Recognizing Emotion From Facial Expressions: Psychological and Neurological Mechanisms

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Recognizing emotion from facial expressions draws on diverse psychological processes implemented in a large array of neural structures. Studies using evoked potentials, lesions, and functional imaging have begun to elucidate some of the mechanisms. Early perceptual processing of faces draws on cortices in occipital and temporal lobe that construct detailed representations from the configuration of facial features. Subsequent recognition requires a set of structures, including amygdala and orbitofrontal cortex, that links perceptual representations of the face to the generation of knowledge about the emotion signaled, a complex set of mechanisms utilizing multiple strategies. Although recent studies have provided a wealth of detail regarding these mechanisms in the adult human brain, investigations are also being extended to nonhuman primates, to infants, and to patients with psychiatric disorders.

Key Words: cognition, cognitive neuroscience, emotion, facial expression, neuropsychology

The recognition of emotion from facial expression has been the focus of a large number of psychological studies over the past several decades, complemented more recently by a wealth of neurobiological findings from experiments involving lesions, electroencephalography (EEG, event-related potential [ERP]), magnetoencephalography (MEG), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI). The sheer diversity of findings precludes any simple summary and argues against the isolation of only a few structures. Instead, it is becoming clear that recognizing facial emotion draws on multiple strategies subserved by a large array of different brain structures. This review will focus on those processes and structures whose role we understand best at present and will focus primarily on data from functional imaging and lesion studies. The review will not cover details of face identity processing or of facial emotion processing in psychiatric disorders.

1. What Is Recognition?

1.1 PERCEPTION AND RECOGNITION

How do we recognize emotion from facial expressions? It is useful to begin answering this question by first discussing in more detail the constituent terms of the question, What do we mean by recognition, emotion, or facial expression? The class of processes labeled perception has sometimes been considered distinct from those under the label recognition, a separation first made on the basis of clinical findings (Lissauer, 1890), although the term *perception* nowadays is often used to cover both domains. Perception in this former sense refers to processes that occur relatively early in time subsequent to the onset of the stimulus that are presumed to rely largely on early sensory cortices and that achieve processing of the features of the visual image and their configuration. Perception in this sense would enable performance on tasks that require judgments to be made solely about the visual, geometric properties of stimuli, such as the ability to discriminate differences between two faces that are presented simultaneously.

By contrast to the information on which early perception is presumed to operate, all of which is available in principle from the visual structure of the stimulus, recognition requires additional knowledge that could not be obtained solely from an inspection of the visual features of the stimulus. Recognition requires that we know something about the world; it thus requires memory of some sort. One of the simplest forms of recognition is in fact called recognition memory and might involve simply the ability to hold in memory some information about the early perceptual properties of the visual image, to which another image could be compared subsequently. This form of recognition might be sufficient to discriminate between two faces that are presented at separate points in time.

Whereas the simplest forms of recognition memory could, in principle, utilize only perceptual information (i.e., only information explicitly present in the features of the visual image and their configuration), full-fledged recognition of emotion from facial expressions would of course require additional knowledge regarding the contingencies between the expression and many other stimuli in the world with which that expression has been directly or indirectly associated (I do not intend here to address the difficult issue of whether all knowledge must be acquired by associative mechanisms). Examples of such knowledge would include knowing where one saw the face, what was said about the person whose face it was, how one felt in response to seeing the face, and other contingent events (they need not even be contiguous in time). None of these bits of information can be derived from the perceptual properties of the face in isolation but rather concern covariances between the face and other stimuli.

1.2 CATEGORIES AND CONCEPTS

The above examples are concerned with picking out information that is specific to a particular stimulus, or even a particular presentation of that stimulus. But, we also need to recognize the face as belonging to categories that pick out regularities in the world rather than idiosyncrasies. Knowledge about the categories can be abstracted from knowledge about the particulars, as well as on the basis of rules (Smith, Patalano, & Jonides, 1998) (an open question beyond the scope of this review is the extent to which the latter might be reducible to the former mechanism). An economic architecture for linking a large set of diverse sensory stimuli rapidly to a set of behavioral responses is provided by categories that serve to group stimuli requiring similar responses into the same category and to group stimuli requiring different responses into different categories. Categorization may be of special importance in processing socially relevant information, due to the dual constraints posed by high informational complexity and rapid behavioral response. Examples of the categorical processing of social stimuli come from the categorical perception of auditory social signals, such as birdsongs, frog calls, or human voice phonemes, from the categorical perception of faces (see Section 4 below), as well as from the stereotyped judgment of other people that social psychologists have studied under the rubric "person perception" (Macrae & Bodenhausen, 2000).

One could categorize stimuli on the basis of their visual appearance or on the basis of what one knows about them. Some findings from computer modeling suggest that the geometric properties of facial expressions may suffice to classify them into categories of basic emotions, whereas some cross-cultural studies in humans have argued that the category of emotion expressed by the face is in the eye (and in the cultural background) of the beholder. Neither the reductionist former position nor the relativism of the latter provides the whole answer: Categories can be shaped both by perception and by recognition, depending on the circumstances.

The percept of a facial expression—how it appears—can be seen as distinct from the concept of that expression—what one knows about it. Concepts in this sense are the knowledge that is required for recognition, and they might be thought of as composing all the multiple component pieces of knowledge that pertain to a particular category. One's concept of fear, for instance, would consist of all the various bits of knowledge relevant to answering questions about fear; moreover, these bits of knowledge are not a fixed or even a bounded set but rather depend on the particular use to which the concept is put and are subject to continuous revision (cf. Solomon, Medin, & Lynch, 1999). It should be emphasized that the conceptual knowledge is not "retrieved" in the sense that a storehouse metaphor of memory would erroneously suggest but that it is generated by a multitude of strategies, some of which are very creative—an issue we will revisit in more detail below. It is thus possible—in fact, it is likely—that different subjects (or the same subject on different occasions) may generate conceptual knowledge about a stimulus via a somewhat different set of component strategies (and hence by drawing on a somewhat different set of neural structures). To preview some of the strategies that will be discussed further below: Recognition of fear from a facial expression might proceed by linking the perceptual properties of the stimulus to knowledge components of the concept of fear, to the lexical label fear, to perception of the emotional response (or a central representation thereof) that the stimulus triggers in the subject, or to knowledge about the motor representations required to produce the expression shown in the stimulus.

2. What Are Facial Expressions?

Another important part of our question concerns the nature of facial expressions, which can be considered as aspects both of an emotional response and of social communication (Darwin, 1872/1965; Fridlund, 1994; Russell & Fernandez-Dols, 1997). These dual aspects generally occur together in shaping a facial expression, although certain circumstances can highlight one or the other (e.g., involuntary expressions accompanying intense basic emotional reactions and voluntary expressions modulated by culturally shaped display rules, respectively). The muscular mobility of the face, highly developed in apes and humans, is governed by complex neural control that encompasses both automatic and volitional components. These two components can also be dissociated following brain damage: Whereas lesions in primary motor cortex result in the inability to produce facial expressions to command but leave intact spontaneous emotional expressions, damage in insula, basal ganglia, or pons can result in the converse impairment (Hopf, Muller-Forell, & Hopf, 1992). Neuroanatomical tracing studies in monkeys have shown that innervation of the lower face (via the facial nucleus) originates principally from contralateral motor-associated cortices M1, M4, LPMCv, and LPMCd, whereas innervation of the upper face originates in bilateral M2 and M3, although there is some degree of overlap between all of these (Morecraft, Louie, Herrick, & Stilwell-Morecraft, 2001). Especially interesting are projections to the facial nucleus from M3 and M4, limbic motor cortices in the cingulate gyrus that regulate emotional expressions and that are in turn innervated most densely by the amygdala in regions corresponding to the motor representation of the face (Morecraft, Avramov, Schroder, Stilwell-Morecraft, & Van Hoesen, 1998).

What different types of information might a face convey? One might identify the face's gender, age, identity, emotion, or other socially relevant category. There is evidence to suggest that recognition of many, perhaps most, of these classes of attributes can be dissociated (depending on how finely one decides to carve up the categories), an issue that has received attention from psychological and neurological studies, as well as from computer modeling. A model first made explicit by Bruce and Young (1986) (see Figure 1) emphasized distinct psychological processes for identifying facial expression or facial identity. An important question thus concerns the processing stage at which such a dissociation might take place.

One possibility is that different types of information are processed by subsystems that are distinct already at the level of perception—perhaps at the level corresponding to Bruce and Young's (1986) structural encoding. Some evidence to support such a scheme comes
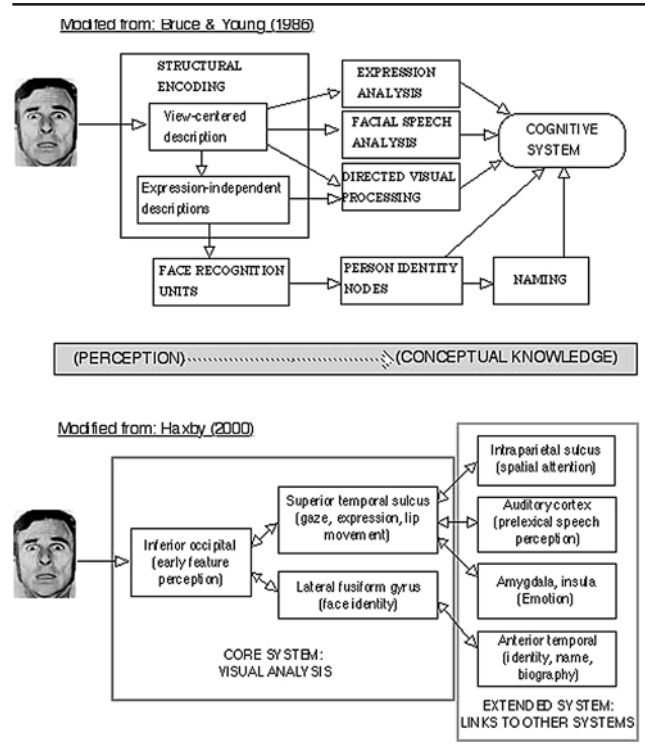

Figure 1: Models of Face Processing.
NOTE: The top of the figure shows the functional model of Bruce and Young (1986), emphasizing separate processes that subserve recognition of identity and of emotion from the face. The model begins with perceptual processing of the features of faces and their configural relations (structural encoding) and progresses through relatively specialized functional modules for recognizing specific types of information from the face, culminating in naming the information that is recognized and in modulating other aspects of cognition on the basis of such information. The model is not intended to be neuroanatomically detailed but rather to provide a description of the computational aspects of face processing carried out by brains, as well as a suggestion for how such processing might be implemented in artificial systems. The bottom of the figure shows the neuroanatomical model of Haxby, Hoffman, and Gobbini (2000), emphasizing perceptual processing of changeable aspects of the face in the superior temporal gyrus, and invariant aspects of the face in the fusiform gyrus. The model explicitly acknowledges the bidirectional connections, and likely bidirectional information flow, between essentially all components. Specific neural regions are assigned to specific functional components, as indicated in the figure. Both models shown in the figure share with the current review the idea that early perceptual processing of the face needs to be linked to many other brain structures to accomplish recognition. Figures modified with permission from data provided by A. Young and J. Haxby.

from computational modeling of face perception. It is possible to examine the statistical structure of face images (that is, the statistical structure of the pixels corresponding to digital images of faces, or input representations thereof) using mathematical techniques such as principal component analysis. In one recent analysis of this type, Calder, Burton, Miller, Young, and Akamatsu (2001) found that expression and identity information from faces exhibit different statistical regularities from one another, such that principal components from

which emotional expressions could be reconstructed were mostly different from the ones from which identity could be reconstructed (similar findings may obtain also in relation to facial gender). Work from functional imaging studies indicates that some of the perceptual processing of information regarding identity involves ventral occipitotemporal regions such as the fusiform gyrus, whereas some of the processing of information regarding expression involves superior temporal cortices (see Section 9.2), perhaps a reflection of differences in processing two aspects of structural information: that which specifies relatively rigid, unchanging configurations of features and that which specifies more dynamic, changeable configurations, respectively (Haxby, Hoffman, & Gobbini, 2000) (cf. Figure 1).

Another possibility is that expressions are processed differently from other face information at a step that is subsequent to perceptual processing, at a level that requires some recognition already. One might imagine a common perceptual format for all information that subsequently engages distinct sets of processes involved in recognizing the gender, the identity, or the expression shown in the face, the view also suggested by the model of Bruce and Young (1986). Evidence to support this view comes from the finding that many of the neurological dissociations reported in fact rely on tasks at the level of recognition (that is, the dissociations concern category-specific agnosias rather than impairments in basic perceptual ability). For instance, specific impairments following brain damage have been reported in the ability to recognize either the emotion or the identity shown in a face, but the ability to discriminate between contemporaneously presented faces often appeared intact in these cases (e.g., Adolphs, Tranel, Damasio, & Damasio, 1994; Tranel, Damasio, & Damasio, 1988). As detailed below, there is evidence to support both the above schemes: Processing of facial expressions draws in part on relatively specialized routes already at the level of early perception and in part on higher level conceptual knowledge.

What are the roles of information concerning specific features and of information concerning their relative configuration? Recognition of face identity depends to a significant extent on configural information about the spatial relations among features (Moscovitch, Winocur, & Behrmann, 1997; Sergent, 1984), recruited especially when viewing the face right side up (Searcy & Bartlett, 1996; Yin, 1969; A. W. Young, Hellawell, & Hay, 1987), and is perhaps "holistic" in the sense that it cannot be decomposed merely to the sum of perceptual processing of the individual features (Tanaka & Farah, 1993). Although a substantial effort has gone into understanding feature-based and configuration-based processing for the identity of faces, this issue is less well understood

in the case of facial expressions. Some evidence that feature-based processing could be sufficient, in principle, to classify facial expressions into emotion categories comes from computer models that demonstrate such an ability (Cottrell, Dailey, Padgett, & Adolphs, 2001). In contrast, some studies in human subjects indicate that perception of facial emotion requires at least some configural processing of the relations between multiple facial features (Calder, Young, Keane, & Dean, 2000). It may also be that feature-based processing and configuration-based processing play differential roles depending on the emotion: For instance, it may be that one could infer happiness by detecting a single feature, the smile, whereas discriminations among negatively valenced emotions might require additional information about the configuration of the face.

3. What Is an Emotion?

Although facial expression encompasses a broad range of social signals, expressions of emotions constitute the aspect that is best understood. Neurobiologists and psychologists alike have conceptualized an emotion as a concerted, generally adaptive, phasic change in multiple physiological systems (including both somatic and neural components) in response to the value of a stimulus (e.g., A. R. Damasio, 1995, 1999; Plutchik, 1980; Scherer, 2000). An important issue, often overlooked, concerns the distinction between the emotional reaction (the physiological emotional response) and the feeling of the emotion (presumed in some theories to rely on a central representation of this physiological emotional response) (A. R. Damasio, 1999). It is also essential to keep in mind that an emotional response typically involves concerted changes in a very large number of somatic parameters, including endocrine, visceral, autonomic, and musculoskeletal changes including facial expression, all of which unfold in a complex fashion over time.

It is debatable to what extent our concept of emotions picks out a homogeneous kind of state (Griffiths, 1997), and it is further debatable to what extent our concepts of individual emotions pick out discrete states rather than regions of a more continuous manifold. Different psychological theories (see Scherer, 2000, for a review) argue that emotions should be thought of as discrete states (such as the ones we have names for in language and that subjects assign as labels to facial expressions) (Ekman, 1992), as regions falling in a low-dimensional space (for instance, a two-dimensional space with axes of arousal and valence; see Figure 2) (Russell, 1980), or as assembled dynamically from a large possibility of component processes (Scherer, 1984), depending on the appraisal of the situation (Scherer, 1988) (see Box 1). Although facial expressions of emotion are categorized
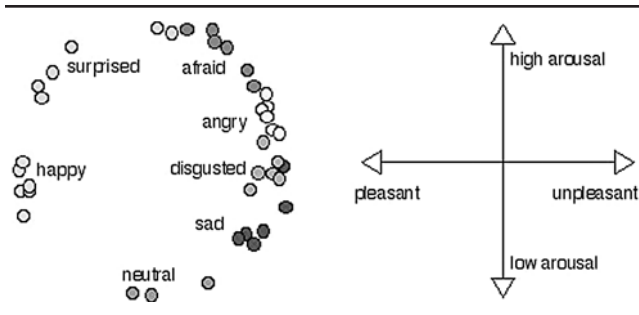
Figure 2: The Dimensional Structure of Emotion Categories.

into discrete categories, and although there is even evidence for categorical perception of such facial expressions (see Section 4), it is also clear that expressions are typically members of multiple emotion categories, that the boundaries between categories are fuzzy at the level of recognition (Russell & Bullock, 1986), and that the categorization of an emotional facial expression depends to some extent on the contextual relation to other expressions with which it may be compared (Russell & Fehr, 1987). Some mathematical models further argue that emotions shown in facial expressions could be thought of in a more abstract fashion that might exhibit features both of discrete emotions and continuous dimensions (Calder, Burton, et al., 2001).

A face space is a mathematical way of representing relatedness between different faces, defined by its number of dimensions (the number of parameters according to which faces vary in the representation) and its metric (how distances between faces scale as a function of absolute position). There are two approaches to representing faces in a space: One can use the geometric structure of the facial image as the starting point, or one can begin with the structure of the judgments that humans make about the face. In the former, one generates a representation of the physical relatedness between faces, in the latter, a representation of their psychological relatedness (as in Figure 2). Methods such as principal component analysis are popular tools for generating the former, and nonmetric multidimensional scaling is often used for the latter purpose.

There is debate regarding the structure of emotion categories: On one hand, emotions appear discrete; on the other hand, they can be mapped onto a continuum. An example of a dimensional account of emotions is given in Figure 2, which shows the similarity structure among facial expressions of emotion. Ratings of the emotional expressions from normal subjects were averaged and subjected to a multidimensional scaling algorithm. The colored dots in the figure correspond to the facial expression stimuli used in the task (color-coded according to their emotion category), and the distance between different stimuli represents their derived dis-

Face Space and the Structure of Emotion Categories

There are many schemes for thinking about emotions, ranging from very simple categories defined solely on the basis of behavior to the huge diversity of social emotions that have different names in a given language (see Table 1). Motivational states, basic emotions, and social emotions are all superordinate categories into which individual emotion states can be grouped. Although emotions overlap substantially with the broader category of motivational states, they differ from motivational states, such as thirst, hunger, pain, or mood, in a number of respects. First, emotions (unlike moods) are best thought of as phasic, like actions: They have an onset, a finite duration, and an offset. Second, emotions (unlike pain, hunger, or thirst) feature prominently in social communication. Certain classes of emotions—the so-called social, moral, or self-conscious emotions—function explicitly to regulate social behavior. This class of emotions includes shame, embarrassment, pride, and guilt. Feeling such social emotions requires a more extensive self-representation than does the feeling of the basic or primary emotions, as it involves representing oneself situated in a web of social relations and requires representing the internal mental states of other individuals (e.g., representing how others feel about oneself). The vast majority of emotion models, and certainly those that have been used to guide neurobiological research, fail to take into account the diversity of social behaviors that are regulated by the social emotions. Providing a fine-grained account of how social emotions are differentiated is a major challenge for the future and will likely require close collaboration between social psychologists and neuroscientists.

similarity. Shown on the right is one interpretation of this representation, in which the axes correspond to valence and arousal.

There are several ways in which digital images of faces can be processed to yield images that are intermediates and to generate a continuous series of images in face space. This involves computations on the smallest components of digital images, their pixels. One such manipulation is to align two faces in terms of their corresponding features and then simply to change the luminance values of the pixels between the two images to generate a "fade" that interpolates gray scale values of the constituent pixels (see Figure 3a). Another manipulation is to maintain the luminance value of pixels but to alter their positions to "warp" one image into another (see Figure 3b). The most common manipulation involves the conjunction of these two methods: Two faces are "morphed" into one another by simultaneously changing their pixel luminance and warping their pixel position (see Figure 3c). Morphing can thus generate continuous, physically linear changes in a face image. This transformation can be applied not only between two faces but can be extrapo-

lated beyond the actual face to yield an exaggeration of that face relative to the other face: a "caricature" (see Figure 3d).

Interesting findings arise when one attempts to merge face spaces that represent the geometric, physical structure of faces with face spaces that represent their psychological structure: In general, the two show some similarities but are not identical (Busey, 1998). This is certainly the case when one examines a simple morph space: The morphing of an expression of one emotion into an expression of another generates intermediates that are never actually observed as facial expressions in real life, and the rate of change of the transition of one expression into the other does not map linearly onto the rate at which one perceived emotion category changes into the other.

In addition to exhibiting a similarity structure that can be mapped into two dimensions, as shown in Figure 2, basic emotion categories are hierarchically related (see Figure 4). Normal subjects categorize basic emotional facial expressions into the superordinate categories happy and unhappy, as well as into more subordinate categories. This hierarchical structure can also be revealed following brain damage and remains an important issue to consider in the interpretation of impairments in the recognition of selective emotions (see Section 15). As for the recognition of concrete entities (e.g., A. R. Damasio, Damasio, Tranel, & Brandt, 1990), damage to temporal neocortices can result in impairments in recognition of subordinate emotion categories with sparing of the recognition of superordinate emotion categories. A recent study of a patient with extensive bilateral damage to temporal cortex revealed precisely such a pattern: Categorization of emotional facial expressions could proceed only to the superordinate stage of happy versus unhappy but not to more subordinate levels (Adolphs, Tranel, & Damasio, in press-a) (see Figure 4).

There is evidence that the recognition of at least a subset of emotions from faces is carried out similarly by different cultures. This evidence is strongest for the so-called basic emotions (see Table 1), which appear to be categorized similarly from facial expressions in different cultures (Ekman, 1994), even though those cultures may have different ways of linking the concepts to the name (Wierzbicka, 1999) and even though those cultures have different social rules for expressing the same emotions in faces under various circumstances (Fridlund, 1994). Although the role of culture in shaping concepts and categories is a hotly debated issue, it would appear that a reconciliatory view can acknowledge that certain expressions are processed similarly at the perceptual level but then linked to different sets of social conceptual knowledge depending on the cultural context within which that conceptual knowledge has been acquired. The simi-
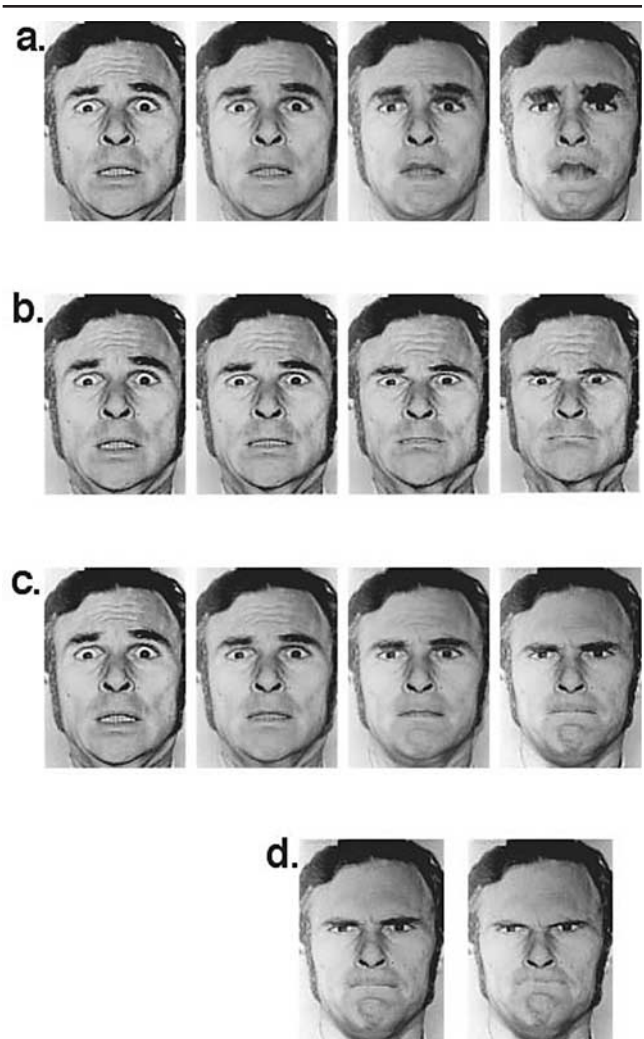

Figure 3:   Morphing Between Facial Expressions of Fear (left) and Anger (right).
NOTE: In the figure, (a) shows a luminance transform, (b) a spatial warping, (c) a combination of both, and (d) a caricature obtained when the morphing process is continued past the end anger image. See text for details.

larities in processing of emotional facial expressions across different cultures might therefore be most apparent at the level of discrimination and perceptual categorization (cf. Russell, Lewicka, & Niit, 1989), whereas the differences might be most apparent at the level of the retrieval of complex and symbolic knowledge, such as the names for the different emotions (Wierzbicka, 1999).

Although the majority of research on facial expression uses the emotion categories for which we have names in English (in particular, the basic emotions indicated in Table 1), or, somewhat less commonly, a dimensional approach (often in terms of arousal/valence as depicted in Figure 2), there are three further frameworks that seem worth exploring in more detail. Two of these arose primarily from animal studies. A behaviorist-
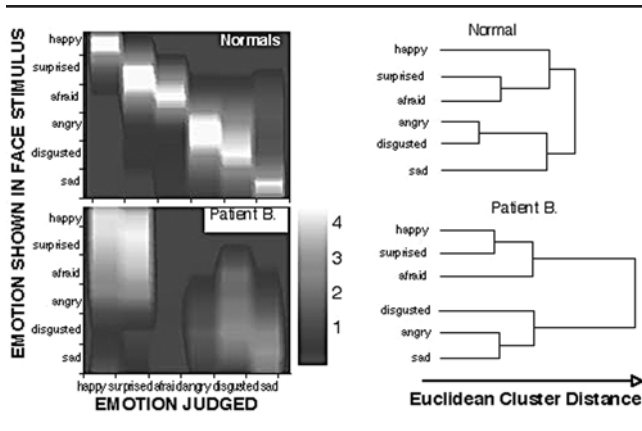
Figure 4: Hierarchical Organization of Emotion Categories.
SOURCE: Adolphs, Tranel, & Damasio (in press-a).
NOTE: A hierarchical structure can be revealed from a variety of data, in this case data from rating the intensity of each basic emotion judged to be signaled by a given facial expression. Section (a) shows a 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 4 (*very much*). Bright regions correspond to categories distinguished by the subjects. Data are from 7 normal controls (mean shown) and from a lesion subject (Patient B) who has extensive bilateral damage to temporal lobe. These data were analyzed with a complete-linkage hierarchical clustering algorithm to generate the solutions shown in Section (b), in which 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. The data from normals and from Patient B support the idea that pleasant/happy and unpleasant/unhappy are two superordinate emotion categories.

inspired scheme proposed by Rolls (1999) also maps emotions onto a two-dimensional space, as do some other psychological proposals, but in his case the dimensions correspond to the presentation or omission of reinforcers: roughly, presentation of reward (pleasure, ecstasy), presentation of punishment (fear), withholding of reward (anger, frustration, sadness), or withholding of punishment (relief). Another scheme, due to Panksepp (1998), articulates a neuroethologically inspired framework for categorizing emotions; according to this scheme, there are neural systems specialized to process classes of those emotions that make similar requirements in terms of the types of stimuli that trigger them and in terms of the behaviors that are associated with them (specifically, emotions that fall under the four broad categories of seeking, panic, rage, and fear). Both of these approaches (Panksepp, 1998; Rolls, 1999) would appear to yield a better purchase on the underlying neurobiological systems, but both leave unclear how exactly such a framework will map onto all the diverse emotions for which we have names (especially the social ones) (cf. Table 1). A third approach takes a more fine-grained psychological analysis of how people evaluate an emotional situation and proposes a set of "stimulus eval-

uation checks" that can trigger individual components of an emotional behavior, from which the concerted response is assembled as the appraisal of the situation unfolds (Scherer, 1984, 1988). This latter theory has been applied to facial expressions, with some success (Wehrle, Kaiser, Schmidt, & Scherer, 2000). Although rather different in many respects, all three of these frameworks for thinking about emotion share in common the idea that our everyday emotion categories are probably not the best suited for scientific investigation. Future studies, both psychological and neurobiological, could use aspects of these frameworks in their formulation of tasks.

MECHANISMS FOR RECOGNIZING EMOTION FROM FACES

We begin with an outline of the different possible mechanisms for recognizing emotions from facial expressions. In the following sections, these possible mechanisms will then be tied to specific neural structures and their interconnections. One conclusion will be that a given brain structure typically participates in multiple strategies and that performance on a recognition task also often engages different strategies and, hence, different sets of neural structures.

4. Recognition as Part of Perception

One possibility is to consider recognition as a part of perception. Arguably, recognition of simple features of a stimulus, or recognition that one stimulus differs from another, is really an aspect of perception. Perhaps we do not need to know anything about the world to recognize an emotion but are able to discriminate, categorize, and identify emotions solely on the basis of the geometric visual properties of a stimulus image. It is even conceivable (in principle) that such perceptual processing could be linked directly to language-related regions of the brain sufficient to produce the name of the emotion, in the absence of retrieving any other information associated with the stimulus (something akin to paired associate learning, for instance).

This notion of recognition is of course an impoverished version. Nonetheless, it could suffice to produce normal performance on some tasks, such as discriminating between different emotions, sorting different emotions into categories, perceiving borders between different categories, picking out prototypes within a category, and perhaps even labeling the emotion in forced-choice matching tasks when the labels of the emotion words are provided. However, this notion of recognition would not be sufficient to retrieve associated knowledge about the concept of the emotion.

TABLE 1:A Sampling of Some Ways to Categorize Emotions

Behavioral State	Motivational State	Moods, Background Emotion	Emotion System	Basic Emotion	Social Emotion
Approach	Reward	Depression	Seeking	Happiness	Pride
Withdrawal	Punishment	Anxiety	Panic	Fear	Embarrassment
		Mania	Rage	Anger	Guilt
	Thirst		Fear	Disgust	Shame
	Hunger	Cheerfulness		Sadness	Maternal love
	Pain	Contentment		Surprise	Sexual love
	Craving	Worry		Contempt	Infatuation
					Admiration
					Jealousy

There is some evidence both from psychological studies in humans and especially from computer models that supports the idea that a fairly substantial amount of processing can be carried out solely from the information present in the geometric properties of the stimulus. Mathematical analyses have revealed that structure present in images of facial expressions is sufficient, in principle, to generate some of the structure of the emotion categories that humans perceive (Calder, Burton, et al., 2001). The categorization of morphed images (see Box 1) generated from the expressions of two different emotions has been explored in normal subjects (Calder, Young, Perrett, Etcoff, & Rowland, 1996; de Gelder, Teunisse, & Benson, 1997; Etcoff & Magee, 1992; A. W. Young et al., 1997) and has been investigated in a neural network model trained to classify faces (Cottrell et al., 2001; Cottrell, Padgett, & Adolphs, 1998; Padgett & Cottrell, 1998). These studies have found evidence for categorical perception of facial emotion: People, and the network models, judge there to be a sharp perceptual difference between expressions, even when the expressions are structurally very similar, provided that they straddle the boundary of an emotion category (analogous to the way in which we segment a rainbow into bands of color despite linear changes in wavelength). This finding is in line with the idea that categorical perception plays a role in communication of social signals by parsing stimuli that can vary along a continuum into discrete categories that carve out relevant communication signals (Ehret, 1987; Macrae & Bodenhausen, 2000). It seems plausible that categorical perception of facial expressions in humans relies predominantly on perceptual information, and this is certainly the case with the network models because they do not possess any conceptual knowledge at all. (A separate difficult issue concerns the extent to which lexical labels, independently of the concepts they denote, can help in structuring perception of the categories—even the network models are trained to begin with using labels that carve out the categories, and aphasic humans who lack proper use of lexical labels but have normal conceptual knowledge make surprising errors in categorizing emotional facial expressions [Davidoff, 2001, and unpublished observations]. But, this may show only that labels aid perceptual categorization by providing a convenient way to structure the percepts not that conceptual knowledge is required for the categorization.)

Thus, one surprising conclusion from the above studies is that entirely perceptual processing apparently can yield a category structure for emotions that is isomorphic with the semantic structure of the emotion concepts. That is, the physical, geometric similarity between different facial expressions reflects the structure of our concepts of the emotions. In this respect, communication by emotional facial expressions differs fundamentally from language: If it were like language, facial expressions would be expected to be symbolic, and the particular configuration of the expression would bear only an incidental relationship to the emotion/feeling concept that it denotes. Although the precise implications of these findings remain to be fully understood, they strongly suggest that the perception, expression, and experience of emotion may be intimately related sets of processes.

5. Recognition via the Generation of Associated Knowledge

However, recognition typically involves more than just perceptual information. When we see a facial expression of fear, we can relate it not only to the percepts of other facial expressions in terms of its structure, but we can recognize that the person whose face we see is likely to scream, is likely to run away, has probably encountered something scary, and so on. None of that knowledge is present in the structure of the stimulus; it is present in our past experience with the world (and, to some limited extent, may even be present innately). A complex question concerns the precise mechanisms by which such knowledge might be retrieved. In general,

the knowledge is not stored in any explicit format but rather relies on recipes for reconstructing knowledge by reactivation of the representations that were originally associated with one another when the knowledge was acquired (e.g., A. R. Damasio & Damasio, 1994). The simplest example of such a mechanism would be literal association, as when we see a face of fear and hear a scream at the same time and link the two henceforth in memory. In general, linking other knowledge with a perception of the facial expression will be vastly more complex and will rely on multiple higher order associations that may be fairly separated in time (e.g., seeing a face of fear and seeing the chasing tiger some time later), as well as on symbolic representations that, in humans, rely substantially on language (e.g., seeing a face of fear and merely being told that the person was afraid because he or she was running away from a tiger).

The general neural scheme for implementing the above mechanisms requires the "binding" of information between separate neural representations so that they can be processed as components of knowledge about the same concept. In the perceptual case, a stimulus activates multiple neural regions that represent particular aspects of its visual properties, and the coherent ensemble of these different bits of knowledge (the representations of the different properties of the stimulus) constitutes the perceptual mechanism that we discussed in Section 4 above. But, this mechanism can be extended beyond those neural regions that represent the visual properties of the stimulus to include those that represent knowledge not of the stimulus itself but of that with which it has been associated. The demand for integrating neural representations that are spatially separated in the brain would require extensive feedback connections as well as feedforward connections between different neural regions. One might thus envision a continuous dynamic interplay between feedforward, feedback, and horizontal information flow from which the brain constructs representations of visual stimuli (cf. Lamme, Super, & Spekreijse, 1998, for review). Schemes such as Ullman's (1995) "counter streams" or Edelman's (1987) "re-entry" both capture this idea: The representation of the stimulus itself, and of its associated knowledge, evolves contemporaneously such that the one continuously modulates the other and perception and recognition become parts of the same process.

6. Recognition via the Generation of a Simulation

The above mechanisms, although they rightly can be considered creative, are relatively direct: On linking together the various representations that give rise to components of the conceptual knowledge about the emotion that is signaled by the stimulus, the subject has available all the information necessary to recognize the emotion; all that is required to perform most recognition tasks now is an implementation of the reconstructed conceptual knowledge in terms of language so that the subject can tell us what he or she knows. But, there are less direct routes that might come into play also. It may be that the explicit knowledge triggered in the above scheme is insufficient to recognize an emotion, perhaps because that particular emotion was never seen before or because the recipe for reconstructing knowledge about it provides insufficient detail. Another mechanism might attempt to generate conceptual knowledge using an inverse mapping that seeks to trigger those states normally antecedent to producing the facial expression. Such a mechanism would attempt to simulate in the observer the state of the person shown in the stimulus by estimating the motor representations that gave rise to the observed stimulus. Once the observer has generated the state that the other person is presumed to share, a representation of this actual state in the observer could in turn trigger conceptual knowledge. Simulation thus still requires the triggering of conceptual knowledge, but the basis of the trigger is not a representation of someone else but rather a representation of ourselves (simulating the other person).

The simulation hypothesis has recently received considerable attention due to experimental findings that appear to support it. In the premotor cortex of monkeys, Rizzolatti and colleagues have reported neurons that respond not only when the monkey prepares to perform an action itself but also when the monkey observes the same visually presented action performed by someone else (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Gallese & Goldman, 1999; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Various supportive findings have also been obtained in humans: Observing another's actions results in desynchronization in motor cortex as measured with MEG (Hari et al., 1998) and lowers the threshold for producing motor responses when transcranial magnetic stimulation (TMS) is used to activate motor cortex (Strafella & Paus, 2000); imitating another's actions via observation activates premotor cortex in functional imaging studies (Iacoboni et al., 1999). Moreover, such activation is somatotopic with respect to the body part that is observed to perform the action, even in the absence of any overt action on the part of the subject (Buccino et al., 2001). It thus appears that primates construct motor representations suited to performing the same action that they visually perceive someone else perform, in line with the simulation theory.

The specific evidence that simulation may also play a role in recognition of the actions that compose emotional facial expressions comes from disparate experiments. The experience and expression of emotion are

correlated (Rosenberg & Ekman, 1994) and offer an intriguing causal relationship: Production of emotional facial expressions (Adelman & Zajonc, 1989) and other somatovisceral responses (Cacioppo, Berntson, & Klein, 1992) can lead to changes in emotional experience. Producing a facial expression to command influences the feeling and autonomic correlates of the emotional state (Levenson, Ekman, & Friesen, 1990) as well as its EEG correlates (Ekman & Davidson, 1993). Viewing facial expressions results in expressions on one's own face that may not be readily visible but that can be measured with facial EMG (Dimberg, 1982; Jaencke, 1994) and that mimic the expression shown in the stimulus (Hess & Blairy, 2001); moreover, such facial reactions to viewing facial expressions occur even in the absence of conscious recognition of the stimulus, for example, to subliminally presented facial expressions (Dimberg, Thunberg, & Elmehed, 2000). Viewing the facial expression of another can thus lead to changes in one's own emotional state; this in turn could result in a remapping of one's own emotional state, that is, a change in feeling. Although viewing facial expressions does indeed induce changes in feeling (Schneider, Gur, Gur, & Muenz, 1994; Wild, Erb, & Bartels, 2001), the mechanism could also operate without the intermediate of producing the facial expression, by the direct modulation of the somatic mapping structures that generate the feeling (akin to Damasio's "as-if" loop) (A. R. Damasio, 1994, 1999). That the simulation theory requires the possibility of such a direct, central mechanism is borne out by the finding that patients with congenital facial paralysis are able nonetheless to recognize facial emotion (Calder, Keane, Cole, Campbell, & Young, 2000).

7. The Development of Emotion Recognition

The ability to discriminate and to recognize emotion from facial expressions develops in a complex fashion in infancy (Nelson, 1987; Saarni, Mumme, & Campos, 1997) and matures somewhat earlier in females than in males (see McClure, 2000, for a review). The evidence is best for the mechanisms outlined above in Sections 4 and 6, principally because their assessment relies less on lexical competence than does the assessment of conceptual knowledge per se (see Section 5 above). In line with the view that perception is a prerequisite for recognition, one would expect that Mechanism 4 might be active fairly early in life (e.g., Bushnell, Sai, & Mullin, 1989). Infants already orient to face-like stimuli at birth (Valenza, Simion, Macchi-Cassia, & Umilta, 1996), and there is some evidence that this may depend primarily on subcortical pathways, as indicated by the fact that they appear to process faces preferentially in temporal visual fields (Simion, Valenza, Umilta, & DallaBarba, 1998). Some basic emotions can be discriminated by 7-month-olds (Nelson, Morse, & Leavitt, 1979; Soken & Pick, 1992), and responses in temporal visual cortices show some selectivity to the sight of faces in 2-month-old monkeys (Rodman, O Scalaidhe, & Gross, 1993). There is also evidence that Mechanism 6 above, recognition by simulation, may be engaged early on in life: Newborns already possess an innate ability to mimic some simple facial gestures (such as someone sticking out their tongue) (Meltzoff & Moore, 1983) that may be precursors to a more extensive ability to mimic and simulate others.

Given the importance of communicating via facial expressions and other visual social signals, one would expect that infants who are born blind would be impaired in their social and emotional development. Although it has been exceedingly difficult to obtain unequivocal data on this issue, some studies do indeed suggest such an effect: Although even congenitally blind children express a range of facial emotions both spontaneously and volitionally, their expressions are not entirely normal (Cole, Jenkins, & Shott, 1989; Galati, Scherer, & Ricci-Bitti, 1997), and there is some suggestion that socioemotional development may be subtly abnormal as well (Troester & Brambring, 1992). The ability to recognize facial expressions at age 5 has been found to predict later social and academic competence (Izard et al., 2001), although it remains uncertain to what extent this correlation reflects a causal relationship.

In adults, there is evidence both for the consistent recognition of facial emotion across the life span (Moreno, Borod, Welkowitz, & Alpert, 1993) as well as for a slight decrease in accuracy in recognizing emotions with increasing age (Adolphs, Damasio, Tranel, & Damasio, 1996). In general, factors such as age and gender have not been investigated in detail for their contribution to differential performances in the experiments reviewed below. Although gender (Kesler-West et al., 2001) and age differences (Iidaka et al., in press; Pine et al., 2001) in processing facial emotion do turn up in functional imaging studies, the evidence so far suggests that the effect sizes of these factors are relatively small compared to the effects of brain damage in lesion studies (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Adolphs et al., 1996).

STRUCTURES FOR PERCEIVING EMOTION FROM FACES

Early perceptual processing of faces will of course draw on many of the same brain structures involved in processing visual stimuli in general. There are two principal divisions: (a) subcortical mechanisms that bypass striate cortex, usually presumed to be limited to relatively coarse, automatic processing perhaps especially of

visual transients and certain highly salient visual features, and (b) processing involving occipital and temporal visual neocortex, usually presumed to be required when more extensive, fine-grained perceptual representations need to be constructed. This division of labor has been studied best in relation to emotional auditory stimuli: In rats, there is auditory processing via the thalamus and the amygdala that is sufficient for fear conditioning to simple tones, whereas fear conditioning to complex auditory stimuli requires auditory cortex (LeDoux, 1996).

8. Subcortical Routes to Perception: Blindsight and the Amygdala

Ever since the discovery of blindsight in humans (see Weiskrantz, 1996, for a review), and of its experimental analogues in animals (Cowey & Stoerig, 1995), it has been known that visual processing can occur in the absence of striate cortex (although this conclusion in humans has been debated) (see Fendrich, Wessinger, & Gazzaniga, 1992). Although it is clear that visual processing in the absence of striate cortex is impoverished and, in both humans and monkeys, fails to achieve conscious visual experience, it has also been clear that it can be sufficient to guide behavior in response to visual stimuli under certain conditions. The pathways that mediate blindsight involve projections from the retina to the superior colliculus, hence to the pulvinar nucleus of the thalamus, and hence to extrastriate visual cortices, where one can in fact record neuronal responses to visual stimuli despite a complete lack of input from striate cortex (e.g., Rodman, Gross, & Albright, 1989).

How extensive can perceptual processing be without the contribution of striate cortex? It was generally considered that such processing can only encode very crude information about the stimulus, such as its spatial location, its direction of motion, and some spectral information (Cowey, 1996; Stoerig & Cowey, 1989). However, recent studies indicate that the processing may be much more detailed than initially presumed: Patients with blindsight appear able to discriminate facial expressions of emotion (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999)! Because they do so in the absence of conscious visual experience, it is probably inaccurate to refer to their performance as "recognition." The anatomical route described above has been corroborated by functional imaging studies: There is correlated activation of the superior colliculus, the pulvinar thalamus, and the amygdala (on the right) in response to subliminally presented facial expressions that have been associated with an aversive stimulus (J. S. Morris, Ohman, & Dolan, 1999). These same structures were recently found to be activated also in a participant with blindsight when discriminating emotional facial expressions in the blind visual field (J. S. Morris, de Gelder, Weiskrantz, & Dolan, 2001). Furthermore, processing of subliminally presented facial expressions of fear activates the amygdala in normal subjects (Whalen et al., 1998), possibly reflecting the operation of this same circuit. These data thus indicate that perceptual processing sufficient to discriminate certain emotional facial expressions from others can occur via circuits that largely involve subcortical structures. However, it is premature to assume that such processing excludes neocortex: Even in the blindsight cases, sectors of extrastriate cortex are presumably engaged, and it may well be those extrastriate cortices that are doing most of the perceptual work. The subcortical route provides an entry point into face perception that is likely to be more rapid and more automatic and to operate in parallel with the cortical route discussed below; an open issue is the extent to which such processing might utilize information about specific features or about the configuration of the stimulus.

9. Cortical Routes to Perception: The Fusiform Face Area and the Superior Temporal Gyrus

9.1 PROCESS CONSIDERATIONS

Cortical processing of faces begins with occipital cortices that perform early perceptual processing on the individual features of a stimulus and that relate the structure and configuration of those features to one another and distinguish them from background features of an image. Figure-ground segmentation and feature binding permit such early perceptual processing to construct a representation of the stimulus that might occur in a bottom-up fashion to a considerable extent (i.e., solely on the basis of information present in the image). Faces present the brain with particular computational problems and are consequently processed using particular strategies that may not be shared with other classes of visual stimuli. In particular, we need to be able to discriminate among a huge number of faces that are all structurally very similar, we need to be able to do so rapidly, and we need to be able to quickly relate perceptual representations of a face with knowledge about the socially relevant categories of which it is a member. Because our social relations with other people operate in large part at the level of the individual, face perception requires categorization at the most subordinate level, the level of the unique person. In general, we cannot recognize chairs, books, or cars at the unique level (although with training, people can become experts at categorizing such objects at the unique level).

Early perceptual processing probably sufficient to categorize faces as distinct from other visual objects draws on sectors of occipitotemporal cortex, importantly including the fusiform gyrus. Evidence from lesion and

functional imaging studies (see below), from MEG, as well as from recording surface and intracranial evoked electrical potentials (ERP) has demonstrated the importance of this region in processing the perceptual properties of faces. ERP and MEG studies show that some coarse categorization of visual images occurs in occipitotemporal cortex as early as 50 ms to 90 ms after stimulus onset (Seeck et al., 1997; Van Rullen & Thorpe, 2001), consistent with gender categorization of faces at latencies of 45 ms to 85 ms (Mouchetant-Rostaing, Giard, Bentin, Aguera, & Pernier, 2000), although such early responses do not yet correlate with behavioral discrimination (Van Rullen & Thorpe, 2001). More subordinate categorization of faces proceeds subsequent to this, with the earliest activity that discriminates among emotional facial expressions seen in midline occipital cortex as early as 80 ms (Pizzagalli, Regard, & Lehmann, 1999) to 110 ms (Halgren, Raij, Marinkovic, Jousmaki, & Hari, 2000), followed by temporal cortical activity around 140 ms to 170 ms (Streit et al., 1999). Peak activity related to face-specific processing near the fusiform gyrus is seen around 170 ms (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Halgren et al., 2000; Jeffreys, Tukmachi, & Rockley, 1992) and also may be part of a similar response measured in ventral occipitotemporal cortices near 200 ms with intracranial recordings (Allison et al., 1994). This response at 170 ms is not influenced by the familiarity of the face (Bentin & Deouell, 2000; Bentin et al., 1996; Eimer, 2000a), thus, presumably corresponding to bottom-up aspects of perceptual processing (akin to early structural encoding in the model by Bruce & Young, 1986). Postperceptual processing of faces, such as recognition of identity, relies on anterior temporal cortices (Tranel, Damasio, & Damasio, 1997) and occurs with latencies in excess of 200 ms (Seeck et al., 1993). Later activity in occipital regions that discriminates between different emotions is also seen after 500 ms and is influenced by the particular task, presumably reflecting top-down modulation (Krolak-Salmon, Fischer, Vighetto, & Mauguiere, 2001). Whereas the construction of a detailed structural representation of the global configuration of the face thus seems to require about 170 ms (Eimer, 2000b), it appears that some rapid, coarse categorization of gender and emotion can occur with substantially shorter latencies, presumably indicating coarse perceptual routes parallel to a full structural encoding. It should be noted, however, that the short latencies reported for gender and emotion categorization relate to individual instances of stimuli rather than to sustained categorization rates; continuous emotion categorization of images presented in a rapid serial stream can occur at rates of up to 5 Hz (Junghofer, Bradley, Elbert, & Lan, 2001, although that study did not specifically use faces). There is evidence that rapid processing occurs perhaps

disproportionately for expressions of those emotions that signal threat or danger: Compared to happy faces, facial expressions of anger show preattentive pop-out in visual displays (Ohman, Lundqvist, & Esteves, 2001), and facial expressions of fear paired with electric shock can elicit conditioned responses when subsequently presented subliminally (Esteves, Dimberg, & Ohman, 1994).

9.2 ANATOMICAL CONSIDERATIONS

Particular attention has been focused on a region of occipitotemporal cortex in the fusiform gyrus. This region of cortex in humans is activated in functional imaging studies by faces (often bilaterally but more reliably on the right than on the left) when contrasted with other objects or scrambled images (Kanwisher, McDermott, & Chun, 1997), can be modulated by attention (Haxby et al., 1994), and may be relatively specific for faces especially on the right (McCarthy, Puce, Gore, & Allison, 1997). The fusiform gyrus is also activated by nonface objects when subjects are forced to engage in subordinate-level categorization (Gauthier, Anderson, Tarr, Skudlarski, & Gore, 1997) or automatically when subjects are experts at subordinate-level categorization of those objects (e.g., in people who are expert at recognizing particular species of birds or makes of car [Gauthier, Skudlarski, Gore, & Anderson, 2000] or artificial objects [Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999]). This so-called fusiform face area participates in constructing perceptually detailed representations of the structural, and primarily static, properties of faces, which can then be linked to the retrieval of knowledge regarding that specific face.

Nearby cortical regions surrounding the occipitotemporal junction appear to serve a similar function and link perceptual representations to the retrieval of knowledge required to categorize the face at the unique level (i.e., for recognition of the individual person whose face it is). Damage to these regions can result in an impaired ability to recognize individual faces despite intact perceptual discrimination, and despite an intact ability to recognize the face in terms of its emotional expression, gender, or age (Tranel et al., 1988). Recognition of the identity behind a face (independent of naming the face) requires temporal polar cortex in the right hemisphere (Tranel et al., 1997), and naming the person whose face one recognizes requires left temporal polar cortex (H. Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996).

Given the ecological importance of faces, and the need to retrieve rapidly different types of social knowledge connected to the face, one might expect that higher order visual cortices consist of an assembly of relatively specialized "expert" systems that process distinct attributes of faces, a prediction borne out by a series of

detailed studies that recorded intracranial field potentials in humans (Allison, Puce, Spencer, & McCarthy, 1999; McCarthy, Puce, Belger, & Allison, 1999; Puce, Allison, & McCarthy, 1999). Whereas the fusiform face area is involved in processing the structural, static properties of faces that are reliable indicators of personal identity, regions more anterior and dorsal in the temporal lobe process information about the changeable configurations of faces, for example, facial expressions, eye movements, and mouth movements (Haxby et al., 2000) (see Figure 1), although there is likely some overlap among the different types of facial information represented in these two regions (Allison, Puce, & McCarthy, 2000). Functional imaging using such visual motion stimuli from the face has found activations in cortices in and near the superior temporal gyrus (Puce, Allison, Bentin, Gore, & McCarthy, 1998), possibly reflecting visual inputs to this region that carry both structural and motion-related information (Seltzer & Pandya, 1994). The fusiform face area, the superior temporal gyrus, and other as yet less well-specified regions of occipitotemporal cortex could thus be thought of as an interconnected system of regions that together construct a spatially distributed perceptual representation of different aspects of the face.

9.3 DATA FROM SINGLE NEURONS

Findings in monkeys have elucidated some of the single-unit correlates of face perception in temporal cortical regions. Neurons located in the inferior temporal cortex show a variety of response properties that are relatively selective for the sight of faces (Perrett, Rolls, & Caan, 1982) and other categories of objects (Gross, Rocha-Miranda, & Bender, 1972). Moreover, specific neurons modulate their response preferentially with specific information about faces, such as their identity, social status, or emotional expression. The selectivity of neurons in inferior temporal cortex for the identity of faces can already be conveyed in the earliest components of their visual response (less than 100 ms latency) (Oram & Perrett, 1992) and exhibits a sparse population code that can be represented in a relatively low-dimensional space (M. P. Young & Yamane, 1992). There is some evidence that neurons in temporal cortex are anatomically segregated in terms of the type of information that they encode: Whereas neurons in the superior temporal sulcus encode information about the emotional expression of a face, those more ventral in the inferior temporal cortex primarily encode information about the identity of the face (Hasselmo, Rolls, & Baylis, 1989). These findings at the single-unit level should probably be thought of in analogy with findings from functional imaging studies in humans reviewed above: They reveal which regions of the brain are involved in certain pro-

cesses but not which are necessary, as indicated by the finding that in monkeys, lesions of superior temporal cortex (wherein one finds neurons with responses selective for faces) do not produce a behavioral impairment in face recognition (Heywood & Cowey, 1992). Whereas the earliest possible visual responses of neurons in monkey inferior temporal cortex exhibit latencies as short as 20 ms to 50 ms (Tovee, Rolls, Treves, & Bellis, 1993), the information that they encode about faces varies in time: The evolution of responses encoding fine-grained, subordinate information sufficient to distinguish emotion categories shown in facial expressions lags behind responses encoding more superordinate information sufficient to distinguish faces from other objects by approximately 50 ms (maximal rates of information transmission, which are skewed toward the beginning of the response, occur near 170 ms versus 120 ms, respectively) (Sugase, Yamane, Ueno, & Kawano, 1999).

Information about visual stimuli is encoded in both the rates and the timing of action potentials. It appears that a relatively greater proportion of information about the visual stimulus is encoded in the temporal structure of spikes the more "high-level" the visual cortex from which one is recording (McClurkin, Optican, Richmond, & Gawne, 1991). Some structures, such as orbitofrontal cortex and amygdala, have very low firing rates, and it seems likely that they encode a considerable proportion of information in spike timing, perhaps even in the latency between stimulus onset and the first spike (for a recent example of such coding in somatosensory cortex, see Panzeri, Petersen, Schultz, Lebedev, & Diamond, 2001). Information-theoretic techniques are now being used to quantify the information that neuronal spikes can encode about stimuli such as faces (Oram, Foldiak, Perrett, & Sengpiel, 1998; Sugase et al., 1999). It remains to be fully understood how patterns of neuronal spikes in disparate regions of the brain and at different points in time are coordinated to produce the constructive information processing that evidently occurs as we recognize emotion from facial expressions. A future goal is to combine data available from multiple methods with differing spatiotemporal resolution and to combine data from studies in both human and nonhuman animals.

10. Lateralized Perception of Emotion: The Right Cerebral Hemisphere

There is a long history of the right hemisphere's disproportionate role in emotional and social processing, encompassing perception as well as recognition (many studies do not distinguish between the two). There is evidence also that processing of faces in general draws differentially on the left and on the right cerebral hemispheres: People recognize their own faces more rapidly with their right hemispheres than with their left

(Keenan et al., 1999; Keenan, Nelson, O'Connor, & Pascual-Leone, 2001), and face agnosia appears to draw more on damage in right hemisphere than in left (De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994) (although in general bilateral damage is required) (A. R. Damasio, Tranel, & Damasio, 1990). The right hemisphere appears to contain systems for social communication that are in many ways complementary to the left hemisphere's specialization for language (Bowers, Bauer, & Heilman, 1993). Moreover, the right hemisphere's role encompasses a variety of channels, including voice, face, and others (Borod, 1993). Earlier studies showed that damage to the right hemisphere can impair discrimination, recognition, and naming of emotional faces or scenes (DeKosky, Heilman, Bowers, & Valenstein, 1980) and that electrical stimulation of right temporal visual-related cortices can disrupt the perception, recognition, and memory for faces (Fried, Mateer, Ojemann, Wohns, & Fedio, 1982). There is evidence that emotion is processed preferentially by the right hemisphere already in 5-year-olds, who show ERPs in the right, but not in the left, hemisphere that discriminate among facial expressions (de Haan, Nelson, Gunnar, & Tout, 1998).

Despite the consensus that the right hemisphere plays a key role in emotion processing, there is debate regarding the details. Two main theories have been put forth: that the right hemisphere participates in processing all emotions (the "right hemisphere hypothesis") or that the right hemisphere is relatively specialized to process negative emotions, whereas the left hemisphere is relatively specialized to process positive emotions (the "valence hypothesis") (see Borod et al., 1998, and Canli, 1999, for reviews). To date, there is evidence pointing both to the right hemisphere hypothesis (e.g., Borod et al., 1998; Burt & Perrett, 1997), as well as data supporting the valence hypothesis (e.g., Canli, 1999; Jansari, Tranel, & Adolphs, 2000; Reuter-Lorentz & Davidson, 1981); additional complications may arise from an interaction with gender effects (Van Strien & Van Beek, 2000). Some modifications propose that the valence hypothesis may indeed hold for the experience and perhaps the expression of emotions but that the perception of emotion is better described according to the right hemisphere hypothesis (Borod, 1992; Bryden, 1982; Canli, 1999; Davidson, 1993). On the other hand, there is evidence that both the perception of emotion and aspects of the experience (awareness of the details of one's feelings) rely on the same right hemisphere mechanisms (Lane, Kivley, Du Bois, Shamasundara, & Schartz, 1995).

Measurements of the expression of emotions on specific sides of the face have been largely supportive of the valence hypothesis, in both human (Brockmeier &

Ulrich, 1993) and nonhuman primates (Hauser, 1993), although this finding appears to rely primarily on expression in the lower half of the face (Richardson, Bowers, Bauer, Heilman, & Leonard, 2000). In regard to the perception and recognition of emotion, some studies with brain-damaged subjects have provided data in support of the valence hypothesis (Borod, Koff, Lorch, & Nicholas, 1986; Mandal et al., 1999; Schmitt, Hartje, & Willmes, 1997), whereas others have provided more support for the right hemisphere hypothesis (Adolphs et al., 2000; Borod et al., 1998). Findings from functional imaging have contributed little to the question of cortical hemispheric asymmetry because hemispheric contrasts have usually not been explicitly calculated (but they have investigated asymmetric involvement of subcortical structures) (cf. Section 11.2).

The bulk of the data has come from normal subjects, also providing mixed support for the above hypotheses. Some studies have used chimeric faces, which show an emotion on one half side of the face and a neutral expression on the other. Whereas a series of studies by Levy and colleagues (Hoptman & Levy, 1988; Levy, Heller, Banich, & Burton, 1983; Luh, Rueckert, & Levy, 1991) found support for the valence hypothesis, other studies in humans (Christman & Hackworth, 1993) and chimpanzees (R. D. Morris & Hopkins, 1993) supported the right hemisphere hypothesis. Studies using tachistoscopically presented stimuli have generally supported the valence hypothesis: a left visual field bias for perceiving negative valence and a right visual field bias for perceiving positive valence (Davidson, Mednick, Moss, Saron, & Schaffer, 1987; Reuter-Lorentz & Davidson, 1981). Under free viewing conditions, Jansari et al. (2000) found that perceptual discrimination of faint morphs of emotional faces from neutral faces was better if the emotional face was shown horizontally to the viewer's right of the neutral face in the case of positively valenced faces but was better if the emotional face was shown to the viewer's left of the neutral face in the case of negatively valenced faces, results that also fit with the valence hypothesis.

Consistent with the findings from Jansari et al. (2000), and in line with the valence hypothesis, Adolphs, Jansari, and Tranel (2001) found that in the same task, right hemisphere damage decreases the normally superior accuracy for discriminating sad faces shown on the viewer's left, whereas left hemisphere damage decreases the normally superior accuracy for discriminating happy faces shown on the viewer's right. However, this study also reported the counterintuitive finding that subjects with damage in either left or right hemisphere were significantly superior to normal subjects in discriminating happy from neutral faces when the happy faces were shown on the viewer's left. One possibility that might

explain these data is an active process, in normal brains, that impairs discrimination of happy faces shown on the left. That is, when normal subjects see a happy face to the left of a neutral face, they perceive the two faces to be more similar (harder to discriminate)—either because the happy face is given a negatively valenced tone or because the neutral face is given a positively valenced tone.

The roles of the left and right hemispheres in recognizing facial emotion provide a good example of the complexities encountered when subjects can engage multiple strategies on a task. A study in a split-brain patient (Stone, Nisenson, Eliassen, & Gazzaniga, 1996) found that whereas both hemispheres were equally adept at recognizing facial emotions on standard tasks, providing an explicitly nonverbal matching task revealed a distinct right hemisphere advantage; however, this advantage disappeared when the instructions on the same task were altered slightly so as to encourage a verbal mediation strategy (perhaps by generating labels for the faces and internally comparing the labels, rather than directly comparing the faces without generating the label).

Taken together, the findings from normal subjects and from subjects with unilateral brain damage broadly support the idea that the left and right hemispheres are differentially important in processing emotion, but they are not unanimous in providing support for either the valence or the right hemisphere hypothesis. The bulk of the data supports the idea that the right hemisphere plays a disproportionate role in perceiving emotions of negative valence, but a clear asymmetry in perceiving emotions of positive valence has not emerged. One possibility that might reconcile at least some of the findings is that hemispheric specialization is asymmetric not with respect to valence but with respect to arousal, specifically, that the right hemisphere may be specialized to perceive expressions of high arousal. A lesion study with a large sample size found evidence to support this view (Peper & Irle, 1997), and it should be noted that many negatively valenced emotions also are systematically of higher arousal than are positively valenced emotions. In further support of this idea, emotional responses to conditioned facial expressions show the largest autonomic arousal to negatively valenced and highly arousing faces shown to the right hemisphere (Johnsen & Hugdahl, 1993), and damage to right hemisphere, more than damage to left, results in impaired autonomic arousal to a variety of emotionally charged stimuli (Morrow, Vrtunski, Kim, & Boller, 1981; Tranel & Damasio, 1994; Zoccolotti, Scabini, & Violani, 1982).

Another finding related to hemispheric asymmetry is an anomia for emotions. Lesions with damage in right posterior neocortex, including white matter, can result in a specific anomia for emotional facial expressions. Subjects in these studies were able to perceive faces normally and able to recognize identity from the face, and they were also able to show some recognition of the emotion shown in the face in matching tasks that did not require knowing the name of the emotion. However, they were impaired when asked to retrieve the name of the emotion. Two subjects studied by Rapcsak et al. (Rapcsak, Comer, & Rubens, 1993; Rapcsak, Kaszniak, & Rubens, 1989) had damage in middle temporal gyrus and underlying white matter, and a patient studied by Bowers and Heilman (1984) had damage to white matter in right parietal and temporal lobe. Given the selective anomia found in these subjects, it appears unlikely that their impairment resulted from a defect in recognizing the emotion, as might result from damage that included parietal cortices in right hemisphere concerned with representing body state information (cf. Section 13.1). Instead, it is plausible that these patients suffered from a disconnection of high-level visual information about the expression shown in the face, on one hand, and the left hemisphere networks required for lexical retrieval of the name of the emotion, on the other hand—an idea made plausible by the direct connections between right visual temporal cortex and Broca's area in humans (Di Virgilio & Clarke, 1997).

STRUCTURES FOR RECOGNITION OF EMOTION FROM FACES

The previous sections thus point to regions in occipital and temporal neocortex that construct fine-grained perceptual representations of faces and of such regions, especially in the right hemisphere, that encode perceptual information about the emotion shown in the face. How are these perceptual representations linked to the retrieval of conceptual knowledge from the face? A large number of different structures participate in recognizing the emotion shown in a face: right occipitotemporal cortices, right parietal cortices, bilateral orbital frontal cortices, left frontal operculum, bilateral amygdala, insular cortex, and basal ganglia, among others (see Figure 5) (Brothers, 1990). The issue is further complicated by the fact that most studies also make demands on other cognitive processes, such as attention or memory; a recent study that investigated some of these issues found evidence for a network of structures participating in emotion recognition, including amygdala, orbitofrontal cortex, anterior cingulate cortex, and ventral striatum (Vuilleumier, Armony, Driver, & Dolan, 2001).

In interpreting the lesion studies described below, one needs to distinguish among four ways in which lesions could result in impaired recognition or naming of the emotion shown in a face: (a) because of a percep-
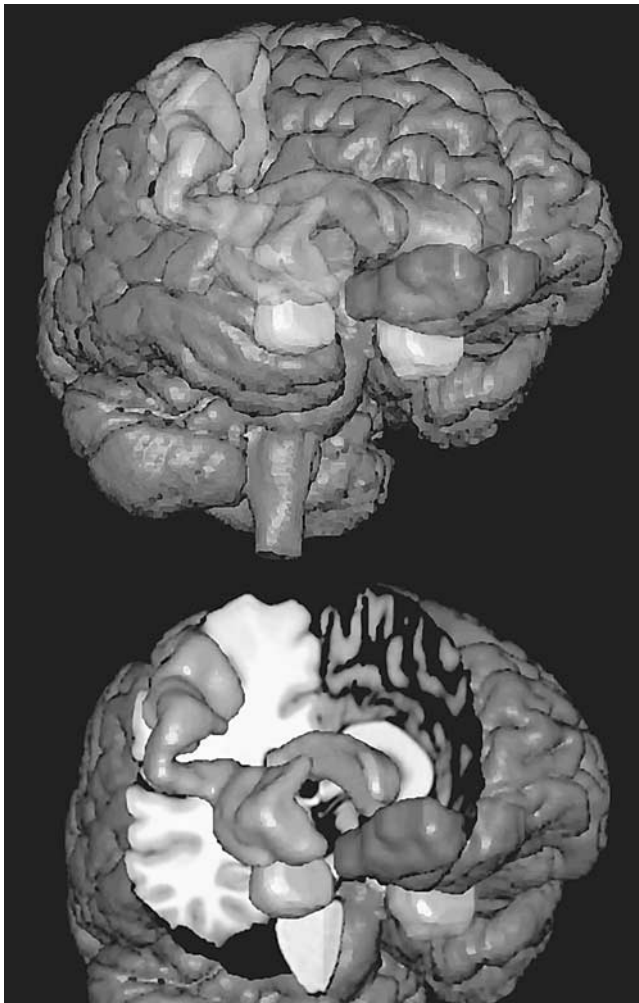
Figure 5: Neuroanatomy of Some of the Key Structures Implicated in Recognition of Facial Emotion.
NOTE: Three-dimensional renderings of the amygdala (yellow), ventromedial prefrontal cortex (red), right somatosensory cortices (S-I, S-II, and insula) (green), and, for orientation, the lateral ventricles (light blue) were obtained from segmentation of these structures from serial magnetic resonance images of a normal human brain. The structures were corendered with a three-dimensional reconstruction of the entire brain (top) and a reconstruction of the brain with the anterior right quarter removed to clearly show location of the internal structures (bottom). Images prepared by Ralph Adolphs, Hanna Damasio, and John Haller, Human Neuroimaging and Neuroanatomy Laboratory.

tual deficit (e.g., lesions in striate cortex), (b) because of a disconnection of perceptual information from structures bona fide involved in recognition (e.g., white matter lesions in right occipitotemporal regions and possibly lesions to cortex in those same regions), (c) because of damage to structures that themselves contain associations between fine-grained perceptual information and conceptual knowledge associated with the face—such structures could in and of themselves reconstruct some conceptual information, and they could do so also by activating remote regions that are the proximal substrate

for representing components of conceptual knowledge. (d) The ensemble of these latter remote regions would in turn constitute possibility: the neural substrate for conceptual knowledge about the world in general. Some of the above possibilities are not interesting and will not be considered further: Possibilities (a) and (d) are in general nonspecific because they destroy perception in general or because they destroy conceptual knowledge in general (e.g., respectively, in someone who is blind or demented). The structures under Possibility (c) are the ones that will be of primary concern.

11. The Amygdala

We encountered the amygdala already as a structure presumed to be involved in the rapid, coarse, perceptual processing of facial expressions that relies on subcortical mechanisms. However, it also receives highly processed cortical information about faces and participates in recognition—a good indication that a single structure may participate in multiple processes that probably operate at different temporal scales.

The amygdala plays a complex and ubiquitous role in emotion and in social behavior (Aggleton, 2000). The mechanisms that underlie this role are best understood in animals, especially rodents, where they have been shown to draw on the amygdala's ability to modulate a large variety of response components and cognitive processes based on the emotional significance of the stimulus. Thus, the amygdala modulates attention, memory, and decision making, as well as many components of an emotional response (including behavioral, autonomic, and endocrine components). Specific nuclei within the amygdala are involved in certain subsets of these processes, as well as in processing certain classes of stimuli, further complicating the picture. Shared in common by all these diverse mechanisms is the ability to associate stimuli with their emotional/social value. The representations required for such an association draw on visual neocortex (for representing the stimuli) and on brainstem and hypothalamic nuclei (for representing and implementing the emotional value).

The amygdala's functional complexity is mirrored in its vast array of connections with other brain structures: High-level sensory neocortices provide information about the stimulus, primarily to the lateral nucleus, and the amygdala projects back to much of neocortex, as well as to basal forebrain, hippocampus, and basal ganglia to modulate cognition and to hypothalamic and brainstem nuclei to modulate emotional response. It is precisely because of the complexity of the various processes in which the amygdala participates that it can effect a concerted change in cognition and behavior that plays out as an organized emotional reaction.

The amygdala's role in processing facial emotion reviewed below is complemented by findings at the single-neuron level: In both human (Fried, MacDonald, & Wilson, 1997) and nonhuman primates (Leonard, Rolls, Wilson, & Baylis, 1985; Nakamura, Mikami, & Kubota, 1992; Rolls, 1992), neurons in the amygdala respond differentially to faces, consonant with the broader responses of amygdala neurons that have been recorded in monkeys in response both to the basic motivational significance of stimuli (Nishijo, Ono, & Nishino, 1988) as well as to their complex social significance (Brothers, Ring, & Kling, 1990).

11.1 HUMAN LESION STUDIES

Following earlier indications that amygdala damage might impair aspects of face processing (Jacobson, 1986), the first study to demonstrate a selective impairment in recognition of emotion from faces also found this impairment to be relatively restricted to certain highly arousing emotions, especially fear (Adolphs et al., 1994) (see Figure 6). Subsequent studies in several additional patients confirmed an impaired ability to recognize emotion from faces, despite a normal ability to discriminate faces perceptually. Some of these studies found a disproportionately severe impairment in recognizing fear (Adolphs, Tranel, Damasio, & Damasio, 1995; A. K. Anderson & Phelps, 2000; Broks et al., 1998; Calder, Young, Rowland, et al., 1996; Sprengelmeyer et al., 1999), whereas others found evidence for a broader impairment in recognizing multiple emotions of negative valence in the face, including, fear, anger, disgust, and sadness (Adolphs, 1999; Adolphs, Tranel, et al., 1999; Schmolck & Squire, 2001) (see Figure 7 and Table 2). In all these cases, the patients had bilateral damage to the amygdala; unilateral damage has been reported to produce milder impairments in emotion recognition that can be more variable and that may achieve statistical significance only in larger samples (Adolphs, Tranel, & Damasio, 2001; A. K. Anderson, Spencer, Fulbright, & Phelps, 2000).

The ability to recognize emotions has been assessed using several different tasks, although the stimuli have generally been drawn from the same set, the Pictures of Facial Affect (Ekman & Friesen, 1976). The two primary tasks used have been a rating task (Adolphs et al., 1994; Russell & Bullock, 1985) and a labeling task (A. W. Young et al., 1995). In the rating task, subjects are asked to rate the intensity with which each of the six basic emotions is judged to be signaled by a stimulus; thus, each face stimulus yields a profile of ratings that reflect its expression of multiple emotions, even though it may be judged to be a member of only a single category (for example, a face of fear could be judged to look afraid categorically yet would also be judged to signal some surprise and
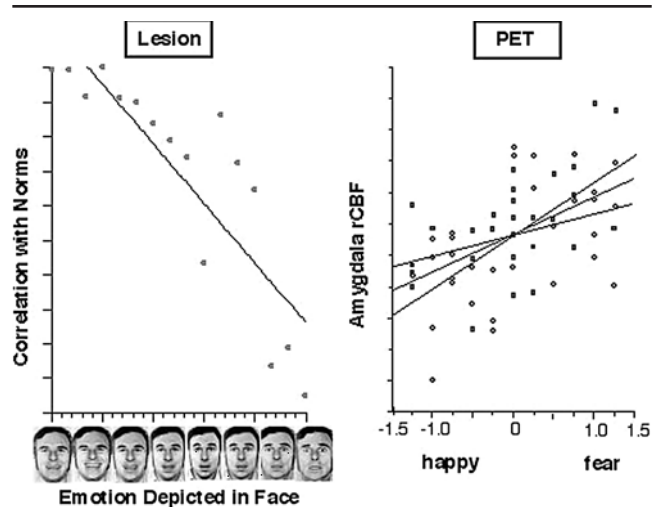

Figure 6: The Amygdala's Role in Recognition of Fear.
NOTE: PET = positron emission tomography. Section (a) shows that bilateral damage to the amygdala can result in selective impairment in the recognition of fear. Shown is the performance of subject SM in rating morphs of emotional facial expressions. The y-axis shows the correlation of SM's ratings with mean normal ratings, and the x-axis shows the stimuli, which are morphs from happy to surprise and from surprise to fear. SM's recognition score becomes progressively worse the closer the expression is to fear. Modified from Adolphs and Tranel (2000); copyright John Wiley. Section (b) shows that viewing facial expressions of fear results in activation of the amygdala in normal subjects. Regional cerebral bloodflow (rCBF) in the left amygdala (y-axis) shows a linear correlation with the degree of fear shown in morphs between facial expressions of happiness (−1 on the x-axis) and fear (+1 on the x-axis). Lines indicate regression line and 95% confidence intervals. Modified with permission from J. S. Morris et al. (1996); copyright Macmillan.

anger) (Russell & Bullock, 1986). Ratings given to the face can be examined for each emotion that is rated or can be considered as a vector in a multidimensional face space that quantifies the intensity of all the different emotions a subject judges to be signaled by the stimulus. In the labeling task, subjects are asked to provide a single categorical label to the stimulus, usually by matching the face with one label from a given list of the words for basic emotions. In addition to these two tasks, various others have been used: matching faces to descriptions of emotions, sorting faces, and judging the similarity between emotions shown in pairs of faces (cf. Adolphs & Tranel, 2000).

Across the majority of studies, impairments in recognition of emotion as assessed by one or more of the above tasks have been found despite an often normal ability to discriminate perceptually among the same stimuli. Most of the patients with bilateral amygdala damage perform in the normal range on the Benton Face Matching Task (often misleadingly called the Facial Recognition Test) (Benton, Hamsher, Varney, & Spreen, 1983), in which subjects are asked to match different views of the same, unfamiliar person's face. Some patients with complete bilateral amygdala damage also
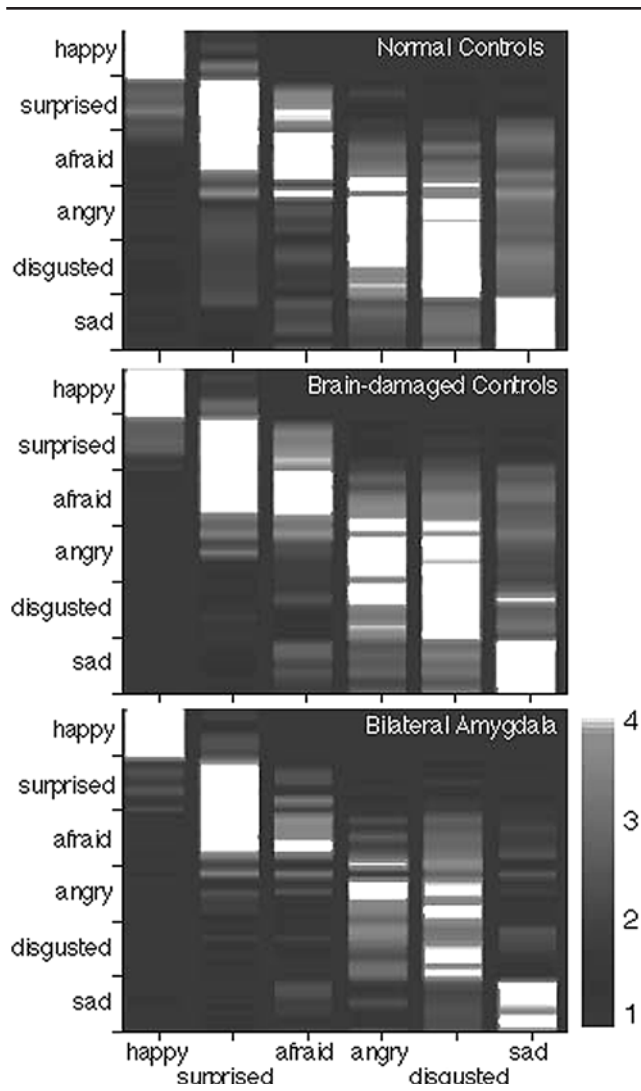
Figure 7: Bilateral Amygdala Damage Impairs Recognition of Multiple Negative Emotions.

SOURCE: Adolphs, Tranel, et al. (1999); copyright Elsevier Science. **[PERMISSION NEEDED?]**

NOTE: Whereas subject SM (see Figure 6) shows a disproportionate impairment in the ability to recognize fear, most subjects with bilateral amygdala damage show broader impairments in multiple negatively valenced emotions. Raw rating scores of facial expressions of emotion are shown from 7 normal controls, from 16 brain-damaged controls with no amygdala damage, and from 8 subjects with bilateral amygdala damage (from Adolphs, Tranel, et al., 1999). The emotional stimuli (36 faces; 6 each of the six basic emotions indicated) are ordered on the y-axis according to their perceived similarity (stimuli perceived to be similar, e.g., two happy faces or a happy and a surprised face, are adjacent; stimuli perceived to be dissimilar, e.g., happy and sad faces, are distant). The six emotion labels on which subjects rated the faces are displayed on the x-axis. Gray scale brightness encodes the mean rating given to each face by a group of subjects, as indicated in the scale. Thus, a darker line would indicate a lower mean rating than a brighter line for a given face; a thin bright line for a given emotion category would indicate that few stimuli of that emotion received a high rating, whereas a thick bright line would indicate that many or all stimuli within that emotion category received high ratings. Because very few mean ratings were less than 1 or greater than 4, we truncated the graphs outside these values. Data from subjects with bilateral amygdala damage indicate abnormally low ratings of negative emotions (thinner bright bands across any horizontal position corresponding to an expression of a negative emotion).

TABLE 2:Studies of Facial Emotion Processing in Subjects With Bilateral Amygdala Damage

Lesion Study	Finding
Sprengelmeyer et al. (1999)	Impaired recognition of fear from faces, body postures, and sounds
Rapcsak et al. (2000)	Impaired recognition on labeling task but no specificity for fear when analyzed according to profile in normal subjects
Jacobson (1986)	Impaired face perception and social behavior in a psychiatric patient
Adolphs, Russell, & Tranel (1999); Adolphs & Tranel (2000); Adolphs, Tranel, Damasio, & Damasio (1994, 1995)	Patient SM is selectively impaired in rating the intensity of fear, the arousal of negatively valenced expressions, and judging similarity between expressions
Adolphs (1999)	Summary from several patients with bilateral amygdala damage showing variable impairments across several negative emotions
Adolphs, Tranel, et al. (1999)	Nine subjects with bilateral amygdala damage showed impaired fear recognition as a group but considerable heterogeneity with impairments on various negative emotions
A. K. Anderson & Phelps (2000)	Patient could not recognize fear on others' faces but could express it on her own face
Broks et al. (1998)	Impaired recognition of facial expressions in several subjects with bilateral amygdala following encephalitis, especially severe for fear
Calder, Young, Rowland, et al. (1996)	Impaired recognition of facial expressions, especially severe for fear
Hamann et al. (1996)	Normal rating profiles in 2 subjects with complete bilateral amygdala damage, when correlations were used
Hamann & Adolphs (1999)	Normal similarity measure from ratings, using MDS in same 2 subjects with complete bilateral amygdala damage
Schmolck & Squire (2001)	Three patients with complete bilateral amygdala damage, including the 2 from the Hamann et al. (1996) studies above, were impaired on some negative emotions when data analyzed differently
A. W. Young et al. (1995); A. W. Young, Hellawell, Van de Wal, & Johnson (1996)	One patient with bilateral amygdalotomy (not complete) was impaired in learning new faces, in matching emotional expressions to the words, and in detecting direction of gaze

NOTE: MDS = nonmetric multidimensional scaling.

have a normal ability to discriminate subtle changes in facial expression, even for facial expressions that they are nonetheless unable to recognize (Adolphs & Tranel, 2000; Adolphs, Tranel, & Damasio, 1998). Perhaps the most compelling evidence for intact perceptual processing in subjects with bilateral amygdala damage comes

from three patients with normal performance on a series of very difficult visuoperceptual tasks that have also been used in monkeys (Stark & Squire, 2000). A final piece of evidence for normal face perception is that some of the amygdala subjects are able to recognize a person's identity (Adolphs et al., 1994), as well as gender and age (A. K. Anderson & Phelps, 2000) from the face, even though they fail to recognize aspects of its emotional expression.

A patient with partial bilateral amygdala damage, as well as minimal damage to extra-amygdalar structures (A. W. Young et al., 1995), was impaired in recognizing emotion on the labeling task, in learning the identity of faces, as well as in discriminating the direction of eye gaze from the face. A disproportionate impairment in labeling fear in facial expressions was documented in subsequent studies with the same patient (Calder, Young, Rowland, et al., 1996) and a number of others who had complete, but nonselective, bilateral amygdala damage (Broks et al., 1998).

A particularly well-studied subject, SM, has been especially informative because of the specificity of both her lesion and her impairment (Adolphs & Tranel, 2000; Tranel & Hyman, 1990). SM is a woman in her mid-30s who has complete bilateral amygdala damage due to calcification from a rare disease. She also has minor damage to anterior entorhinal cortex, contiguous with her amygdala damage, but no damage elsewhere in the brain. On a series of tasks, she shows a relatively disproportionate impairment in recognizing the intensity with which facial expressions signal fear and a lesser impairment also in recognizing the intensity of related emotions such as surprise and anger. Her impairment is restricted to this class of emotions when asked to rate the intensity of basic emotions; however, she also has a broader impairment in rating the degree of arousal of all negatively valenced emotions (Adolphs, Russell, & Tranel, 1999), as well as in making social judgments concerning the trustworthiness and approachability of people from their faces (Adolphs et al., 1998). We have proposed that her impairments across these diverse tasks reflect the amygdala's role in recognizing signals that indicate potential threat or danger, a hypothesis motivated by the amygdala's broader role in mediating emotional responses to this class of stimuli (Adolphs & Tranel, 2000; Adolphs, Tranel, et al., 1999).

Whereas some subjects with bilateral amygdala damage are impaired on both the labeling and the rating tasks described above, several with complete amygdala damage have been found to be impaired on one task but not the other, or variably impaired depending on how the data are analyzed. However, on closer analysis all such subjects are indeed impaired on at least some measure of facial emotion recognition but not all in the same way. Two subjects with complete bilateral amygdala dam-

age resulting from encephalitis gave profiles on the rating task that correlated well with normal rating profiles (Hamann et al., 1996), unlike the ratings given by SM (Adolphs et al., 1994) and some other subjects with amygdala damage (Adolphs, Tranel, et al., 1999). These two subjects were nonetheless impaired when the data from the rating task were analyzed in more detail and also when given the labeling task: Their impairment was especially evident when asked to make judgments concerning emotions other than the prototypical one shown in the stimulus (Schmolck & Squire, 2001). Subject SM, on the other hand, was severely impaired on the rating task but performed normally on the labeling task, provided that she was given the list of labels to choose from (she was impaired if asked to generate the labels herself without matching to a list) (Adolphs & Tranel, 2000). This variance in performance on particular tasks emphasizes that the amygdala cannot be completely essential for all aspects of emotion recognition. The story is more complicated than that and will need to take into account the amygdala's role as one component of a network of structures that participate in various aspects of recognition, depending on the particular strategy a subject is using to perform a given task. This conclusion suggests the need to design tasks that restrict the options among different available strategies, for instance by providing time constraints.

A second source of confusion comes not from variable performances across different tasks but from variable emotions whose recognition is impaired, regardless of task. Whereas SM shows the most severe impairment, across multiple tasks, in recognition of fear, other subjects show an impairment that is much less specific, or even show impairments that are disproportionately severe for negative emotions other than fear, such as sadness (Adolphs, 1999; Adolphs, Tranel, et al., 1999; Schmolck & Squire, 2001). This source of variance is more difficult to explain: It seems unlikely to arise simply from different performance strategies and may reflect instead a broader or more heterogeneous function of the amygdala in emotion recognition. It has been argued that the amygdala is not involved principally in processing stimuli related to threat and danger, as we have suggested (Adolphs & Tranel, 2000; Adolphs, Tranel, et al., 1999) but that it instead triggers cognitive resources to help resolve ambiguity in the environment—under this explanation, both facial expressions of fear and of anger signal threat/danger, but fear differs from anger in that the source of the threat is ambiguous. It would then be the imperative to resolve this ambiguity that engages the amygdala (Whalen, 1999). This latter explanation would also fit with the substantial evidence for the amygdala's modulation of attentional processes in both animals (Holland & Gallagher, 1999) and

humans (A. K. Anderson & Phelps, 2001), including a speculative role for modulating spatial attention to facial expressions (Vuilleumier & Schwartz, 2001). Another explanation is that the amygdala is involved in processing a class of emotions that are of negative valence and high arousal (Adolphs, Russell, et al., 1999), which may carve out an ecologically salient emotion category of which threat/danger is a subset. Yet a further possibility is that the emotions whose recognition depends most on the amygdala are related to behavioral withdrawal (A. K. Anderson et al., 2000), where again threat/danger or fear is a subset of this class. Clearly, we do not yet have a final picture of how the amygdala relates to specific emotions, and it is conceivable that none of our current conceptualizations does full justice to the amygdala's role. In the face of these difficulties, and in the face of the diverse and complex role of the amygdala in aspects of emotion other than facial emotion recognition, it seems plausible that the amygdala may instead participate primarily in a set of more basic biological processes that can all come into play in emotion recognition but that do not translate neatly into any particular categories of emotion.

Although the bulk of the data from subjects with amygdala damage has come from the two recognition tasks described above, some other studies help elucidate further the nature and specificity of the amygdala's role in emotion recognition. A. K. Anderson and Phelps (2000) have studied a patient with bilateral amygdala damage who is impaired in her ability to recognize fear in others' faces but who is able to produce fear on her own face and who can also recognize fear from her own facial productions. General declarative knowledge regarding fear, for instance when asked to describe situations that normally induce fear (Adolphs et al., 1995), appears to be intact in all subjects whose damage is relatively restricted to the amygdala (if the damage extends to temporal cortex, general impairments in conceptual knowledge of emotion can result) (Adolphs et al., in press-a). Subject SM has been tested on a large number of tasks, including ones that do not require verbal mediation; all these provide evidence of her selective impairment in recognizing fear, suggesting that lexical processing is not at the root of the impairment (Adolphs & Tranel, 2000). The findings thus suggest that the amygdala cannot be thought of as a repository of conceptual knowledge about emotions or as a necessary ingredient for all aspects of emotional response. Its role appears to be more mediational, in linking perception of facial expressions with the reconstruction of some components of conceptual knowledge.

As mentioned briefly above, unilateral damage to the amygdala does not appear to result in the same magnitude of impaired recognition of emotion from facial expressions as does bilateral damage (Adolphs et al.,

1995). However, when larger samples of subjects are tested, some impairments can be found: An impaired ability to learn new emotional facial expressions correlated with the extent of unilateral amygdala damage (Boucsein, Weniger, Mursch, Steinhoff, & Irle, 2001), and both Adolphs, Tranel, et al. (2001) (sample $N = 26$) and A. K. Anderson et al. (2000) (sample $N = 23$) found evidence that subjects with right temporal lobectomy were impaired, as a group, in their recognition of some negative emotions from facial expressions, despite intact basic visual perception (cf. Mendola et al., 1999). The impairment was especially striking for fear (Adolphs, Tranel, et al., 2001) but may extend to emotions related to withdrawal in general (A. K. Anderson et al., 2000). It is important to keep in mind that the patients in these studies had damage in addition to the amygdala, including temporal polar cortex and rhinal cortex, structures bidirectionally connected with the amygdala (Amaral, Price, Pitkanen, & Carmichael, 1992) that have been shown to modulate emotional behaviors in animal studies (Aggleton & Young, 2000).

Both studies (Adolphs, Tranel, et al., 2001; A. K. Anderson et al., 2000) involved epileptic patients with neurosurgical temporal lobectomy and reported that earlier age of seizure onset correlated with worse recognition of emotion, also raising an important issue of relevance to the data from subjects with bilateral amygdala damage: To what extent does the age of onset of the amygdala damage contribute to the nature of the impairment? Subject SM had damage that was acquired relatively early in life, and it has been suggested that this early onset may account for some of the features of her impairment (Hamann et al., 1996; Schmolck & Squire, 2001). Although preliminary findings from functional imaging indicate that the amygdala is activated by viewing emotional facial expressions certainly by adolescence, and probably earlier (Baird et al., 1999), and although lesion studies in monkeys have shown a role for the amygdala in early social development (Bachevalier, 1991; Bachevalier, Malkova, & Mishkin, 2001), the amygdala's possible contribution to the acquisition of knowledge about a facial expression remains largely unknown. There is of course a clear role in those aspects of knowledge acquisition that rely entirely on associative mechanisms, supported by the amygdala's role in fear conditioning. Although the acquisition of declarative knowledge appears not to require the amygdala essentially (Bechara et al., 1995), there is an established role in modulating such acquisition (Adolphs, Cahill, Schul, & Babinsky, 1997; Cahill & McGaugh, 1998; Hamann, Ely, Grafton, & Kilts, 1999), indicating diverse contributions to knowledge about emotional stimuli via multiple mechanisms (cf. Desmedt, Garcia, & Jaffard, 1998). Some evidence that the amygdala may contribute to

acquisition of conceptual knowledge of emotions during development comes from the finding that subjects who sustained bilateral amygdala damage early in life, but not those who sustained similar damage as adults, have impaired knowledge of the degree of emotional arousal of negatively valenced emotions (Adolphs, Lee, Tranel, & Damasio, 1997; Adolphs, Russell, et al., 1999), an intriguing finding that still awaits replication and further interpretation. A fuller understanding of the human amygdala's contribution to the development of facial emotion recognition will require longitudinal studies in subjects who sustained amygdala damage early in life, some of which are currently underway in our laboratory.

11.2 FUNCTIONAL IMAGING STUDIES

The initial findings that bilateral amygdala damage impairs recognition of facial emotion were quickly complemented by data from functional imaging studies in normal subjects (see Table 3). Such studies have provided evidence that viewing facial expressions, especially fear, automatically engages the amygdala in normal individuals and that abnormal amygdala activation can be seen in certain psychiatric populations with disorders of emotion. Although corroborating the data from lesion studies, these findings have led to the further insight that the amygdala may process faces rather automatically and transiently, and in conjunction with other neural structures wherein activity is correlated with amygdala activation.

Two early studies, one using PET (J. S. Morris et al., 1996) and the other blocked fMRI (Breiter et al., 1996), found that the amygdala is activated by facial expressions of fear, even though neither study asked subjects to judge the emotion shown in the stimulus. The study by J. S. Morris et al. (1996) provided a parametric approach to the stimuli (morphs between happy and fearful faces) that found a significant linear correlation between the intensity of fear shown in the face and the degree of amygdala activation, findings very much in line with the increasingly impaired recognition of a morphed expression of fear in subject SM who has amygdala damage (cf. Section 11.1 and Figure 6). However, as in the case of the lesion studies, other investigations have found evidence for amygdala processing of expressions other than fear, including either activations (Breiter et al., 1996) or deactivations (J. S. Morris et al., 1996) to happy faces, as well as activations to sad faces (Blair, Morris, Frith, Perrett, & Dolan, 1999; but see Kesler-West et al., 2001, and Phillips et al., 1998). As for the lesion studies, this heterogeneity may reflect the differential engagement of processes, depending on the subject and the experiment. It is noteworthy that the functional imaging studies have not in general asked subjects to process the emotion shown in the face but rather have asked them to perform an unrelated task or simply to view the stimuli passively. This of course leaves the processes subjects might engage somewhat unconstrained: They could be encoding the stimuli into memory; they could be thinking about associated facts, episodes, or emotions; or they could be allocating attention to certain aspects of the stimuli. One fMRI study that speaks to this issue in fact found that perceptual processing of facial expressions of fear and anger activated the amygdala, whereas requiring subjects to label the emotion instead resulted in a deactivation of the amygdala; the authors proposed that inhibition and regulation of emotional responses under the labeling condition might account for this finding (Hariri, Bookheimer, & Mazziotta, 2000).

A more specific indication regarding the particular contribution that the amygdala might make to the processing of emotional expressions has come from studies finding rapid activation and habituation of the amygdala and activation in response to stimuli that are presented very briefly. Breiter et al. (1996) found that amygdala activation to fearful faces habituated rapidly on repeated presentations of the face, and Whalen et al. (1998) found amygdala activation to fearful faces that were presented briefly and backward masked so as to render their perception subliminal. These studies provide support for the idea that the amygdala is engaged in relatively rapid and automatic processing of facial expressions.

In contrast to the data from lesion studies, functional imaging has generally pointed to unilateral amygdala participation in processing facial expressions of emotion (see Table 3). Some studies have assigned specific roles to these lateralized activations: J. S. Morris, Ohman, and Dolan (1998) found evidence that the right amygdala is activated more in processing of emotional facial expressions that are presented subliminally, whereas the left amygdala is activated more by those that are presented supraliminally. Wright et al. (2001) found greater habituation to emotional facial expressions in the right than in the left amygdala, suggesting that the right amygdala is involved in dynamic, and the left in sustained, emotional evaluation. However, the conclusion that therefore unilateral amygdala activation is sufficient to recognize emotion from the face is probably spurious for several reasons. As mentioned above, it is not clear which among several possible processes triggered by seeing the face are reflected in the amygdala activation, and such activation may have little to do with actual recognition of the emotion because this is usually not required of subjects in the studies. Another important point derives from the statistical treatment of the data obtained in activation studies: The fact that one amygdala rather than both happen to achieve statistical significance does not

TABLE 3:Studies of Facial Emotion Processing Using Functional Imaging That Have Found Amygdala Activation

Functional Imaging Study	Stimuli	Key Finding
Iidaka et al. (In press)	Gender discrimination of emotional faces	Activation in left amygdala to expressions of fear declined with age
J. S. Morris, de Gelder, Weiskrantz, & Dolan (2001)	Emotional faces presented to blind hemifield	Correlated activation in amygdala, thalamus, and superior colliculus to unseen faces of fear
J. S. Morris, Friston, et al. (1998)	Gender discrimination of emotional faces	Left amygdala activation to faces of fear predicted activity in visual cortices
J. S. Morris, Friston, & Dolan (1997)	Fear-conditioned facial expressions	Correlated activity in right amygdala, pulvinar, and basal forebrain
J. S. Morris et al. (1996)	Morphs of fearful and happy faces	Left amygdala activation correlated with degree of fear shown in the face
J. S. Morris, Ohman, & Dolan (1998)	Fear-conditioned facial expressions	Fear-conditioned angry faces activated the right or left amygdala when shown subliminally or supraliminally, respectively
J. S. Morris, Ohman, & Dolan (1999)	Fear-conditioned facial expressions	Right amygdala increased functional connectivity with pulvinar and superior colliculus to unseen stimuli
Breiter et al. (1996)	Neutral, fearful, and happy faces	Amygdala was activated by fear and, to a lesser extent, happy faces but habituated rapidly
Schneider et al. (1997)	Sad and happy faces used to induce mood	Left amygdala activated by sad faces and, to some extent, by happy faces
Schneider, Gur, Gur, & Muenz (1994)	Sad and happy faces used to induce mood	Left amygdala activated by sad faces
Schneider, Habel, Kessler, Salloum, & Posse (2000)	Sad and happy faces used to induce mood	Left amygdala activated by sad faces in men but not in women
Phillips, Bullmore, et al. (1997)	Happy, sad, and neutral faces	Right basal ganglia activated by sad faces
Phillips et al. (2001)	Fearful and neutral faces	Right amygdala response habituated to fear, and potentiated to neutral, more rapidly than in left amygdala
Phillips et al. (1998)	Fearful, disgusted, and neutral faces	Amygdala activated by fear, insula and basal ganglia by disgust, and STG by both
Phillips, Young, et al. (1997)	Fearful, disgusted, and neutral faces	Amygdala activated by fear, insula and basal ganglia by disgust
Whalen et al. (1997)	Fearful and happy faces masked by neutral faces	Amygdala and BNST activated by subliminally presented fear faces
Whalen et al. (1998)	Fearful and happy faces masked by neutral faces	Amygdala activated by subliminal fear faces
Blair, Morris, Frith, Perrett, & Dolan (1999)	Gender discrimination of morphs of sad and angry faces	Increasing sadness correlated with activation in left amygdala and right temporal pole, and increasing anger correlated with orbitofrontal and anterior cingulate
Hariri, Bookheimer, & Mazziotta (2000)	Perceptual or recognition tasks on emotional faces	Fear and anger activated bilateral amygdala in the perceptual but not the recognition task
Critchley, Daly, Phillips, et al. (2000)	Rapid presentation of happy and angry faces	Amygdala activation in a gender discrimination (implicit) task but not a labeling (explicit) task
Wright et al. (2001)	Fearful and happy faces	Rapid habituation in right amygdala, and larger response to happy than to fearful faces in left amygdala
Killgore, Oki, & Yurgelun-Todd (2001)	Fearful faces	Females, but not males, showed an age-dependent shift in activation from left amygdala to left frontal
Thomas et al. (2001)	Happy and fearful faces	Adults showed left amygdala activation to faces of fear, 12-year-olds did not; 12-year-old males showed habituation to faces of fear
Vuilleumier, Armony, Driver, & Dolan (2001)	Fear faces	Attentional modulation to fear faces in fusiform gyrus but not in left amygdala
Rauch et al. (2000)	Masked fearful and happy faces	Exaggerated amygdala response in patients with post-traumatic stress disorder
Baird et al. (1999)	Sad facial expressions	Facial expressions activated amygdala in 12- to 17-year-old adolescents
Critchley, Daly, Bullmore, et al. (2000)	Explicit and implicit tasks for faces (as above?)	Autistics fail to activate amygdala in the implicit task and FFA in the explicit task
Kawashima et al. (1999)	Direct and indirect eye gaze from the face	Whereas left amygdala activated under both conditions, the right activated more during direct than indirect gaze

NOTE: STG = superior temporal gyrus; BNST = bed nucleus of the stria terminalis; FFA = fusiform face area.

mean that one amygdala was significantly more activated than the other amygdala; the latter statement would require a direct contrast between activation in one versus the other amygdala, but this is typically not calculated in the studies (cf. Davidson & Irwin, 1999, for a discussion of this very issue). It seems likely that both amygdalae are engaged in the majority of functional imaging studies but that one may be somewhat more activated than the other to a degree sufficient for crossing a statistical threshold.

11.3 TEMPORAL ASPECTS OF AMYGDALA PROCESSING

Whereas lesion and functional imaging studies have investigated primarily the spatial aspects of emotion recognition, it is also of interest to consider at what point in time the amygdala might participate in such recognition. As mentioned earlier, it is fallacious to draw an anatomical separation, independent of a temporal separation, between perception and recognition: Even early visual cortices are in a position to participate in high-level recognition via feedback connections from more anterior temporal cortex as well as from amygdala and frontal cortex. This idea is supported both by behavioral and by physiological findings: For instance, perception of visually degraded or ambiguous images is influenced by prior recognition of the same images (Dolan et al., 1997), and activity in V1 can be driven entirely via top-down influences from V2 (Mignard & Malpeli, 1991).

In regard to the amygdala, studies using MEG (Ioannides, Liu, Kwapien, Drozdz, & Streit, 2000) and fMRI (J. S. Morris, Friston, et al., 1998) have found a correlation between activation in the amygdala and in occipitotemporal visual cortices in response to facial expressions of emotion, consistent with a top-down neuromodulatory role for the amygdala. A recent lesion study showed that patients with amygdala damage are impaired in the attentional modulation of rapid serial presentation of visual stimuli on the basis of the emotional significance of the stimuli: Specifically, emotionally salient words modulated the "attentional blink" in normal subjects but not in a subject with bilateral amygdala lesions (A. K. Anderson & Phelps, 2001).

One might thus envision a first, feed-forward sweep of information processing proceeding along occipital and temporal neocortices that extracts perceptual information from faces and that, by around 100 ms in humans, has coarsely categorized the stimulus as expressing an emotion or not, on the basis of the structural properties of the image. Amygdala responses to emotional facial expressions ensue shortly thereafter (at around 120 ms) (Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994), show differential effects as a function of emotion category at about 150 ms (Liu, Ioannides, & Streit, 1999),

and might be correlates of relatively automatic, implicit categorization of facial emotion (Critchley, Daly, Phillips, et al., 2000). As discussed above, some of this fast, initial processing within the amygdala could rely also on the amygdala's connections with subcortical structures, a component whose contribution is unmasked in situations where conscious perception of the stimulus is prevented (J. S. Morris et al., 1999, 2001). It should also be noted that most studies that have provided data regarding processing in the amygdala at millisecond resolution cannot distinguish between activity within the amygdala and activity in adjacent cortex because techniques such as EEG and MEG lack the spatial resolution to do so.

Subsequent to such bottom-up processing, the amygdala could participate in the processes whereby we recognize the emotion from the face in at least three distinct ways: (a) The amygdala could modulate perceptual representations via feedback. A possible role for structures such as the amygdala in modulating activity in visual cortices is supported by electrophysiological data: Field potentials in human temporal visual cortex are modulated by emotional or social information (Puce et al., 1999), and single neurons in monkey temporal cortex encode information about the emotion shown in the face at a point in time later than they encode information about superordinate categories that simply distinguish the face from nonface objects (Sugase et al., 1999). (b) The amygdala could also trigger associated knowledge via its projections to other regions of neocortex and to the hippocampal formation. (c) The amygdala could participate in triggering an emotional response in the subject that permits reconstruction of conceptual knowledge via simulation of the emotional state observed in the face stimulus. These three mechanisms correspond to the ones discussed previously under Sections 4 to 6.

12. The Orbitofrontal Cortex

An additional key structure in emotion processing, with which the amygdala is intimately connected (Amaral et al., 1992), is the orbitofrontal cortex. Experiments in animals have shown that amygdala and orbitofrontal cortex both participate in processing the rewarding or punishing contingencies of stimuli, and these structures have been shown to operate as two components of a system in disconnection studies (Baxter, Parker, Lindner, Izquierdo, & Murray, 2000; Gaffan, Murray, & Fabre-Thorpe, 1993). Prefrontal and temporal cortices have broadly been shown to have an intimate reciprocal connectivity necessary for normal processing of visual stimuli and the knowledge previously associated with them (Fuster, Bauer, & Jervey, 1985; Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999), and there is recent evidence that the prefrontal cortex

can respond very rapidly to faces and facial expressions (Kawasaki et al., 2001; Marinkovic, Trebon, Chauvel, & Halgren, 2000). The extensive connections between temporal visual regions and prefrontal cortex (Seltzer & Pandya, 1989) provide for an effective source of perceptual input to orbitofrontal cortex and also make it plausible that orbitofrontal cortex could play a role in recognizing facial emotion via direct modulation of activity in temporal cortex via feedback, as outlined above for the amygdala. Building on the close anatomical and functional relationship between amygdala and orbitofrontal cortex, Emery and Amaral (1999) proposed that the prefrontal cortex may provide contextual modulation of the amygdala's processing of social facial signals, much as it modulates a large variety of basic emotional responses mediated by the amygdala (e.g., Jackson & Moghaddam, 2001; Kalin, Shelton, Davidson, & Kelley, 2001; Quirk, Russo, Barron, & Lebron, 2000).

The prefrontal cortex has been implicated in self-regulation, response inhibition, and strategy selection during development (see for a review Case, 1992; Diamond, 1990; Schore, 1994), findings that are broadly in keeping with the striking pattern of cortical development in this region, which shows an early spurt around 3 years of age (Thompson et al., 2000) followed by a surprisingly late maturation subsequent to adolescence (Sowell, Thompson, Holmes, Jernigan, & Toga, 1999), as well as with the consequences of developmental damage to this structure (S. W. Anderson, Bechara, Damasio, Tranel, & Damasio, 1999; Eslinger, Grattan, Damasio, & Damasio, 1992). There is preliminary evidence of a developmental redistribution of processing within prefrontal cortex and amygdala: Killgore, Oki, and Yurgelun-Todd (2001) found that in females, there was an increase with age in the activation of prefrontal cortex relative to amygdala when subjects were shown facial expressions of fear. The authors proposed a shift in cerebral functions during adolescence from subcortical structures to prefrontal cortex, perhaps implementing the development of greater self-control over emotional behavior.

In terms of social behavior, the prefrontal cortex, and in particular its orbital region, has been linked to the regulation of interpersonal relationships, social cooperativity, moral behavior, and social aggression (see for reviews A. R. Damasio, 1994; Davidson, Putnam, & Larson, 2000; Schore, 1994). Its role here has been stressed particularly in the context of social development and its pathologies. Developmental psychopathy, for example, has been associated with morphological abnormalities of the prefrontal cortex (e.g., Raine, Lencz, Bihrle, LaCasse, & Colletti, 2000). Although the contribution of the ability to recognize facial expressions in this context will no doubt be complex, Blair (1995) proposed that recognizing facial displays of submission

(of which fearful expressions may be an instance) normally triggers an inhibition of aggressive behavior and that such inhibition depends on the integrity of the orbitofrontal cortex; dysfunction in this system might thus help explain why psychopaths show abnormal aggressive behavior toward other individuals even when confronted with submissive displays.

Although some studies have linked impairments in recognizing facial emotion to the prefrontal cortex broadly (Kolb & Taylor, 2000), most of the evidence points to those sectors of the prefrontal cortex connected with amygdala and other structures that regulate emotion and autonomic function: principally ventral and medial sectors (Öngür & Price, 2000). A study by Hornak, Rolls, and Wade (1996) first explicitly demonstrated impaired recognition of emotion from facial expressions, and from the voice, following damage to orbitofrontal cortex. Their patients had unilateral and bilateral damage to medial and lateral aspects of the orbital cortex (right unilateral damage was much more frequently associated with impaired emotion recognition than was left unilateral damage). In apparent discrepancy with this study, other lesion studies failed to find similar impairments (Adolphs et al., 1994, 1995, 2000; Adolphs, Tranel, & Damasio, in press-b); however, the latter studies did not directly investigate the orbitofrontal cortex and thus had relatively small numbers of subjects with damage in that region. Moreover, whereas Hornak et al. used a labeling task, the studies by Adolphs et al. used a rating task. These findings from a lesion study (Hornak et al., 1996) may be related also to the activation of left ventrolateral prefrontal cortex in a PET study, in which subjects had to hold in mind a mental image of a happy face (Dolan et al., 1996), and to activation in right orbitofrontal cortex in an fMRI study when comparing presentation of fearful to neutral faces (Vuilleumier et al., 2001). Also of interest, Hornak et al. reported that subjects' experience of certain emotions, notably fear, decreased considerably following their lesion, supportive of the idea that the orbitofrontal cortex may participate in both experience and recognition of emotion, possibly with a primary role in the former that contributes to the latter (see below).

Other data implicating regions of prefrontal cortex in emotion recognition are provided by a recent study that used TMS to transiently disrupt processing within medial prefrontal cortex (Harmer, Thilo, Rothwell, & Goodwin, 2001). Subjects were asked to match to labels faint morphs of emotional facial expressions. Upon TMS, subjects showed significantly longer reaction times on this task in response to morphs of angry facial expressions but not in response to happy facial expressions, indicating a role for the medial prefrontal cortex in recognition of angry faces. Whereas some functional imag-

ing studies have reported broader activations to multiple emotional expressions in frontal cortex (George et al., 1993), a more specific role for prefrontal cortex in the recognition of anger is also supported by a recent PET study, which found increased activation in orbitofrontal and anterior cingulate cortex when subjects were shown facial expressions of anger but not of sadness (Blair et al., 1999). The converging evidence for orbitofrontal and anterior cingulate cortices in processing fear and anger fits with the fact that these two emotions involve the highest autonomic arousal, a function regulated in part by these regions of prefrontal cortex (Öngür & Price, 2000).

Some intriguing data come from field potential and single-unit recordings in two patients who had depth electrodes implanted for the purpose of monitoring seizures. Both patients had depth electrodes in right prefrontal cortex. In one patient, field potentials first showed selectivity for faces over objects near the right inferior temporal sulcus around 120 ms, followed by selectivity in right inferior frontal gyrus around 150 ms (a selectivity that became statistically significant only later, near 180 ms) (Marinkovic et al., 2000). Unfortunately, responses to emotional facial expressions were not assessed in this study; however, behavioral performance in labeling facial expressions of emotion was assessed in the same patient after surgical resection of right prefrontal cortex and revealed a severe impairment that was relatively selective for expressions of fear (Marinkovic et al., 2000). In another patient, single-unit responses were obtained in right ventromedial prefrontal cortex to presentation of facial expressions of fear (Kawasaki et al., 2001); although first signs of neuronal discrimination between fearful and happy expressions appeared around 120 ms, this discrimination only became significant at 160 ms (Kawasaki et al., 2001; unpublished observations). Single-neuron responses to faces have also been recorded in various sectors of prefrontal cortex in the monkey, including ventromedial and ventrolateral regions (O Scalaidhe, Wilson, & Goldman-Rakic, 1997).

Overall, there is clear evidence for some regions in prefrontal cortex in processing emotional facial expressions, but the detailed anatomy and the details of the emotion categories remain to be specified. The studies to date point to a relatively disproportionate role for medial and ventral sectors in processing highly arousing emotions, such as fear and anger, and further suggest that this function may be lateralized toward the right hemisphere. There is also the indication that impairments in recognizing emotions in others goes hand in hand with impairments in feeling emotions in the patients themselves, additional evidence that the recognition and experience of emotion are closely related

and, in principle, consistent with the idea that the orbitofrontal cortex participates in emotion recognition via triggering an emotional response in the observer, as proposed for the amygdala above. Taken together with the findings on the amygdala, one can make a case that the amygdala subserves mostly rapid, automatic processing of emotional stimuli, whereas the prefrontal cortex modulates such amygdala-mediated processing depending on the context and the task (Emery & Amaral, 1999). This picture is supported both by direct manipulation of these structures in animal studies as well as by recent functional imaging studies in humans. Conditioned physiological changes mediated by the amygdala can be inhibited by direct electrical stimulation of medial prefrontal cortex (Zbrozyna & Westwood, 1991), an effect possibly mediated by a modulatory influence of prefrontal projections onto interneurons in the amygdala that serve to gate sensory inputs to the basolateral amygdala (Rosenkranz & Grace, 2001). As for the imaging studies, as mentioned earlier, several studies have found a reduced activation of the amygdala to facial expressions of emotion when subjects were asked to engage in a cognitively demanding task (e.g., Hariri et al., 2000), and amygdala activation is generally greater when subjects are not explicitly asked to make judgments about the emotion but rather about another attribute such as gender (Critchley, Daly, Phillips, et al., 2000). By contrast, explicit rather than implicit processing of facial emotion activates medial and ventral sectors of prefrontal cortex (Nakamura et al., 1999; Narumoto et al., 2000).

13. Somatosensory-Related Cortices

Recent findings have elucidated the role of specific sectors of cortex that represent somatic/visceral information about body states in the recognition of emotion. It seems likely that these cortices participate in the mechanism outlined in Section 6 above: construction of knowledge via the generation of a simulation.

13.1 THE RIGHT PARIETAL CORTEX

As reviewed in Section 10, there is a large literature linking the cortex in the right hemisphere to processing of emotion, but very few of these studies have examined particular cortical regions more closely. It seems plausible that discrete sectors within the right hemisphere would subserve somewhat different functions in processing emotion.

A study examining the lesion overlaps of subjects who were impaired in recognizing emotion from facial expressions found evidence for an association between impaired emotion recognition and damage in right parietal and right medial occipital cortex (Adolphs et al., 1996), consistent with some other findings from lesion
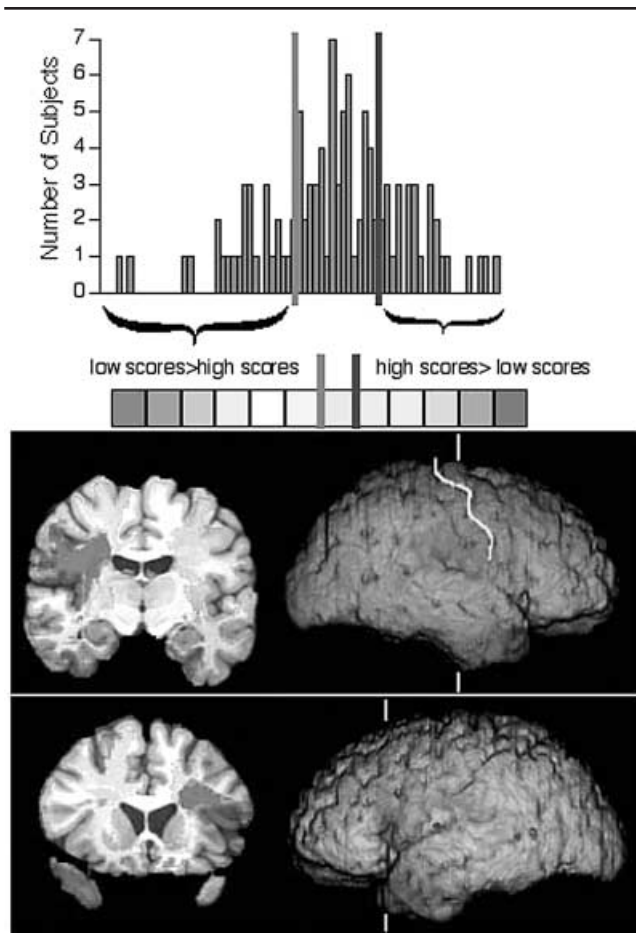
Figure 8: Distribution of Lesions as a Function of Emotion Recognition.
NOTE: Section (a) is a histogram of the performance scores of 108 subjects with focal cerebral lesions. Scores are the Z-transformed correlations between a subject's rating profile and normal ratings; thus, higher values on the x-axis indicate more normal performance, and lower values indicate more impaired performance. For analysis, we divided the subject sample into two groups according to their performance score. In this case, we examined only those 25% of the 108 subjects (27 subjects) with the lowest performance scores (to the left of the red line) and those 25% of the 108 subjects with the highest performance scores (to the right of the blue line). To investigate the possibility that there would be lesions systematically associated with either a high or a low performance, we computed the overlaps of lesions from subjects within each of these two groups, shown in Section (b). Section (b) shows the distribution of lesion overlaps from the most impaired and the least impaired 25% of subjects. Subjects were partitioned as indicated in Section (a). Lesion overlaps from the 27 least impaired subjects were subtracted from those of the 27 most impaired subjects; data from the middle 54 subjects were not used. Color (scale at top) encodes the difference in the density of lesions between those subjects with the lowest scores and those with the highest scores. Thus, red regions correspond to locations at which lesions resulted in impairment more often than not, and blue regions correspond to locations at which lesions resulted in normal performance more often than not. For instance, bright red regions indicate that there were 6 more subjects from the bottom 25% group who had lesions at given location than there were subjects from the top 25% group who had lesions at that location, bright green regions indicate that an equal number of subjects from each of these two groups had lesions at that location, and so on. Coronal cuts are shown on the left, and 3-D reconstructions of brains that are rendered partially transparent are shown on the right, indicating the level of the coronal cuts (white lines) and location of the central sulcus (green). Lesions in right somatosensory cortex (S-I and S-II) as well as right insula and anterior supramarginal gyrus, and in left frontal operculum, were systematically associated with impaired recognition of emotion from facial expressions. Data are from Adolphs, Damasio, Tranel, Cooper, and Damasio (2000).

and functional imaging (Gur, Skolnick, & Gur, 1994) studies. The study by Adolphs et al. (1996) used a sample of moderate size ($N = 37$ lesion subjects) and examined the association between lesion site and task performance only with respect to the overlaps of lesions in two dimensions on fixed medial and lateral views of the cortical surface within each hemisphere. The study found a strong association between impaired recognition of negatively valenced emotions, especially fear, and damage in right ventral occipital cortex, as well as in right ventral and lateral parietal cortex, with an emphasis on posterior supramarginal and superior temporal gyrus.

A subsequent study (Adolphs et al., 2000) used a larger sample size ($N = 108$ subjects) and mapped lesion overlaps in 3-D. This study also used a somewhat different method for partitioning the sample into subjects with different performances for computing lesion overlaps (see Figure 8). Across all lesion locations, subjects performed best in recognizing happy faces and worst in recognizing some faces that expressed negative emotions, including fear, consistent with the prior study (Adolphs et al., 1996). However, when one examined the subjects who had the lowest performance scores on each

emotion, regardless of absolute performance, a consistent pattern emerged for all emotions: Lesions in right ventral parietal cortex were systematically and significantly associated with impaired recognition of emotion (see Figure 8). The sites within which lesions systematically resulted in impaired emotion recognition tended to be located more anteriorly than in the previous study (Adolphs et al., 1996) and focused on ventral S-I and S-II, with a lesser involvement in insula and anterior supramarginal gyrus. The task in both of the above studies used ratings of the intensity of all the emotions expressed by a stimulus and thus assessed subjects' knowledge of all basic emotions for each expression shown.

Given the significant association between lesions in somatosensory cortex and impaired recognition of facial emotion revealed in the study by Adolphs et al. (2000), one would predict that somatic sensation and emotion recognition should be correlated. The study indeed found evidence for such an association: There was a significant rank-order correlation between the degree to which touch perception was impaired and the degree to which subjects were impaired in recognizing facial emotion, but only in subjects with damage in right, not in left,

parietal cortex. The close relationship between the somatosensory system and emotion recognition suggested by these findings is thus in line with what one would expect on the basis of the simulation hypothesis discussed in Section 6.

The rating task used in the studies just reviewed makes demands on at least two distinct abilities: knowledge of the name of the emotion (because the names define the emotion that is rated) and conceptual knowledge other than the name (because this is required to judge the numerical intensity). Additional investigations with other tasks provided some insight into the neural structures that might be shared in common, or that might differ, between these two sets of processes (Adolphs et al., 2000). The labeling task commonly used to investigate emotion recognition (A. W. Young et al., 1995) was found to rely on the same right parietal sectors revealed with the rating task; similarly, subjects' ability to sort pictures of the facial expressions into piles on the basis of their judged similarity of the emotion shown depended on the integrity of right somatosensory cortices. Somatosensory regions thus appear necessary to perform all three tasks—rating the intensity, matching the face to the lexical label, and sorting the faces into categories. In addition to this commonality, the three tasks drew on other neural regions that varied from task to task. Rating the intensity and matching to label also depended on frontal cortex, especially left frontal operculum, as well as on right temporal cortex, consistent with the likely involvement of these two regions in naming emotions. Sorting the faces into categories, by contrast, depended primarily on somatosensory regions in the right hemisphere, especially the insula. These findings using several different tasks thus indicate that lesions in frontal operculum or in right temporal lobe may impair recognition of facial emotion by interfering primarily with lexical processing related to the emotion, whereas lesions in right somatosensory-related cortices including the insula may impair recognition of facial emotion by interfering with simulation processes that can generate conceptual knowledge related to the emotion independent of language.

13.2 THE INSULAR CORTEX

If primary and secondary somatosensory cortices play a role in the recognition of facial emotion in virtue of their ability to help construct a somatosensory image of the body state associated with an emotion, one would predict that other somatosensory cortices could be drawn on as well. The insular cortex, a visceral somatosensory cortex that has direct connections with the amygdala and that participates in regulating autonomic tone, would be a good candidate in this regard. Although insular cortex was also implicated in the study

by Adolphs et al. (2000) discussed in the above section, a more specific role has been elucidated by recent functional imaging and lesion studies.

Functional imaging studies first showed that insular cortex was activated relatively selectively by facial expressions of disgust, as opposed to facial expressions of other emotions such as fear (Phillips et al., 1998; Phillips, Young, et al., 1997; Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998). Those studies have now been complemented by lesion studies: A patient with damage to left insula and basal ganglia showed pronounced impairments both in the ability to recognize facial expressions of disgust as well as in the ability to experience the emotion himself (Calder, Keane, Manes, Antoun, & Young, 2000), and another patient with bilateral damage to insula in addition to extensive temporal lobe damage was severely impaired in the ability to recognize and experience disgust from all types of stimuli (Adolphs et al., in press-a). In addition to the insula, there is good evidence that recognition of disgust requires the integrity of the basal ganglia (see below), as well as the integrity of other somatosensory-related cortices in the right hemisphere (Adolphs et al., 2000), indicating a distributed neural network for processing this emotion. The above findings again emphasize the close connection between the experience and the recognition of emotions and provide further support for the idea that the latter may depend in part on the former.

13.3 SOMATOSENSORY PROCESSING AND SIMULATION

The above experimental findings thus provide considerable support for the idea that we obtain knowledge about other people's emotions by simulating components of their presumed body state, as discussed in detail in Section 6 (it seems likely that such simulation generally occurs below the level of conscious awareness and is certainly not usually driven volitionally). It remains somewhat unclear how precisely the findings on action perception reviewed in Section 6 might relate to emotion recognition. Emotional facial expressions can, of course, be thought of as facial actions and as such would be expected to draw on some of the same simulation mechanisms found for action perception in general. But if we begin to spell this out in detail, unanswered questions remain: Does the recognition of an emotion from a facial expression rely on the internal generation of a motor or somatosensory representation of the face alone? or Does it rely on the generation of a more comprehensive representation that simulates the entire state of the body associated with the emotion shown by the face? Both would involve somatosensory-related structures, but to differing extents. It seems plausible that the depth of detail to which the body state associated with an

emotion needs to be simulated might depend on the demands made by the recognition task: Coarser, easier tasks requiring recognition only at a superordinate level may engage no simulation or only a very rudimentary simulation of a few components of the emotional body state, whereas fine-grained, difficult tasks requiring recognition at subordinate levels may engage the subject in a much more comprehensive reconstruction of an emotional body state, perhaps requiring topographic body-state representation in primary somatosensory cortex. This idea would be consistent with the general use of imagery in obtaining coarse or fine-grained information, for example, the finding that retrieving knowledge of the shape of your house may not require visual cortices at all, that retrieving knowledge of the number of windows in your house may draw on visual imagery in higher order visual cortices, and that detailed knowledge of the exact positions and shapes of the windows might require a visual image that draws on all visual cortices down to topographic representations in striate cortex (cf. Kosslyn et al., 1999, for discussion).

Although our emphasis has been on the role of somatosensory cortices, there are of course other processes involved in the simulation. Most notably, we might expect motor and/or premotor cortices to be an essential intermediate: Perception of the face could be linked to motor representations of the commands necessary to produce such an expression, which could in turn trigger a somatosensory representation of what such an expression would feel like if produced in the subject. Given the lack of evidence for an essential role for motor/premotor cortices in recognizing emotion, it might be that the somatosensory representations can be triggered directly from the percept without the mediation of motor structures. Alternatively, it may be that basal ganglia or nuclei in brainstem tegmentum, rather than motor cortices, are a critical route for generating motor responses to viewing facial emotions (see below). In either case, to trigger an image of the somatosensory state that is entirely centrally generated, or to actually trigger components of an emotional bodily response that could in turn be perceived and thus represented in somatosensory cortices, we would require structures that link perception of the stimulus (the facial expression seen) to a somatic response or directly to the representation thereof. We have already encountered precisely such structures: the amygdala and the orbitofrontal cortex. Both these structures mediate emotional responses to a wide variety of emotional stimuli and are thus well positioned also to trigger the components of an emotional response (or central image thereof) that could be used in obtaining knowledge via simulation. The different strategies for recognizing facial emotions that we outlined in Sections 4 to 6 thus need not map onto different neural structures; rather, a partly overlapping network of structures is likely to participate in implementing each of them.

14. The Basal Ganglia

There is a long history of studies showing that the basal ganglia, especially on the right, participate in the recognition of facial emotion. Some studies have reported that lesions to the basal ganglia in either hemisphere can contribute to impaired recognition of emotion from a variety of stimuli (Cancelliere & Kertesz, 1990). Functional imaging studies have reported differential activation in the right basal ganglia when comparing the perception of happy faces to fearful faces (J. S. Morris et al., 1996) or when comparing sad faces to neutral faces (Phillips, Bullmore, et al., 1997). Both lesion and functional imaging studies suffer from their relatively poor spatial resolution in investigations of the basal ganglia, which consist of many different nuclei and white matter tracts in close spatial proximity. Some additional insights are offered by diseases that preferentially damage certain sectors of the basal ganglia.

Three diseases that involve the basal ganglia have been investigated in some detail regarding recognition of facial emotion: obsessive-compulsive disorder, Parkinson's disease, and Huntington's disease. Subjects with obsessive-compulsive disorder, who experience abnormal feelings of anxiety and disgust, are impaired disproportionately in the recognition of facial expressions of disgust (Sprengelmeyer et al., 1997), and one of the neural correlates of this impairment may be the dysfunction of sectors of the basal ganglia affected in this disease. The evidence regarding Parkinson's disease is less decisive: Whereas some studies have reported impaired recognition of facial emotion in this disease (Blonder, Gur, & Gur, 1989; Breitenstein, Daum, Ackerman, & Larbig, 1996; Jacobs, Shuren, Bowers, & Heilman, 1995), others have failed to find any such impairment (Adolphs, Schul, & Tranel, 1997). The best evidence comes from Huntington's disease, which results in impairments in recognizing facial expressions (Jacobs, Shuren, & Heilman, 1995) that appear to be disproportionately severe for disgust (Sprengelmeyer et al., 1996). Especially intriguing is the finding that subjects who carry the gene for Huntington's disease show impairments in recognition of disgust prior to the onset of any other symptoms (Gray, Young, Barker, Curtis, & Gibson, 1997), possibly making the recognition impairment one of the earliest phenotypic markers of the disease. As with other evidence accrued in the discussions above, the involvement of the basal ganglia in emotion recognition points to the close relationships between emotional experi-

ence, motor production of facial expressions of emotion, and recognition of the emotion. It is of interest to note here that electrical stimulation of the basal ganglia (probably primarily in the substantia nigra) in a neurosurgical patient resulted in the acute and intense experience of emotion (a feeling of sadness, in this case) as well as of its expression in the face (Dejjani et. al, 1999) (the recognition of emotion was not examined in this study).

The basal ganglia are of course intimately connected with several of the other structures discussed in the preceding sections. Both dorsal (Han, McMahan, Holland, & Gallagher, 1997) and ventral sectors of the basal ganglia (Everitt & Robbins, 1992) function in concert with the amygdala, and there are topographic connections between basal ganglia and the prefrontal cortex (Berendse, Galis-de Graaf, & Groenewegen, 1992), notably including the orbitofrontal cortex (Eblen & Graybiel, 1995). The close functional relationship between amygdala, orbitofrontal cortex, and the ventral striatum has been explored in regard to decision making, reward, and drug addiction (Everitt et al., 1999; Everitt & Robbins, 1992; Schultz, Tremblay, & Hollerman, 2000). It seems likely that these structures should similarly be thought of as components of an integrated system when it comes to processing social information in general (Brothers, 1990) and facial emotion in particular. An open question that remains is the extent to which such a system might be specialized for processing complex social stimuli, such as facial expressions; possibly, its function is better construed in more basic terms, as linking perception of stimuli with their punishing or rewarding contingencies, a primary mechanism that would also be utilized when we recognize facial emotion (cf. Rolls, 1999, for such a scheme). On the other hand, the diversity of different categories of social knowledge to which faces need to be linked seems to surpass the complexity of nonsocial processing. An alternate scheme might envision some structures, such as perhaps amygdala and ventral striatum, in implementing more basic reward/punishment associations and other structures, notably prefrontal cortex, in implementing a further refinement that permits differentiation among different social stimuli and within different social contexts (Emery & Amaral, 1999). Such a hierarchical arrangement might also be the most consistent with both evolutionary and developmental findings on facial emotion recognition.

15. The Issue of Task Difficulty

When reporting impairments that are specific to certain domains, it is important to ensure that the specificity observed could not be attributed to other factors, often lumped simply under the term *task difficulty*. One might imagine the following factors that could give rise to relatively selective impairments in recognizing certain emotions from facial expressions: (a) The expressions whose recognition is impaired are more difficult to process at a perceptual level; in this case, we would expect that certain emotional expressions simply might be more difficult to discriminate than others, perhaps because they are configurally more ambiguous, are more complex, or make special demands on perceptual systems in some other way. (b) Recognition of certain expressions might be impaired not because of perceptual factors but because different demands are made on the retrieval of knowledge. One possibility is that the categorization of certain expressions requires the subject to classify those expressions at a more subordinate level than other expressions; in this case, we might find that subjects can categorize expressions at superordinate levels (e.g., happy versus unhappy) but not at more subordinate levels (e.g., a fearful surprise versus a happy surprise).

A recent comprehensive study by Rapcsak and colleagues (2000) used a labeling task to investigate the issue of task difficulty in a large sample of brain-damaged subjects, as well as in normal controls. The study found that recognition of fear was less accurate than recognition of other emotions even in normal subjects and that when this general difficulty is accounted for in the analysis, subjects with damage to amygdala or to right parietal cortex are in fact not impaired disproportionately in recognizing fear. Instead, the evidence pointed to an overall, nonspecific impairment in performing the task (that is, a global impairment in recognizing all emotions from facial expressions) in brain-damaged subjects, with no evidence that damage to certain regions resulted in impairments in recognizing certain emotions. This conclusion is at odds with the majority of the studies reviewed in the preceding sections. However, there are several further issues to consider in interpreting the data.

First, it is important to note that it is not the case that fear is more difficult to discriminate from a neutral expression than are any of the other emotions. Nor is it the case that fear is more difficult to discriminate from facial expressions of other basic emotions, when subjects are only required to make same/different judgments. Unpublished data from our laboratory using morphed facial expressions as stimuli demonstrate that fear does not stand out as the most perceptually difficult to discriminate as an emotion. Actually fear, together with surprise and happiness, is quite easy to discriminate from neutral, whereas sadness and especially disgust are more difficult to discriminate. This is what one would expect because happiness, surprise, and fear are the most

configurally distant from the configuration of a neutral face (e.g., happiness and fear have very large changes in the configuration of the mouth, with open mouth and teeth showing). Possibility (a) above is thus rather implausible.

However, fear does indeed turn out to be relatively more ambiguous to match to a label when offered a choice between the labels for the six basic emotions; critically, this ambiguity depends on there being a choice between the labels fear and surprise. The problem with this particular forced-choice task is that it does not control for the different confusability between the six choices: Not all choices are equally distinct. This is a consequence in part of the different levels of categorization required of subjects in the labeling task. One could think of happiness as a superordinate category and all the basic negatively valenced emotions as more subordinate categories of the superordinate category unhappy, as indicated also in Figure 4. This may explain in part why impairments are observed more commonly on negatively valenced emotions than on happiness: The negatively valenced emotions are more subordinate and more confusable with one another than with happiness. The errors typically made by brain-damaged subjects when they fail to recognize a negatively valenced emotion correctly are to mistake it for another negatively valenced emotion but not for happiness. It is conceivable that fear and cheerful surprise are two instances of an even more subordinate category, in the sense that they could be considered categories of a general surprise (which could be a positively or negatively valenced surprise). As Rapcsak et al. (2000) pointed out in their article, if the confusion between fear and surprise is scored as incorrect, one obtains an erroneous performance score based on the mistake of assuming that all six choices are equally discriminable, when in fact they are not. One would very likely obtain the same pattern of impairment using stories that depict fear, fearful sounds, or any other stimulus depicting fear—it is not the stimuli that are the problem here, it is the task and the analysis used to assess recognition.

There are at least two ways to get around this problem: Either control for the different label confusabilities in how data from this matching task are analyzed or use a different task. Some modifications of the labeling task could use a different array of label options; for instance, modifying the surprise label to read happy surprise would probably increase dramatically the accuracy in labeling expressions of fear, in virtue of eliminating "incorrect" matches to the previously ambiguous surprise label. The rating task described above, which we have generally favored in our studies, also circumvents the problem by asking subjects explicitly to rate both the intensity of fear and of surprise judged to be expressed

by a face (subjects typically give facial expressions of fear high ratings on both emotion labels). With either task, one would want to analyze the data from brain-damaged subjects in relation to the profile of performance given by normal controls, to take into account whatever differential performance normal subjects give across different emotions, rather than using only the normal modal response. Rapcsak et al. (2000) did this by computing accuracy scores in relation to the pattern of normal performance on their task, and we have done so by calculating correlation scores between the ratings given by brain-damaged subjects and by normal subjects in our studies.

A finding that is often used to argue for the specificity of an impairment, and for its link to particular brain structures that are damaged, is the double dissociation—a finding also available in regard to the recognition of emotions from facial expressions (Calder, Lawrence, & Young, 2001). As reviewed above, there are clear cases of subjects (e.g., SM) who are disproportionately impaired in recognition of fear following selective amygdala damage, and there are cases of subjects relatively impaired in recognition of emotions other than fear, such as disgust, following damage to the insula and basal ganglia but not the amygdala (Calder, Keane, Manes, et al., 2000). Similarly, differential activations to different emotional expressions in functional imaging studies have been used to argue for systems specialized to process certain emotions (Blair et al., 1999; J. S. Morris et al., 1996; Phillips et al., 1998; Phillips, Young, et al., 1997; Sprengelmeyer et al., 1998). Of course, these findings do not exclude the likely possibility that there also are brain structures more generally involved in recognition of all emotions from faces, as may be the case for right parietal cortices, nor do they suggest that there would be a specific neural system specialized to recognize each of the basic emotions. Indeed, it would make sense to suppose that fear and disgust are the only two emotions for whose recognition there evolved relatively specialized circuitry, given the ecological relevance and phylogenetic ubiquity of these two emotions.

Unfortunately, the evidence from double dissociations is somewhat less decisive here than the importance usually accorded to it might suggest. In and of itself, finding that one subject performs worst on fear whereas another performs worst on disgust is not particularly unexpected because individual differences in performances will always produce differential profiles of scores across different emotions. Double dissociations only become convincing evidence of neuroanatomical specialization when the performance differences (a) are of large magnitude and (b) cannot be attributed to factors other than the brain damage. These criteria are not fully met in the majority of reports of emotion-specific recog-

nition impairments, which typically report variably worse recognition of negative emotions compared to happiness. The performance in recognizing fear (or disgust) as compared to other emotions is typically less than overwhelmingly different, and one instead sees a broader profile of low performance across several negatively valenced emotions (e.g., Adolphs, Tranel, et al., 1999). Dramatically disproportionate impairments in recognizing a specific emotion (e.g., Adolphs et al., 1995) are the exception rather than the rule.

This more cautious interpretation of differential impairments notwithstanding, it remains the case that certain structures, notably the amygdala and the insula, are good candidates for participation in the recognition of specific emotions (fear and disgust, respectively), because of the weight of the evidence from multiple studies taken together. In the case of the amygdala, at least one subject (Adolphs et al., 1995) does show a rather striking selectivity in the impaired recognition of fear, corroborated by most functional imaging studies and to some extent by lesion studies with other amygdala patients and neatly consistent with a large body of work in both animals and humans that implicates the amygdala in mediating various emotional responses of fear. Whether the category fear carves out best the amygdala's role here, or whether a related category such as threat or danger is a more appropriate concept, remains a separate question.
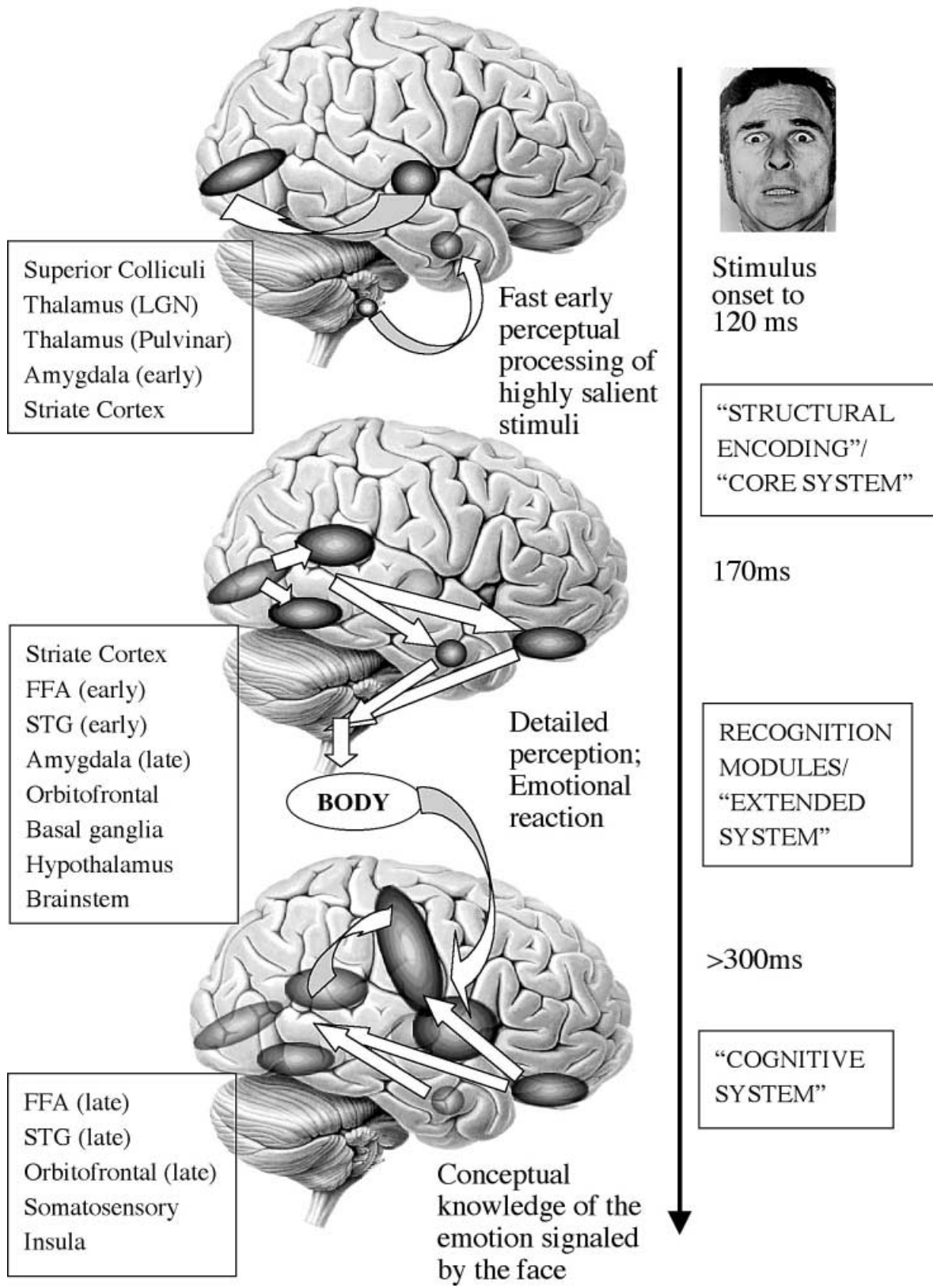
But the issue of task difficulty is by no means resolved. It remains a cause for concern that the two emotional expressions for which there is the clearest evidence of selective impairment, fear and disgust, are also the two expressions whose basic-level categorization is among the most difficult. In the case of fear, this difficulty arises if subjects are asked to distinguish among the categories surprise and fear. Our concept of disgust has a different problem: Metaphorically, disgust has come to be applied not only to unclean and unpalatable stimuli but to a much larger class of stimuli, including people, that one finds disapproving or "distasteful" in this extended sense (Rozin, 1996). The elaborated concept of disgust comes to overlap considerably with the concepts of other negative emotions, notably anger. Some of the difficulties with categorization of fear and disgust can be circumvented by judicious choice of tasks: For categorization of fear, surprise could be omitted as an option; for categorization of disgust, it could be clarified that the sense of disgust pertains to disgusting tastes and smells rather than general disapproval of other people (where the concept disgust then overlaps with the concept anger, leading to confusion between these two categories). Future studies might take into account the structure of emotion categories in the design of tasks.

16. A Model for Recognizing Emotion From Facial Expressions

Three models for processing information about facial emotion are outlined in Figures 1 and 9. The functional model of Bruce and Young (1986) and the neuroanatomical model of Haxby et al. (2000) emphasize separate pathways for processing information about emotion and about identity from the face. Both models begin with early perceptual processes and then, by stages, link such processing to conceptual knowledge. An outline of a model discussed in this review is shown in Figure 9: On the left is a list of some of the candidate structures involved and on the far right a list of the corresponding systems/processes in the models shown in Figure 1. Not all of the processes described below are shown on the figure, nor are all of the component structures. The following sets of processes can be outlined.

Once early visual cortices have provided a coarse processing of some aspects of the visual stimulus, regions more anterior and including visual association cortices would construct more detailed perceptual representations that depend more on processing the configuration of the face. Separate representations are constructed that make explicit information useful for recognizing identity or recognizing emotion. It is likely that regions in both dorsal and ventral visual streams would be engaged: To the extent that there is dynamic information present in the stimulus, middle temporal area, middle superior temporal area, and posterior parietal visual cortices may participate in encoding the structure of the stimulus on the basis of motion signals provided by its constituent features. However, facial structure obtained from visual motion cues would feed into temporal cortices that also receive information about facial structure from static cues. Via all these disparate routes, although probably primarily via V1-V2-V4, posterior temporal cortices and cortex in the fusiform gyrus have constructed a detailed structural representation of the face, by about 170 ms poststimulus onset. Superior temporal gyrus contains representations regarding mouth movement, eye movements, and changes in facial expression. Together, fusiform and superior temporal cortices provide information about the facial expression that can be associated with the emotional and social significance of that expression.

Importantly, there would be feedback influences at multiple temporal scales. Within cortical regions, earlier, predominantly M-cell driven activity will be in a position to modulate via feedback later, predominantly P-cell driven activity; a similar feedback role could be assigned to the amygdala. In fact, for almost any realistic stimulus, there will always be a prior context that can serve to modulate the presently occurring visual input. In thinking through a scheme such as that shown in Figure 9, it is

Superior Colliculi
Thalamus (LGN)
Thalamus (Pulvinar)
Amygdala (early)
Striate Cortex

Fast early perceptual processing of highly salient stimuli

Stimulus onset to 120 ms

"STRUCTURAL ENCODING"/ "CORE SYSTEM"

170ms

Striate Cortex
FFA (early)
STG (early)
Amygdala (late)
Orbitofrontal
Basal ganglia
Hypothalamus
Brainstem

BODY

Detailed perception; Emotional reaction

RECOGNITION MODULES/ "EXTENDED SYSTEM"

>300ms

FFA (late)
STG (late)
Orbitofrontal (late)
Somatosensory
Insula

"COGNITIVE SYSTEM"

Conceptual knowledge of the emotion signaled by the face

thus essential to keep in mind that the same structure (e.g., V1) can participate both in early perceptual and in later recognition-related processing and is likely to do so concurrently.

Processes for the recognition of the emotion from the face draw on sets of structures that may participate in somewhat different functions. Amygdala and orbitofrontal cortices serve to link a perceptual representation of the facial expression to three strategies for producing conceptual knowledge of the emotion: (a) via feedback to temporal and occipital visual cortices to modulate the evolution of the perceptual representation of the face in those regions; this mechanism might contribute especially to fine-tuning the categorization of the facial expression and to the allocation of attention to certain of its features; (b) via connections to diverse cortical regions and hippocampus to trigger knowledge associated with the facial expression; this mechanism might contribute especially to retrieval of conceptual knowledge about the emotion; and (c) via connections

Figure 9: Processing of Emotional Facial Expressions as a Function of Time.
NOTE: LGN = lateral geniculate nucleus; FFA = fusiform face area; STG = superior temporal gyrus. On the left are indicated some of the structures shown in the middle on views of a brain; on the right are indicated some of the processes that are occurring and the processing stages outlined in Figure 1 to which they roughly correspond. The figure begins with the onset of the stimulus, a facial expression of emotion at the top, and progresses through perception to final recognition of the emotion at the bottom. Certain brain structures are preferentially engaged in processing structural information of the stimulus (early perception), whereas others participate more in retrieving conceptual knowledge or linking the perceptual representation to the modulation of other cognitive processes or to the elicitation of physiological states (e.g., an emotional somatic reaction to a stimulus). Attempts to localize the perception/recognition of the stimulus in space or in time have trade-offs: Spatial localization permits us to tie aspects of the processing to particular brain structures but suffers from the fact that the same brain structure participates in different components of processing at different points in time. Temporal localization that treats the brain as a dynamical system has the benefit of describing the evolution of perception and recognition more accurately in time, although this will usually encompass a large set of different structures. A full account will need to describe both the spatial and temporal aspects of processing (something like a movie of brain activation), a description that is becoming possible by combining techniques with high spatial resolution, such as functional magnetic resonance imaging, with techniques with high temporal resolution, such as event-related potentials. Note that the figure omits many structures and connections to provide a schematic overview. See text for a detailed explanation. Initial perception of the face modulates activity in subcortical structures as well as in early visual cortices. The subcortical structures implicated include the superior colliculus and the pulvinar thalamus, structures probably specialized for very fast, automatic, and coarse processing of the stimulus and especially of temporally transient signals in the stimulus, such as the visual motion exhibited by dynamic facial expressions. Information from the pulvinar thalamus in turn feeds into early processing within amygdala. The cortical structures would include V1, V2, and other early visual cortices, via input from the lateral geniculate thalamus. The early visual processing may be relatively specialized to extract information about highly salient stimuli, such as facial expressions of fear or anger, and it may rely in large part on information based on specific features that are detected. These processes would likely be fairly automatic and obligatory.

to motor structures, hypothalamus, and brainstem nuclei, whereby components of an emotional response to the facial expression can be triggered; this mechanism might contribute to the generation of knowledge about another person's emotional state via simulation.

Motor structures, including sectors of the basal ganglia, left frontal operculum, and perhaps right frontal cortices as well, may participate in several ways. Basal ganglia may be involved in generating motor components of an emotional response to the face, a mechanism that could play a role in knowledge retrieval via simulation. Left frontal operculum could, of course, also play a role in the same way, but it is also possible that its contribution to recognizing facial emotion is due to its specific role in the production of language. Because the vast majority of tasks used to assess recognition of facial emotion rely on language (and even those that do not explicitly do so may draw on language covertly), it may be that left frontal regions are important here only derivatively because of their importance to language. A third possibility is that left frontal operculum serves a broader role related to simulating actions observed in others and facilitating communication between individuals, a role that might encompass both aspects of language-based and of emotional expression–based social communication (see Rizzolatti & Arbib, 1998, for such a conjecture).

Somatosensory-related cortices in the right hemisphere in turn participate in representing aspects of the body state that define an emotion. Such representations would automatically come into play whenever components of an emotional response occur, as indicated above. They would come into play prominently when there is a substantial emotional reaction to the facial expression in the observer, and they could be utilized to obtain knowledge about the emotion via simulation. It is also likely that such somatosensory representations could be generated without the actual production of an emotional response, directly via connections from higher order visual association cortices, triggered by motor structures such as the basal ganglia or triggered by complex and perhaps volitional strategies in a top-down manner, for instance, from prefrontal cortex.

There is no question that structures in addition to the ones mentioned in this review will play a role in emotion recognition: For instance, nothing has been said regarding the role of brainstem nuclei or of cerebellum in emotion recognition, although these structures likely make some contribution because it is known that they contribute to other aspects of emotion processing. There is also no question that different structures will participate at different points in time in the various processes that permit recognition. One of the main conclusions of this review has been that emotion recognition is not monolithic but consists of a rather diverse array of strategies

and processes, which are drawn on differentially depending on the precise circumstances of an experimental task.

FUTURE DIRECTIONS

Future directions in research on the psychological and neurological bases of facial emotion recognition will build on the findings to date, extend them to broader issues, and attempt to resolve some of the current discrepancies and difficulties. Of special value will be attempts to extend the current findings, almost all of which come from adult humans, to developmental and comparative approaches; studies in infants and in non-human primates will provide valuable insights into the ontogenetic and phylogenetic background of emotion recognition. How do infants see faces, how do they acquire the social knowledge of what the face signals, and how do they learn to express emotions on their own faces? What emotions can other animals show on their faces; for that matter, what emotional states can other animals have at all? These issues will also relate closely to the investigation of facial expressions that signal emotions other than the basic ones. Very little is known regarding how we signal social/moral emotions (such as shame or pride) via the face, and next to nothing is known regarding the neural underpinnings of the recognition of these emotions.

Another important avenue for further studies is the development of stimuli and of tasks with more ecological validity. For instance, nearly all studies to date have used static images of facial expressions, whereas one would want to use dynamic facial expressions and perhaps also extend the presentation to viewing in specific social contexts that include other social information. After all, we do not make judgments about basic emotions shown in pictures of single faces in real life; we make complex social judgments about fleeting, dynamic facial signals encountered together with body posture and voice stimuli in a certain situation with a social background. Needless to say, approaches to the full complexity of real-life emotion recognition need to tackle this issue in small stages. Eventually, one would like to obtain an account that incorporates not only findings from multiple species and from multiple emotions but also those that integrate recognition of emotion from the face, the voice, body posture, and language.

Although there is much to be said for having diverse stimuli and tasks, there is also a lot to be said for having a uniform set of stimuli and tasks that could be used across different studies. This seems especially valuable given the burgeoning functional imaging literature on facial affect, where quite different tasks often make comparisons between different studies problematic. An ideal situation would be a set of stimuli and tasks that could be used in functional imaging and lesion studies with adult humans and that might have straightforward analogues that could also be administered to infants and nonhuman primates. Important components of such tasks would be attention to issues of differential difficulty in processing stimuli that signal different emotions, using some of the analytical approaches outlined earlier (see Section 15).

No less important than these issues of basic research are the ramifications for clinical diagnosis and therapy. Several neuropsychiatric disorders, especially autism, phobias, and depression, also involve alterations in the ability to perceive, recognize, express, or experience emotions. Some such alterations of course fall within the normal variability, and an additional intriguing issue is the investigation of individual differences in the ability to express or to recognize facial emotions and the possible correlations of such differences with personality and with social functioning. As with other domains of cognitive neuroscience, the exploration of facial emotion recognition is bringing together psychologists, psychiatrists, neurobiologists, computer scientists, and philosophers. One of the main challenges is much more practical than any of those mentioned above: the difficulty of integrating knowledge from such disparate fields into a unified framework. It is my hope that the present review has at least sketched some directions in which such an integration might proceed.

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