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Dissociable neural systems for recognizing emotions

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Abstract

This study tested the hypothesis that the recognition of emotions would draw upon anatomically separable brain regions, depending on whether the stimuli were static or explicitly conveyed information regarding actions. We investigated the hypothesis in a rare subject with extensive bilateral brain lesions, patient B., by administering tasks that assessed recognition and naming of emotions from visual and verbal stimuli, some of which depicted actions and some of which did not. B. could not recognize any primary emotion other than happiness, when emotions were shown as static images or given as single verbal labels. By contrast, with the notable exception of disgust, he correctly recognized primary emotions from dynamic displays of facial expressions as well as from stories that described actions. Our findings are consistent with the idea that information about actions is processed in occipitoparietal and dorsal frontal cortices, all of which are intact in B.'s brain. Such information subsequently would be linked to knowledge about emotions that depends on structures mapping somatic states, many of which are also intact in B.'s brain. However, one of these somatosensory structures, the insula, is bilaterally damaged, perhaps accounting for B.'s uniformly impaired recognition of disgust (from both static and action stimuli). Other structures that are damaged in B.'s brain, including bilateral inferior and anterior temporal lobe and medial frontal cortices, appear to be critical for linking perception of static stimuli to recognition of emotions. Thus the retrieval of knowledge regarding emotions draws upon widely distributed and partly distinct sets of neural structures, depending on the attributes of the stimulus.
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1. Introduction

A large number of neuropsychological studies have shown that knowledge of different classes of entities depends on anatomically separable neural systems, as borne out by the finding that recognition and naming impairments subsequent to brain damage is often disproportionate for specific conceptual categories (Damasio, Damasio, Tranel, & Brandt, 1990; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Farah, McMullen, & Meyer, 1991; Hart & Gordon, 1992; McCarthy & Warrington, 1988; Tranel, Damasio, & Damasio, 1997; Warrington & McCarthy, 1994). For instance, brain-damaged patients may be disproportionately impaired in retrieving knowledge of concepts, or in retrieving names, at a specific level of contextual complexity (e.g., unique entities, as opposed to non-unique entities), or with respect to a particular class of entity (e.g., disproportionate impairments in retrieving knowledge of tools, animals, or people), depending on the site of the lesion. These findings, in addition, are consistent with studies using functional imaging (Damasio et al., 1996; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Martin, Wiggs, Ungerleider, & Haxby, 1996) and electrophysiology (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Nobre, Allison, & McCarthy, 1994).

A clear dissociation has also been demonstrated in regard to processing information related to recognition of static visual stimuli, and to the processing of visual motion and related guidance of reaching towards visual targets in space. Findings from studies in non-human primates have provided evidence for two so-called visual streams: a ventral stream leading into the temporal lobe that is critical for object recognition, and a dorsal stream leading into parietal lobe that is critical for localizing objects in space and for visually guided reaching (Felleman & Van Essen, 1991; Ungerleider & Mishkin,

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1982). In humans, this bipartite distinction encompasses both the processing of visual information (object recognition versus reaching for objects under visual guidance; Goodale et al., 1994; Goodale, Milner, Jakobson, & Carey, 1991; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995) and the processing of lexical information (knowledge of nouns versus knowledge of verbs; Caramazza & Hillis, 1991; Damasio et al., in press; Damasio & Tranel, 1993; Gainotti, Silveri, Daniele, & Giustolisi, 1995; Tranel, Adolphs, Damasio, & Damasio, 2001). As in animal studies, there is good evidence that cortices in temporal lobe subserve the former set of processes, while cortices in parietal and frontal lobe subserve the latter set of processes.

Information concerning either overt or implied visual motion is processed by cortices in the middle temporal and middle superior temporal region (MT and MST) in monkeys, and analogues of these regions have been identified in humans. It is noteworthy that a large variety of visual stimuli, including moving stimuli as well as static stimuli that imply or are in some way connected with movement (e.g., pictures of tools), all result in activation in or close to the presumed location of MT/MST in humans (Damasio et al., in press; Kourtzi & Kanwisher, 2000; Martin, Ungerleider, & Haxby, 2000). MT/MST in turn has connections to both the ventral object recognition system, as well as to the dorsal stream in parietal cortex, illustrating the potential availability of information about visual motion to a wide variety of brain regions.

While the above dissociations have been investigated for concrete entities and for actions in a number of studies, they have not been addressed specifically in regard to knowledge of emotions. To investigate such a possible dissociation in retrieving knowledge about emotions, we carried out a series of detailed studies in patient B., who is severely impaired in retrieving conceptual knowledge for many different kinds of entities. It is noteworthy that B. is able to retrieve at basic level the words denoting visually presented actions (Damasio & Tranel, 1993), although he shows impairments in retrieving many of the words that correspond to concrete entities (e.g., nouns; Damasio & Tranel, 1993). We hypothesized that B. might be able to recognize emotions from dynamic stimuli and actions, but not from static stimuli.

We investigated both naming and recognition of emotions in patient B., using several different tasks, some of which required retrieval of words denoting emotions (e.g., naming emotional facial expressions), and some of which did not (e.g., sorting facial expressions according to the emotion displayed). We focused on knowledge of 6 primary (Ekman, 1972; Ekman & Friesen, 1976) emotions (happiness, surprise, fear, anger, disgust, and sadness) as signalled by facial expressions, stories, or verbal labels. Across all tasks, we found a consistent pattern: B. was entirely unable to recognize any emotion except happiness, either from static stimuli or from single words; by contrast, he performed normally for all emotions except disgust when the stimuli showed visual motion, or when they contained explicit information about actions.

2. Methods

2.1. Subjects

Patient B. is a premorbidly normal man who had severe *Herpes simplex* encephalitis in 1975, at age 48. After a 3-day coma, he gradually improved and was discharged from the hospital 1 month later, awake, alert, and neurologically normal except as described below. Since then, he has been evaluated regularly by us, and he has a stable profile both neuroanatomically and neuropsychologically (Damasio, Eslinger, Damasio, Van Hoesen, & Cornell, 1985). He has one of the most severe anterograde and retrograde amnesias ever reported. His retrograde amnesia covers nearly all episodic knowledge, with some minimal sparing of very remote autobiographical events. He is unable to acquire any new declarative knowledge whatsoever, but shows normal learning of motor skills (Tranel, Damasio, Damasio, & Brandt, 1994). Basic visual perception, language, and basic intellectual functions that do not require declarative long-term memory are all intact [e.g., his score on the Benton Facial Recognition Task is 43 (32nd percentile; normal range), indicating that he has no difficulty processing the perceptual features of faces].

Patient B.'s lesion is shown in Fig. 1. On the basis of detailed examinations of his brain in CT and MR

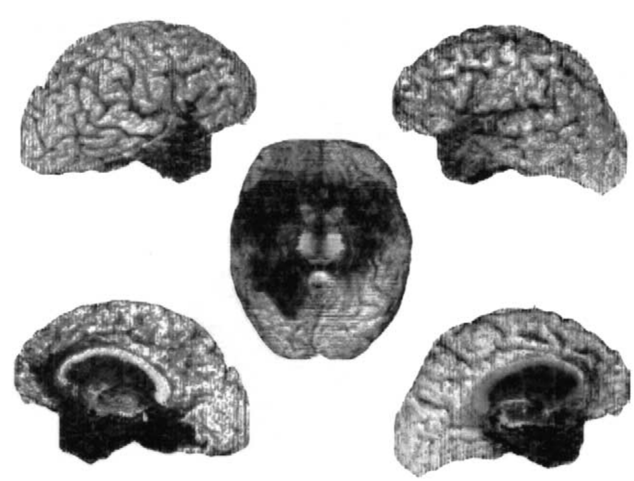

Fig. 1. The brain of patient B. Shown are lateral (top), ventral (middle), and medial (bottom) views of a three-dimensional reconstruction of B.'s brain obtained from serial MR images. The dark regions indicate the extent of his lesion, as described in Section 2.

scans, it is evident that he has complete damage of both amygdalae, hippocampi, as well as adjacent perirhinal, entorhinal, and parahippocampal cortices (greater on the right than on the left). There is also bilateral destruction of temporal neocortical areas 38, 20/21, and most of area 37 on the right. The regions in B.'s brain that are notably spared include posterior inferotemporal cortex, the presumed human homologue of MT/MST, occipito-parietal cortices (laterally, inferiorly, and mesially), as well as dorsal and lateral frontal cortex. There is complete bilateral damage to basal forebrain nuclei, and extensive damage to anterior insula. Parts of the ventromedial frontal cortices, and of the anterior cingulate cortex, are damaged as well.

In the present study, we tested B. in a total of 5 separate sessions. Most of the tasks were repeated at different testing sessions, and his performances were consistent throughout the study. B.'s task performances were compared to those given by normal, adult control subjects (numbers as noted in text). All subjects had corrected-to-normal visual acuity and had given informed consent to participate in these studies, as approved by the Human Subjects Committee of the University of Iowa.

2.2. Stimuli and tasks

There was no time limit for any task. Since B. is severely amnesic, we repeated all instructions frequently throughout each task.

2.2.1. Static facial expressions of emotion

Eighteen normal subjects were shown 36 facial expressions (6 of each primary emotion) from Ekman and Friesen (1976) that normal subjects name correctly at >80% (cf. Adolphs, Damasio, Tranel, & Damasio, 1996; Adolphs, Tranel, Damasio, & Damasio, 1995); B. was shown a subset of 18 of the 36 faces (3 of each emotion). For *Experiment 1*, subjects were asked to generate spontaneously the word that best described the emotion shown in each face. For *Experiment 2*, we showed subjects facial expressions, supplied the name of a basic emotion, and asked the subject to rate the intensity with which the facial expression depicted that particular emotion. Subjects rated the faces on 6 emotional labels (happy, surprised, afraid, angry, disgusted, and sad), on a scale of 0 (not present at all) to 5 (very intense instance of this emotion), as described previously (Adolphs, Tranel, Damasio, & Damasio, 1994). For *Experiment 3*, essentially the inverse of Experiment 1, photographs of 18 faces, 3 of each of the 6 basic emotions, were presented simultaneously on a large table. Subjects were asked to point to all the faces that depicted an emotion stated by the experimenter (e.g., "Point to all the people who look happy"). A normalized score was calculated as (total correct matches/maximum correct matches possible) – (total incorrect matches/maximum number incorrect matches possible).

2.2.2. Recognition of static facial expressions without naming: Experiment 4

Patient B. and 7 normal subjects were asked to sort photographs of 18 facial expressions (3 of each emotion) into 3, 4, 7, and 10 piles (in random order) on the basis of the similarity of the emotion expressed. A measure of similarity between each pair of faces was calculated from this task by summing the occurrences of that pair of faces in a pile, weighted by the number of possible piles, to yield a number between 0 and 24 (Ward, 1977).

2.2.3. Stories about actions: Experiment 5

Patient B. and 29 normal controls were read 30 single sentences (5 of each of the 6 basic emotions) and asked to name the emotion that the story suggested. These stories contained descriptions of events happening to people (e.g., "John was driving down a steep road, and when he stepped down he found that he had no brakes"), or of actions or gestures associated with the emotion (e.g., "John's eyes grew large and he screamed"), but no verbal label of any emotion.

2.2.4. Dynamic facial expressions: Experiment 6

Patient B. and 11 normal controls watched an experimenter produce facial expressions for each of the six basic emotions, in two identical sessions, when seated across from the observing subject. In each case, an intense but natural expression of an emotion was produced after a previously neutral one in rapid succession (<1 s). B. and the controls watched closely as the expression changed from neutral to the target emotion. They were asked to generate spontaneously the name of the emotion, and then to match the expression with the correct name from a list.

3. Results

3.1. Naming and recognition of static emotional facial expressions

3.1.1. Experiment 1 (Fig. 2)

When asked to name the emotions expressed by faces with the words that described them best, normal subjects typically gave spontaneous labels of the emotions as happiness, surprise, fear, anger, disgust, and sadness, which correspond to the "basic-level" (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976) or "entry-level" (Jolicoeur, Gluck, & Kosslyn, 1984) categories. Patient B. consistently named all the stimuli as either "happy," or "sad," thus failing to name most expressions at basic level, and lumping them into two broad categories.

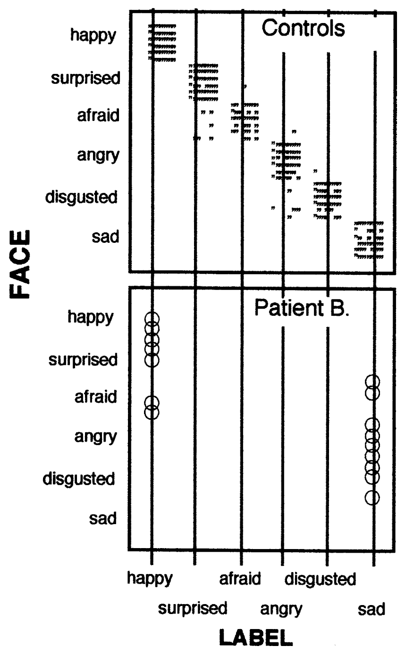

Fig. 2. Spontaneous naming of facial expressions of emotion. Each data point corresponds to the verbal label given to a face by each of 7 normal subjects (top) or by Patient B. (bottom). Patient B. named only 2 categories. For the purpose of displaying these data, some of the names that subjects gave were substituted with synonyms (e.g., "mad" with "angry"); names that were not obviously synonymous with the names in the figure were not plotted (e.g., "guilty" for a sad face).

3.1.2. Experiment 2 (Fig. 3)

To obtain a more detailed analysis of B.'s categorization of the facial expressions, Experiment 2 required him to rate each face with respect to the names for each of the 6 basic emotions. The data from Experiment 2 can be directly visualized to reveal the categories into which B. partitioned the stimuli (he again classified faces according to 2 broad categories, as revealed by the 2 broad peaks in Fig. 3a). We quantified these results with a hierarchical cluster analysis, which confirmed the visual pattern seen in Fig. 3a. The data from normal subjects are consistent with results published in other studies (Russell, 1980; Russell & Bullock, 1985; Russell, Lewicka, & Niit, 1989a). Normal subjects never lump categories together in the way that B. does. Comparisons between B.'s performance and normal performance on this task show that he categorizes the stimuli at an abnormally superordinate level (Fig. 3b).

3.1.3. Experiment 3 (Fig. 4)

When asked to match verbal labels to photographs of emotional facial expressions, B.'s impairment again revealed an inability to retrieve basic-level knowledge of emotions. While he correctly matched happy faces with the label "happy," he failed to match other facial expressions with their correct label. It is worth noting that his low score on sad faces on this task is due primarily to false positives: he tended to label most negative facial expressions as "sad," consistent with the dual classification scheme evident from the above tasks. B.'s inability to connect emotional facial expressions with the names of the emotions at basic level is thus bidirectional: not only is he unable to name the emotion when shown the face, but he also is unable to choose the correct facial expression when given the name.

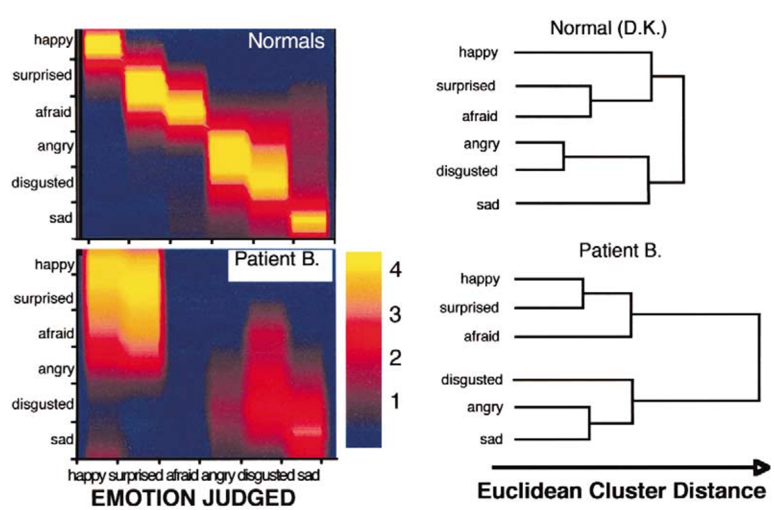

Fig. 3. Ratings of facial expressions of emotion. The x-axis plots emotions in order of similarity as perceived by normal subjects [adjacent emotions are judged to be more similar (Adolphs et al., 1994)]. (a) Direct plot of the intensity of different emotions judged to be expressed by faces. The mean ratings for each face (y-axis) on each verbal label (x-axis) are represented by pixel color on a scale from 0 (not at all) to 5 (very much). Bright regions correspond to categories distinguished by the subjects. Data are from 1 experiment with each of 7 normal controls (mean shown) and 3 experiments with B. These data were analyzed with a complete-linkage hierarchical clustering algorithm (Hartigan, 1975) to generate the solutions shown in (b). A typical normal control (one of the 7 tested, D.K.) is shown; cluster analyses for the other normal subjects were similar. The x-axis measures computed Euclidean distance between emotion categories, corresponding to the subject's perceived dissimilarity between stimulus categories. Closer categories are perceived to be more similar.

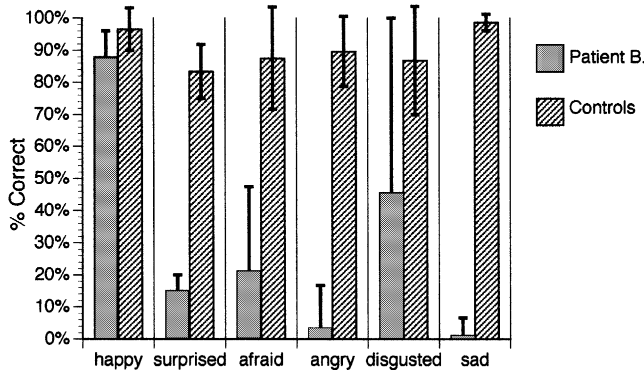

Fig. 4. Normalized accuracy in matching names with visual stimuli. Shown are the mean accuracies in matching of verbal labels with photographs of facial expressions. Scores were corrected for false positives, so that random guessing would be expected to give a score of zero. Patient B. (solid bars) and 7 normal controls (shaded bars) were given the verbal label and asked to choose which facial expressions corresponded to the label. Note that standard error of the mean is shown for B.'s data (for each of the three stimuli within an emotion category), and SDs are shown for the control data.

3.1.4. Recognition without naming: Experiment 4 (Fig. 5)

Performance on the above tasks relies in part on knowing the names for emotions. In a further task that did not require knowledge of the names for basic emotions, we asked B. to sort photographs of the facial expressions into piles of specific size, on the basis of the similarity of the emotion expressed. A derived similarity measure was obtained from these data. B. again categorized emotions dichotomously according to their membership in the superordinate categories of happy or unhappy, whereas normal subjects categorized emotions at their basic level.

We followed up B.'s performance on this task by asking him to sort the photographs into however many piles he thought might constitute emotion categories. He spontaneously sorted the photographs into 2 piles, which he labeled as happy (comprising all 9 happy, surprised, and afraid faces) and sad (comprising all 9 sad, disgusted, and angry faces).

3.2. Recognition of emotions from actions

3.2.1. Experiment 5 (Fig. 6)

When read short stories describing actions associated with emotions, B. spontaneously and without hesitation generated the correct verbal label of the emotion for all primary emotions, with the notable exception of disgust (Fig. 6). Particularly striking is his intact recognition of fear and anger, two emotions which he is entirely unable to recognize in static visual stimuli, and which he cannot describe correctly when given the verbal label (cf. Figs. 2 and 3). It is noteworthy that these stimuli were not simply easier than the stimuli we used in other tasks; as the normative data shown in Fig. 6 attest, B. in fact performed at a level comparable or superior to normal controls on every emotion, with the exception of disgust (interestingly, disgust was the emotion that normal subjects found the easiest). His severely impaired recognition of disgust was more than 5 SD below the mean.

3.2.2. Experiment 6 (Fig. 7)

When shown natural dynamic facial expressions executed by an experimenter, and asked to name the emotion expressed, B. named all primary emotions correctly, with the exception of disgust. Moreover, his responses on this task were immediate and without hesitation. We first asked B. to come up with the emotional label spontaneously, and he correctly labeled happy, fear, anger, and sadness, but mislabeled surprise as "happy" and disgust as "thirsty and hungry." When given a list of the 6 labels of the basic emotions, he correctly matched the label with the dynamic facial

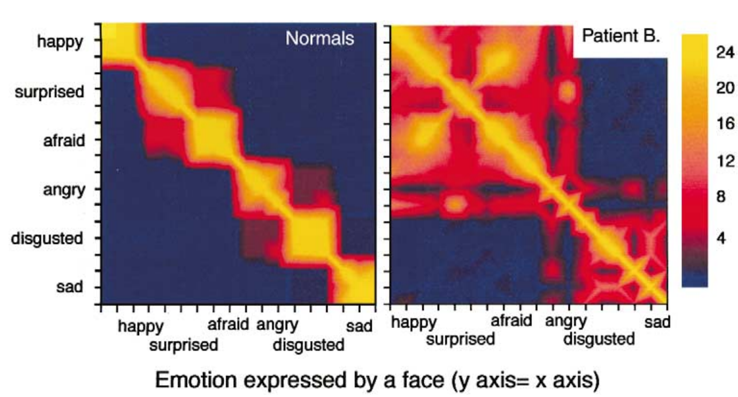

Fig. 5. Hierarchical organization of emotions recognized from facial expressions. Emotion categories were derived from sorting photographs of faces into piles. Normal subjects (left) distinguished the 6 basic emotions, whereas B. (right) distinguished only 2 categories related to happiness and unhappiness. Faces are ordered identically on the *x* and *y*-axes. Pixel color represents the similarity between face *x* and face *y*. Bright regions correspond to faces judged to be more similar to one another. The diagonal shows each face's similarity to itself (maximal similarity); plots are symmetric about the diagonal.

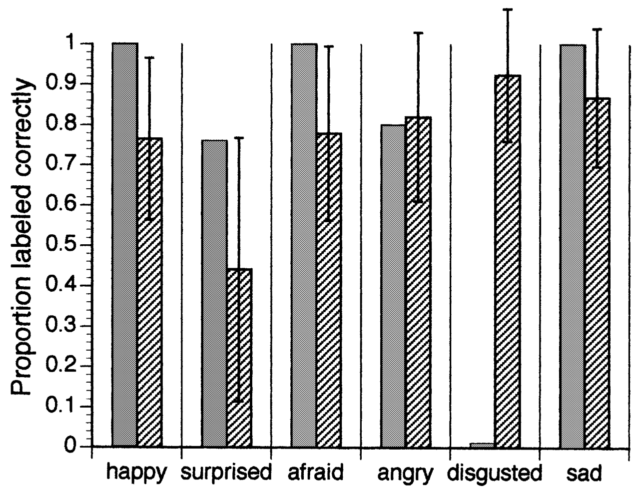

Fig. 6. Patient B.'s naming of short stories describing emotions. B. was read 5 stories depicting each of the 6 basic emotions. The stories stated events happening to people, or depicted the actions of people, that normally are typical of a specific basic emotion, but did not contain the name of the emotion. B. was asked to name the emotion he thought a person in the story would feel; he was not provided with any list of labels from which to choose. B.'s data (solid gray bars) were compared to those obtained from 29 normal controls (hatched bars).

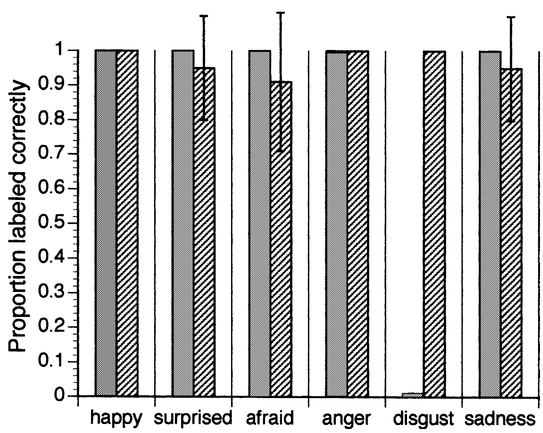

Fig. 7. Patient B.'s labeling of emotions from dynamic facial expressions. Shown are the proportions of stimuli labeled correctly from B. (solid gray bars) and 11 normal controls (hatched bars).

expression for every emotion, except for disgust (proportions correct were 1.0 for all emotions except disgust; 0.0 for disgust). With the exception of disgust, B.'s performances on this task were entirely comparable to those given by normal controls.

We followed up on B.'s severely impaired recognition of disgust by acting out behaviors normally associated with intense disgust. These included eating, and then regurgitating and spitting out of food, accompanied by retching sounds and facial expressions of disgust. In 4 such acted scenarios, by two different experimenters, B. remained entirely unable to recognize disgust, instead indicating that the food was "delicious."

4. Discussion

Patient B. was able to retrieve knowledge about all primary emotions except disgust, when provided with knowledge concerning actions either from (1) viewing dynamic facial expressions, (2) hearing stories about events or situations normally associated with an emotion, or (3) hearing descriptions of the actions that accompany feeling an emotion. The data from Experiments 5 and 6 show that B. can recognize emotions normally at the level of basic categorization, provided that the stimuli contain information about movements or events pertinent to the concept of the emotion. The temporal unfolding of movements or events is an important component of emotion concepts. The fact that B. can use such information to recognize emotions, but fails to recognize or name emotions from static stimuli, suggests that the two kinds of processes rely on partly distinct neural systems.

Patient B. was severely impaired in retrieving knowledge of the emotion signalled by static visual stimuli and by verbal labels. Experiment 4 revealed that his impairment is not restricted to processing the names for emotions, but rather reflects an impairment in the retrieval of conceptual knowledge of emotions at their basic level. However, B. was able to retrieve knowledge about emotions at superordinate levels, since he reliably partitioned stimuli into 2 superordinate categories corresponding to happy and unhappy emotions.

The above data provide evidence that different types of knowledge about emotions may draw upon different neural systems: temporal and limbic-related cortices may be especially important for retrieving information about emotions signalled by static stimuli, whereas regions in the vicinity of human MT/MST, together with parietal and frontal sectors, may be more involved in retrieving knowledge about emotions signalled by actions that unfold in time. An important aspect of the data is the fact that B. is not completely unable to retrieve knowledge about emotions, but rather that his impairment depends on the type of stimuli used to signal the emotion. This indicates that the core structures necessary to reconstruct knowledge about the emotional state associated with stimuli are intact in B.'s brain; candidates for such core structures would be somatosensory-mapping structures, notably including somatosensory cortices (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000). We think it likely that B.'s intact somatosensory cortices permit him to feel, and to recognize, emotions—provided that they can be linked to the relevant perceptual attributes of the stimuli. In the case of actions, such linkage can occur, whereas in the case of static stimuli, it fails.

The set of damaged structures in B.'s brain that are likely to be responsible for his impaired recognition of emotion from static stimuli includes those that previous studies have shown to be important for emotion recognition: bilateral amygdala (Adolphs et al., 1994; Calder et al., 1996; Morris et al., 1996), medial orbitofrontal cortex (Hornak, Rolls, & Wade, 1996), and insula (Calder, Keane, Manes, Antoun, & Young, 2000; Phillips et al., 1997). While B.'s bilateral amygdala damage could account well for impairments in the ability to recognize fear, as well as perhaps other negative emotions, and while his damage to insula could account well for impairments in the ability to recognize disgust (see below), his damage to orbitofrontal cortex might produce broader impairments in recognizing static emotions. It is likely that damage to these limbic-related structures, whose specific role in emotion recognition has been documented, as well as his damage to temporal neocortex, combine to produce the severe impairments that we report here.

4.1. The structure of emotion categories

Since B. classified stimuli similarly whether they were facial expressions or verbal labels, the physical similarity among the stimuli, such as similarity among the features of facial expressions, cannot account for the findings. Rather, the semantic structure of emotion concepts is being revealed by B.'s impairment. (It is, however, entirely possible that semantic structure is constructed in part from the similarity in the features of different stimuli; cf. Small, Hart, Nguyen, & Gordon, 1995.) Put another way, B. does not suffer from a perceptual problem that might explain his performance (as shown also by his entirely normal score on tasks requiring visual discrimination), but rather has a profound defect in the retrieval of the knowledge that normal subjects use when they recognize the emotion depicted by a stimulus. Arguably, the stimuli look the same to B. as they do to a normal subject; but he is unable to classify the emotion that he is seeing because he is unable to link perceptual representations of the stimuli with the emotion that is normally associated with the stimulus.

The above data thus provide some information about how conceptual knowledge of emotions might be organized at subordinate and superordinate levels. The data broadly support the intuition that primary emotion categories are members of the superordinate categories "happy" or "unhappy," essentially a distinction based on valence. The membership of primary emotions in these superordinate categories may explain in part why B. appears to recognize some emotions but not others. He recognizes happiness and sadness in many stimuli, but fails entirely to recognize fear and anger. One explanation of this performance may be that happiness and sadness are basic-level emotions that are also typical instances of the superordinate categories "happy" and "unhappy," and can thus be recognized as such. On the other hand, fear and anger are normally judged to fall between typical instances of happiness and unhappiness, and thus require recognition at basic level in order to be categorized correctly. B.'s impairments in recognizing basic-level emotions from static stimuli thus parallel his impairments in recognizing concrete entities at subordinate levels of categorization (Damasio et al., 1990; Damasio & Tranel, 1993).

There is another possible interpretation of the above findings. Several studies suggest that emotions may be organized in part according to the two factors of valence (pleasantness) and arousal (Johnsen, Thayer, & Hugdahl, 1995; Lang, Bradley, Cuthbert, & Patrick, 1993; Russell, 1980; Russell & Bullock, 1985; Russell, Weiss, & Mendelsohn, 1989b). Although we have not tested this possibility directly in B., our data are consistent with the hypothesis that he fails to retrieve knowledge regarding arousal, but is able to retrieve knowledge regarding valence. In this case, he might organize emotion concepts along a single dimension of pleasantness–unpleasantness. This hypothesis would predict that emotions distinguished by their arousal, such as fear and anger, might be categorized especially abnormally, as is indeed the case with B. It is notable in this regard that he attributes highly abnormal arousal to emotions such as fear and anger, describing these states as relaxing and quiet (unpublished observations). This possibility would find support in a previous study we reported with a patient who had complete bilateral amygdala damage: like B., this patient was severely impaired in recognizing the emotional arousal of negatively valenced emotions, assigning unusually low levels of arousal to emotions such as fear and anger (Adolphs, Russell, & Tranel, 1999).

It remains a task for future studies to distinguish between the above two possible explanations of B.'s impairment. Given the extensive nature of his brain damage, which includes both those regions presumed to be involved in subordinate-level categorical knowledge (temporal neocortex) and in knowledge of arousal (amygdala), it is possible that *both* of the above scenarios operate in combination to generate his severe impairment in recognizing emotions from static stimuli.

4.2. The impaired recognition of disgust

Patient B. was entirely unable to recognize disgust in any of the stimuli we used, including the descriptions of actions or spontaneous labeling of dynamic facial expressions, in which he was able to recognize all other primary emotions. His impaired recognition of disgust was quite striking. For instance, when told a story about a person vomiting, his descriptions of how the person would feel included "hungry," and "delighted," responses he also gave to some of the photographs of disgusted facial expressions. When observing the experimenter act out the apparent vomiting of unpalatable food, B.'s description was that "delicious food was being enjoyed." His performances in regard to disgust are especially striking, because disgust is easy to recognize for normal subjects. In fact, disgust was the emotion that normal subjects found the easiest to recognize of all the emotions in our sentences of actions; yet B. failed to identify correctly a single instance of it (yet recognized the other emotions from such stimuli). These data thus provide support for a disproportionate impairment in all conceptual knowledge regarding disgust: B. appears unable to retrieve knowledge of this emotion, no matter what the stimuli. It has been found that perception of disgusted facial expressions activates the insular cortex (Phillips et al., 1997), and that damage to the insula impairs recognition and experience of disgust (Calder et al., 2000), suggesting that retrieval of knowledge for disgust may rely on specific neural structures, as does fear (Adolphs et al., 1994, 1995; Calder et al., 1996; Morris et al., 1996). The insula, a visceral somatosensory cortex, would be a plausible substrate both for the experience and for the recognition of disgust, at least as this emotion relates to food and ingestive behaviors.

4.3. Possible relationship between recognizing and feeling emotions

We mentioned earlier that a plausible substrate for Patient B.'s intact recognition of some emotions, provided they are presented in dynamic stimuli or actions, are his somatosensory cortices. Lesion studies have indicated that the integrity of somatosensory cortices is critical for the recognition of emotion in others, an ability that we have proposed draws upon an internal reconstruction of what the emotion would feel like via simulation of its associated body state (Adolphs et al., 2000). That is, neural maps of the body state associated with an emotion would be recreated in somatosensory-related cortices, and would permit retrieval of knowledge about the emotion. This proposal builds on theoretical frameworks that have emphasized the role of somatic representation in feeling emotions (Damasio, 1999; Panksepp, 1998). In support of this idea, from our interactions with him, B. appears able to feel emotions, with the exception of disgust, although it is difficult to trigger them from stimuli (it is unclear, however, if he can correctly label all the emotions that he can feel).

The possible close link between knowledge retrieval and feeling of an emotion is also corroborated by B.'s inability to recognize disgust from any stimulus. Our findings with B. are consonant with the fact that insular cortex is a visceral somatosensory cortex that would participate in the representation of body states linked to eating and drinking, such as nausea—states that define the core of the emotion disgust. Patient B. has bilateral lesions in the insular cortices, and such damage is likely to account for impairments in recognizing disgust. Furthermore, our unpublished observations with Patient B. suggest that he appears unable to feel disgust: he ingests items rather indiscriminately, including items that are not edible, and he fails to show any disgust to food-related stimuli (such as pictures of food covered with cockroaches).

In summary, our findings point to three anatomically dissociable sets of processes involved in (1) recognizing emotions from dynamic stimuli/actions versus from static stimuli; (2) recognizing emotions at different levels of categorization, and (3) recognizing specific individual emotions, notably disgust. Furthermore, the data corroborate the idea that the recognition of emotions draws upon the ability to feel the emotion via representation of its associated body state.

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