data relies heavily on case reports, the task should be replicated in larger patient samples to confirm the results and to rule out alternative explanations (e.g. the larger extent of brain damage in patient C.B. or her lower IQ). Our findings complement other recent studies that emphasize the importance of task design in studying the role of temporal lobe structures in face processing and hint at the potential for cognitive remediation strategies to benefit facial evaluation in amygdala-lesioned patients.

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