

# 73 Processing of Emotional and Social Information by the Human Amygdala

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**ABSTRACT** Studies in animals have implicated the amygdala in social and emotional information processing. Within the past decade, the role of this structure has also been investigated in humans, using a variety of techniques. Perhaps best explored is its function in social judgments about facial expressions, the focus of this review. Lesion studies, electrophysiology, and functional imaging have all been brought to bear on this topic, and these approaches have begun to sketch the processes whereby the amygdala links perceptual representations of emotional sensory stimuli with the elicitation of behavioral and cognitive responses. These responses, in turn, both guide social behavior and generate social knowledge. The chapter closes with a preview of future directions that this line of research suggests.

## *A framework for the neurobiology of emotion and social cognition*

In less than a decade, the study of emotion has morphed from a neglected topic to one of the hot frontiers of cognitive neuroscience. This reversal had several causes: the realization that emotion dysfunction is a hallmark of essentially all psychiatric diseases, as well as a highly salient component of healthy function; the development of new techniques, notably functional imaging, that permit an unprecedented examination of its neural substrates; and the development of theoretical frameworks within which new hypotheses can be tested and data can be interpreted. Most important, these frameworks have sought to integrate emotion into the architecture of cognition in general, rescuing the field from its prior isolation. A key contribution to the rapid expansion of the field have been data from lesion studies, because they allow researchers to assign causal roles to neural structures. Lesion studies have demonstrated dissociations between perception and emotion, recognition and emotion, emotion and feeling, and emotion and reason, and thus have outlined the neural systems that process emotionally salient stimuli,

link them to emotional responses, modulate cognition by emotion, and generate emotional feelings.

Despite the deluge of recent data, our understanding of emotion is confused. Different investigators use terms with different meanings, and researchers in different disciplines often find it difficult to understand one another. The reasons for this difficulty are some of the same reasons that make the study of cognition in general difficult, but they are more acute in the study of emotion. They arise from our pretheoretical beliefs about emotions and feelings. Everyone believes that people have emotions, just as they believe that people have thoughts. But when we start taking apart people and investigating the internal mechanisms required for such attributions, we necessarily lose the person we started with. Does it make sense to attribute emotions (or thoughts) to parts of our bodies, including our brains? It probably makes no more sense to attribute an emotion to my stomach, my adrenal glands, or my amygdala than it does to attribute a visual percept to my visual cortices. Processes occurring in these structures are constituents of what makes a whole person have an emotion or a visual percept, but they are not to be confused synecdochically with the organism of which they are a part. Let me reiterate this, as it should be an obvious point. Autonomic responses, neuronal activity in the amygdala or in any other isolated brain region, are never identical with emotions, because emotions depend on a complex, multidimensional pattern of concerted processes occurring in many places at various points in time. What is needed is an account of emotional and social information processing that describes the constituent internal processes and the roles that they play.

What, then, is a starting framework within which we can investigate emotions? It is useful to draw on three different theories of emotion here (there are others that are relevant, but these three serve as a starting point). One theory, in line both with an evolutionary approach to emotion and aspects of appraisal theory, concerns the domain of information that specifies emotion processing. In short, emotions concern, or derive from, information that is of direct

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relevance to the homeostasis and survival of an organism (Darwin, 1872/1965; Frijda, 1986; Damasio, 1994), that is, the significance that the situation has for the organism, both in terms of its immediate impact and in terms of the organism's plans and goals in responding to the situation (Lazarus, 1991). Fear and disgust are obvious examples of such emotions. The notion of homeostasis and survival needs to be extended to the social world to account for social emotions, such as shame, guilt, or embarrassment, that regulate social behavior in groups. Emotions thus pertain to the value of a stimulus or of a behavior—value to the organism's own survival, or to the survival of one's offspring or relatives, or to a larger social group.

This first point, the domain specificity of emotional information, tells us what distinguishes emotion processing from information processing in general, but leaves open two further questions: How broadly should we construe this domain, and how is such specificity implemented? In regard to the first question, the domain includes social and basic emotions, but also states such as pain, hunger, and any other information that has a bearing on survival. Is this too broad? Philosophers worry about such distinctions, but for the present, we as neuroscientists can simply acknowledge that indeed, the processing of emotions should (and, as it turns out, does) share mechanisms in common with the processing of thirst, hunger, pain, sex, and any other category of information that motivates behavior (Panksepp, 1998; Rolls, 1999). In regard to the second question, the implementation of value-laden information, an answer will require information about the perceptual properties of a stimulus to be associated with information about the state of the organism perceiving that stimulus. Such information about the organism could be sensory (somatosensory in a broad sense, meaning information about the impact that the stimulus has on homeostasis) or motor (information about the action plans triggered by the stimulus). This brings us to the remaining two of the three emotion theories.

The first emotion theory, then, acknowledges that emotion processing is domain-specific and relates to the value that a stimulus has for an organism in a broad sense. The second emotion theory of relevance here concerns the cause-and-effect architecture of behavior, bodily states, and central states. Readers will be familiar with the theories of William James, Walter Cannon, and later thinkers that debated the primacy of bodily states (James, 1884; Cannon, 1927). Are we afraid first, and then we run away from the bear, or do we have an emotional bodily response to the bear first, whose perception in turn constitutes our feeling afraid? This debate has been very muddled, for at least two reasons: the failure to distinguish emotions from feelings, and the ubiquitous tendency for a single causal scheme.

It is useful to conceive of emotions as central states that are only dispositionally linked to certain physiological states

of the body, or certain behaviors, or certain feelings of which we are aware. An emotion is thus a neural state (or, better, a collection of processes) that operates in a domain-specific manner on information. However, the mechanism behind assigning value to such information depends on an organism's reactive and proactive response to the stimulus. The proactive component prepares the organism for action, and the reactive component reflects the response to a stimulus. It is the coordinated web of action preparations, stimulus responses, and an organism's internal mapping of these that constitutes a central emotional state. Viewed this way, an emotion is neither cause nor consequence of a physiological response; it emerges in parallel with an organism's interaction with its environment, in parallel with physiological response, and in parallel with feeling. Behavior, physiological response, and feeling all causally affect one another, and none of them in isolation is co-extensive with the emotion, although we certainly use observations of them to infer an emotional state.

The third emotion theory to be considered here is the set of theories concerning appraisal. The issue under debate is the extent to which an emotion (or a social behavior) can ensue automatically and with only a coarse evaluation of a stimulus (Zajonc, 1980), or whether an emotion requires more elaborate cognitive appraisal of the significance that the stimulus has for an organism and of the behaviors appropriate to maximizing an adaptive response (Scherer, 1988; Lazarus, 1991). As with the James–Cannon debate, the answer here is, both. There is good evidence that some stimuli trigger emotional responses very rapidly and in the absence of conscious awareness, but also that elaborate cognitive processing and evaluation play key roles, for instance in emotion regulation. To some extent these components may occur on different temporal scales.

The findings from cognitive neuroscience corroborate the three points made earlier: emotional and social information processing is domain-specific, pertaining to maintenance of homeostasis in a changing and interactive environment; it unfolds in a complex, iterative way over time that involves perception, response, and feeling; and it draws on both relatively fast and coarse perceptual processing and more complex cognitive appraisals. Emotional and social information processing includes multiple perceptual routes, iterative feedback between emotion responses and their representation, and extensive regulation at several levels (Adolphs, 2002; figure 73.1). These multiple perceptual routes result in information processing that is temporally dispersed. The dispersion in time in turn drives emotional responses that also occur on multiple temporal scales: some are rapid and relatively automatic, others require extensive evaluation of the stimulus and are often volitionally modulated. Responses on different time scales interact, as shown clearly in some of the most popular paradigms for studying

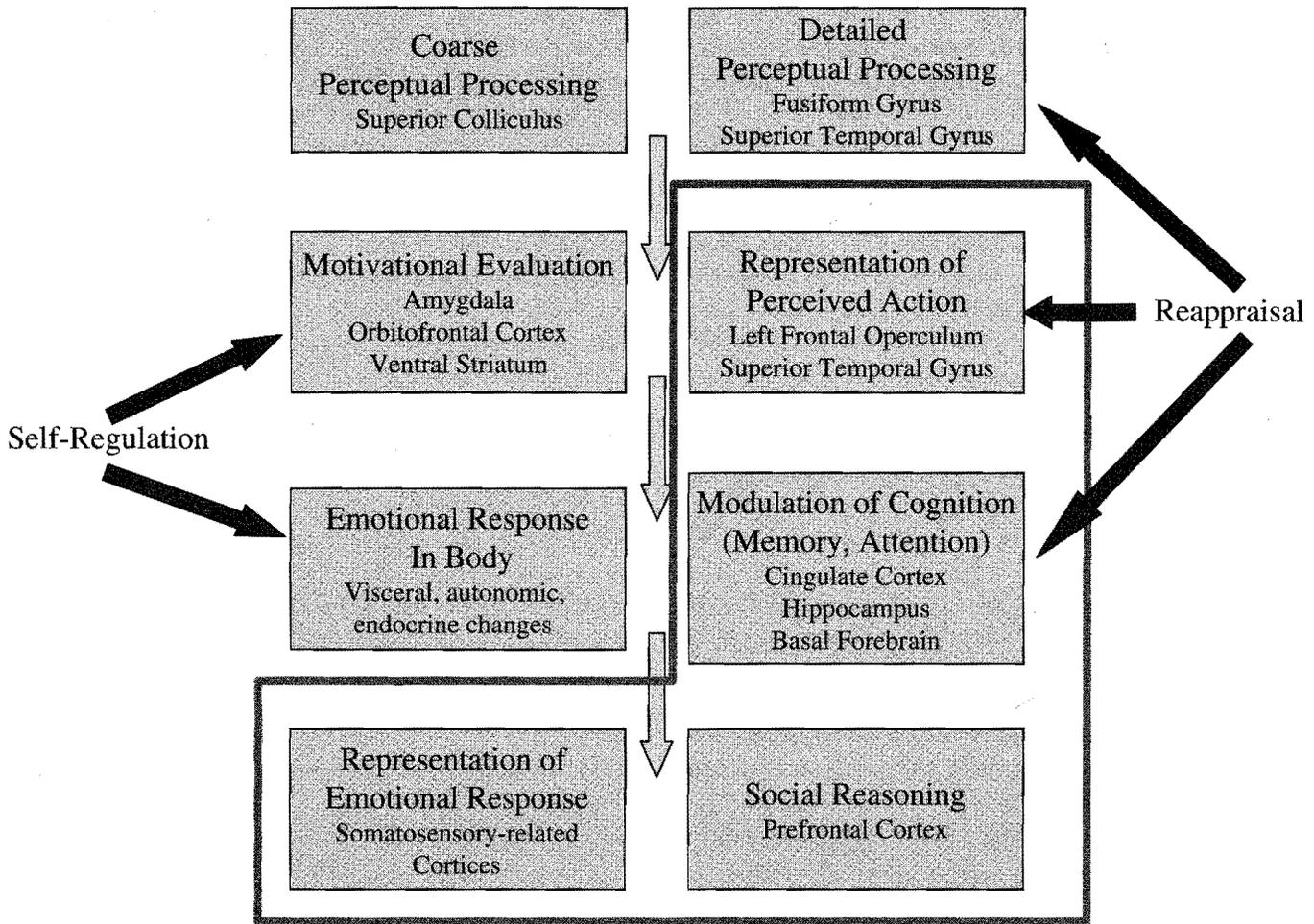


FIGURE 73.1 Processes that contribute to emotional and social information processing. Shown are some of the routes by which socially relevant information guides social behavior. Several features are important to note. There are multiple information processing streams that differ in the extent to which they recruit emotions, in the extent to which they are available for conscious awareness and control, and in their speed and elaboration. The causal relations among these processing components are complex

and include extensive feedback (not shown). There are also notable metacognitive influences: adult humans stand out in the ability to regulate their social behavior based on awareness and effort (arrows indicating Self-Regulation and Reappraisal). This schematic summarizes an overall information processing architecture that includes many more structures than are discussed in the chapter. (Reproduced from Adolphs, 2003.)

emotions. For instance, emotional modulation of the startle reflex shows such an interaction: the startle reflex itself is extremely rapid and automatic, but it is modulated by the valence of visual stimuli via a pathway involving projections from the amygdala to the nucleus reticularis pars caudalis, as well as by cognitive evaluation of stimuli.

Emotional responses to stimuli in turn are represented centrally, and are themselves modulated continuously. The emotional information that is processed thus varies in time, as does the emotional response, and the feeling of the emotion. The subsequent sections of this chapter review what we know about the contribution made by a specific structure, the amygdala, to these processes, with an emphasis on findings gleaned from lesion studies. All of the points made in this introductory discussion will turn out to be relevant for understanding what the amygdala

does as it participates in processing emotionally relevant information.

### *Early perception of socially relevant stimuli*

Certain features of stimuli, such as certain facial configurations that signal emotions, can be processed rapidly, in part by subcortical mechanisms. For instance, processing of subliminally presented facial expressions of fear activates the amygdala (Whalen et al., 1998), possibly reflecting the operation of a circuit from the superior colliculus (SC) to the amygdala via the pulvinar thalamus. This interpretation is in line with functional imaging studies showing correlated activation of the SC, the pulvinar thalamus, and the amygdala in response to subliminally presented facial expressions that had been associated with an aversive stimulus (Morris,

Ohman, and Dolan, 1999), a pattern of activation that was recently replicated in a subject with blindsight when discriminating emotional facial expressions in the blind visual field (Morris et al., 2001).

Regions of nonprimary sensory cortices already appear to be relatively specialized to process certain socially relevant attributes of stimuli. The evidence is best in regard to faces, for which higher-order visual cortices can be regarded as an assembly of modules that process distinct attributes, as borne out by a variety of lesion studies, scalp and intracranial recordings, and a rapidly growing list of functional imaging studies. The data point to the fusiform gyrus in processing the structural, static properties of faces, which are reliable indicators of personal identity, and to regions more anterior and dorsal in the temporal lobe (such as the superior temporal gyrus and SC) in processing information about the changeable configurations of faces, such as facial expressions, eye movements, and mouth movements (McCarthy, 1999; Haxby, Hoffman, and Gobbini, 2000). Activation along the superior temporal sulcus (STS) and superior temporal gyrus (STG) has been found when subjects view stimuli depicting biological motion, such as eye gaze shifts, mouth movements, and point-light displays of whole-body biological motion, and more abstract movements of geometric shapes, likely reflecting the role of this region in processing biological motion information on the basis of which we make social attributions. Processing in this region may draw on both dorsal and ventral visual streams in integrating shape and motion information, and it may reflect a comparison of the observed action with the viewer's simulation of it. The fusiform gyrus, the STG, and other, 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. There is good evidence that activation in all of these regions can be modulated by attention (Vuilleumier et al., 2001) and by the context in which the visual social signal appears (Pelphrey et al., 2003; Wicker et al., 2003).

An important recent lesion study showed that the amygdala is also critical to mediate visual attention. When words are flashed visually in a rapid serial stream, there is a well-known phenomenon called the *attentional blink*: when subjects are asked to identify a particular word that appears in the stream, their ability to detect a subsequent word within a short time window after the initially identified one is severely impaired. However, when the subsequent word to be detected is highly emotional, it can be detected even when it falls within the attentional blink window. Apparently, the initial allocation of attention to a target compromises subjects' ability to detect an immediately subsequent one, but emotional salience provides an independent boost that can override this blink—a boost that depends on the amygdala.

Lesions of the amygdala do not impair the attentional blink itself but the ability of emotion to override it (Anderson and Phelps, 2001). The finding is in line with the idea that the amygdala modulates the access of visual information to subsequent cognitive processing on the basis of the emotional value of the information.

The above anatomical investigations are complemented by data on the timing of face-processing components. Studies using event-related potentials (ERPs) and magnetoencephalography (MEG) show that some coarse categorization, such as sex and emotion categorization, can occur at latencies as short as 100 ms. Peak activity related to face-specific processing near the fusiform gyrus is seen around 170–200 ms (Allison et al., 1994). Although the construction of a detailed structural representation of the face thus seems to require about 170 ms, it appears that some rapid, coarse categorization can occur with substantially shorter latencies, presumably indicating coarse perceptual routes parallel to a full structural encoding of the stimulus. Perception of emotionally and socially relevant stimuli should be seen as an ongoing process extended in time, driven both by a collection of bottom-up processes and by top-down modulation.

### *The amygdala's role in processing emotional and social information*

Although it is difficult to define exactly what constitutes higher-level processing, there are at least three domains that probably qualify: multistep processing that involves volition, thinking about other people's minds, and awareness of one's feelings. There is clear evidence that emotional and social information contributes to decision making, reasoning, and other processes that can be influenced volitionally. By definition, social information processing also includes abilities by which we attribute mental states (such as goals, intentions, and emotions) to other people, dubbed theory of mind. Regions in prefrontal cortex, including ventral and medial prefrontal and cingulate cortex, participate in these processes. Structures that function to construct components of a self model, such as visceral and somatic sensory cortices in parietal lobe and insula, participate in these processes as well and are critical for feeling an emotion (Adolphs, 2003a).

The amygdala's role in these higher processes is quite unclear. Although there have been reports of impaired decision making (Bechara et al., 1999) or theory-of-mind abilities (Stone et al., 2003) in subjects with bilateral amygdala damage, it is plausible to assign the impairments in those cases to a defect in more basic emotional information processing rather than specific to the higher function (Adolphs, 2003a). There is also evidence from functional imaging studies that volitional modulation of emotion modulates activation of the amygdala (Ochsner et al., 2002; Schaefer et al.,

2002), but again, this does not show that the amygdala subserves volitional emotional processing, merely that it can be influenced by such processing. Finally, there is no evidence to suggest that the amygdala itself is critical for feeling emotions (Adolphs, 1999; Anderson and Phelps, 2002).

The evidence thus far points to a role for the amygdala in processing information at a level somewhat “higher” than basic perception but “below” the level of explicit reasoning and thinking about social information. This picture is extremely vague, but it serves to roughly locate the contribution that the amygdala makes at the interface of bottom-up perceptual processing and a whole host of other cognitive processes. What the amygdala does is not like what a reflex does (although it modulates reflexes), nor is it like thinking (although it modulates our thoughts), but rather is something more ubiquitous that pervades the organization of thought and behavior at all levels.

**RECOGNIZING EMOTION FROM FACES** The first definitive demonstration that the human amygdala plays a critical role in recognizing emotion came from two patients with bilateral damage to the amygdala (Adolphs et al., 1994; Young et al., 1995). Both patients had largely normal visuopercep-

tual function but were impaired at recognizing certain kinds of information from faces shown to them. In particular, both showed an inability to recognize normally emotions from facial expressions; that is, they had an emotion agnosia.

The patient my colleagues and I studied, S.M.046, had selective and complete bilateral amygdala damage due to Urbach-Wiethe disease (also known as lipoid proteinosis), a rare genetic disorder of epithelial tissue caused by a mutation in the extracellular matrix protein 1 gene (Hamada et al., 2002). Patients with this disease show medial temporal lobe calcifications and atrophy in about 50% of cases (Hofer, 1973). In S.M.046’s case, the damage was confined to the amygdala and the very anterior portions of entorhinal cortex (Tranel and Hyman, 1990; figure 73.2). Her lesion and her neuropsychological profile have remained stable over more than a decade of study (Adolphs and Tranel, 2000). Despite her normal ability to recognize sex, identity, and other information from faces, S.M.046 is severely impaired in her ability to recognize certain emotions. The impairment is most notable for fear, but includes to some extent emotions that are conceptually close to fear, such as surprise and anger (Adolphs et al., 1994, 1995). Her dysfunction is clearly an agnosia, since S.M.046 is able to

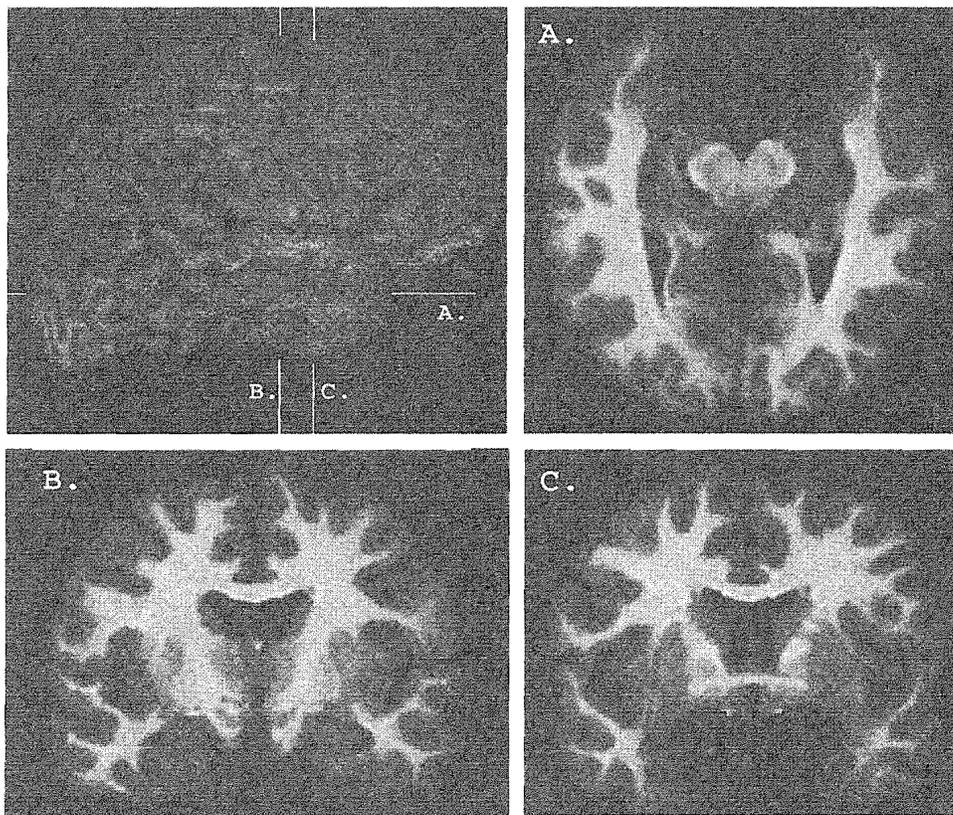


FIGURE 73.2 Neuroanatomy of S.M.046. Shown at top left is a three-dimensional reconstruction of S.M.’s brain from MR images, showing the planes of section of the other cuts. The symmetrical region of low signal in the anteromedial temporal lobe is due to

calcification and atrophy of tissue within the entire amygdala as well as anterior entorhinal cortex. The damage resulted from a rare genetic disease, Urbach-Wiethe disease.

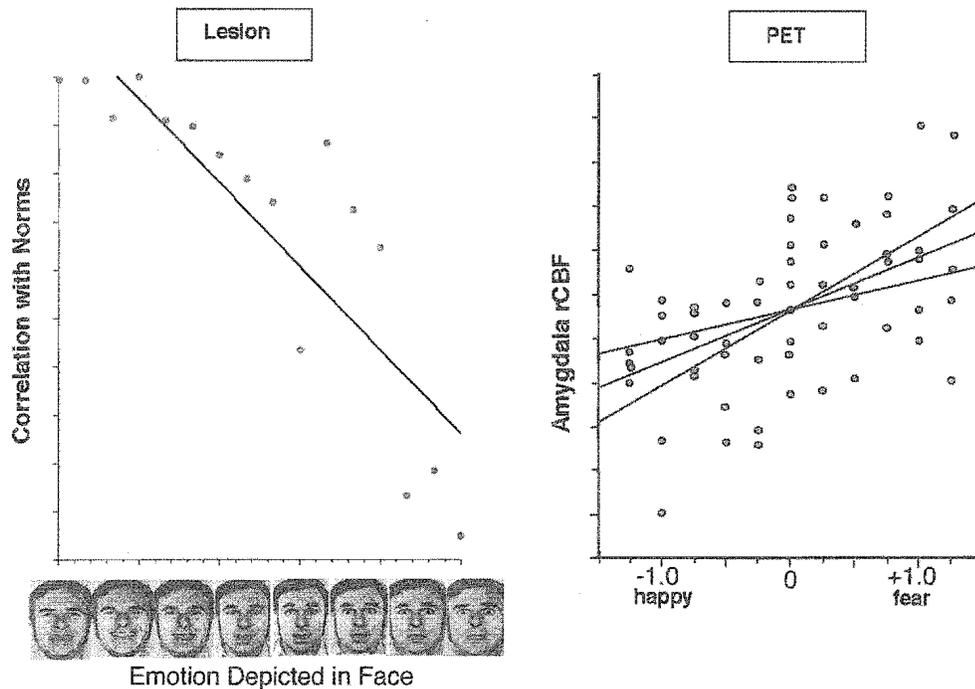


FIGURE 73.3 The amygdala's role in processing fearful facial expressions. *Left*, Impaired recognition of fear following bilateral amygdala damage. Shown are data from S.M.046 on rating the intensity of emotions shown in facial expressions. Subjects were shown morphs of prototypical facial expressions of emotions and asked to rate the intensity of each of the six basic emotions signaled by these stimuli. The x-axis shows the face stimuli and the y-axis shows the correlation of S.M.046's ratings with normal ratings;

discriminate normally even very faint morphs of the same emotions that she failed to recognize (Adolphs and Tranel, 2000). Moreover, she is able to use the word *fear* appropriately in conversation, and is able to generate considerable conceptual knowledge about that emotion. When asked to rate the intensity of emotion signaled by a facial expression, S.M.046 gave very abnormal (low) ratings to expressions of fear (figure 73.3). She also showed a converse impairment: when asked to draw facial expressions of emotions for which we supplied the name, she was able to draw all except fear (Adolphs et al., 1995). She thus showed a bidirectional disconnection between the concept of fear and the facial expressions that normally signal that emotion.

While S.M.046's impairment is strikingly specific to fear, at least on certain tasks, other patients with bilateral damage to the amygdala show impairments in facial emotion recognition that are not as specific but typically encompass several negative emotions, often including but not limited to fear. In a study of nine such patients, we found a pattern of impairments that extended across rating the intensity of multiple negative emotions, especially fear, anger, and disgust (Adolphs, Tranel, et al., 1999; figure 73.4). Other studies have pointed to disproportionate impairments in recogniz-

ing fear (Calder et al., 1996; Broks et al., 1998), more subtle impairments in various negative emotions that depend on the particular task and analysis (Schmolck and Squire, 2001), or impairments that might be attributable to difficulty of the task alone (Rapcsak et al., 2000; Adolphs, 2002).

Data from functional imaging studies have helped to narrow down these possibilities. Although there was an initial flurry of findings showing amygdala activation in response to fearful facial expressions (Breiter et al., 1996; Morris et al., 1996), some aspects of which are still supported by more recent studies (Whalen et al., 2001), those findings are now supplemented by others showing that the amygdala is activated by multiple emotional expressions (Blair et al., 1999; Yang et al., 2002), but differentially so. It does not look as if the amygdala is activated equally by expressions of all emotions or that its activation can be explained merely by the difficulty of the task required. On the other hand, it remains unclear exactly what emotion category it might be specialized to process.

We are thus faced with a key question: How domain-specific is processing in the amygdala? As in some regions of temporal extrastriate cortex, responses within the amygdala seem disproportionate for social visual information such as

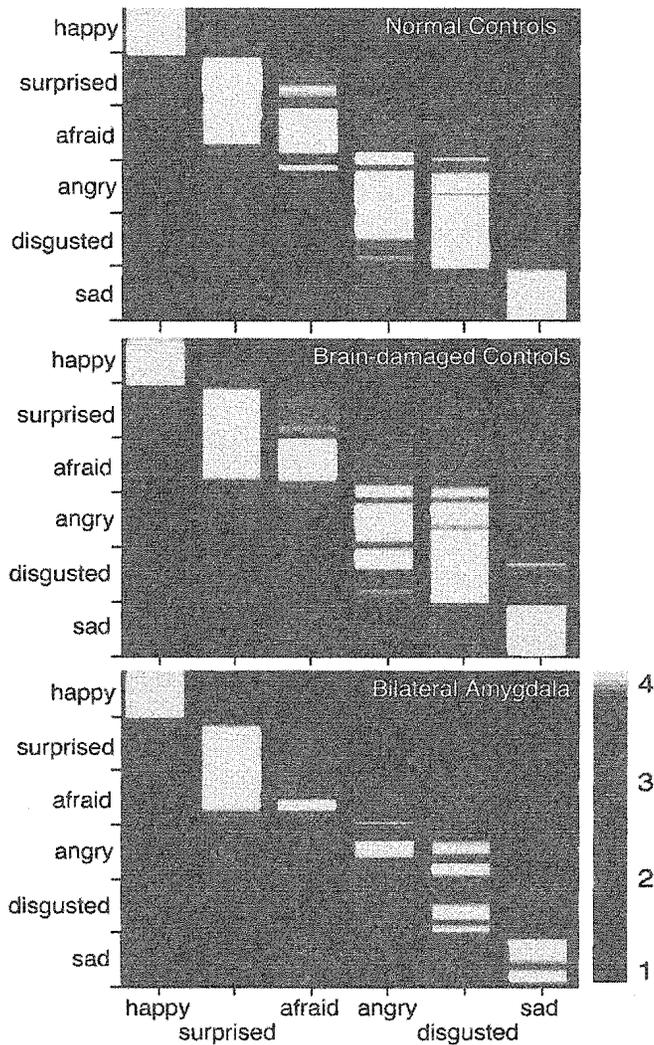


FIGURE 73.4 Impaired recognition of multiple negative emotions in nine subjects with bilateral amygdala damage. On the same task as in figure 73.3, a group of nine subjects with bilateral amygdala damage showed variable impairments across not only fear but also other negatively valenced emotions, compared to either brain-damaged or normal controls. Each of the three graphs shows data for normal controls, brain-damaged controls, and subjects with amygdala damage. The *x*- and *y*-axes represent the labels on which faces are rated and the face stimuli, respectively. The gray scale codes the intensity they assigned to the face on that emotion label.

faces, and the lesion studies certainly point to a role in recognizing only certain negatively valenced emotions, perhaps especially fear; but clearly its role is not restricted entirely to processing information about fear. There are at least three possibilities here: (1) the amygdala is specialized to process a particular basic emotion, fear; (2) the amygdala processes a region of two-dimensional affect space, namely, those emotions that are both negatively valenced and highly arousing; and (3) the amygdala processes a particular ecological category of emotions, for instance those related to threat and

danger (Adolphs, Tranel, et al., 1999; Adolphs, 2002), those requiring the resolution of ambiguity (Whalen, 1999), or perhaps those requiring a mapping of an observed emotional state onto a different emotion in the perceiver (e.g., anger elicits fear, not anger).

There are several further considerations in interpreting the data thus far. The lesion studies are complicated by the fact that different stimuli, different tasks, and different analyses have often been used. The patients present many differences also, both in terms of the details of their lesions and in terms of the cognitive background within which the amygdala damage results in impaired emotion processing. Most of the patients have damage also to extra-amygdalar structures that is often quite substantial. Even within the amygdala, the damage can vary, and studies have not attempted to distinguish between damage in different amygdala nuclei. These difficulties aside, it nonetheless seems possible to extract from the different studies a common pattern of disproportionately impaired recognition of only certain emotions, perhaps those that are both negatively valenced and of high arousal, such as fear. Is this because fearful facial expressions signal a particular type of information whose processing depends on the integrity of the amygdala? Or is processing of fear-related information distinguished in some other ways unrelated to emotion? These are tricky questions to which we as yet do not have definitive answers. There is, for instance, the possibility that certain tasks ask subjects to categorize fear at a level that is subordinate to the level of categorization required for happiness or sadness (which could be thought of as prototypes of the more superordinate categories “happy” and “unhappy”). It might be that fear is simply more confusable with certain emotions, like surprise and anger, than happiness is confusable with any emotion (Adolphs, 2002). In support of such a possibility, we described a patient with extensive bilateral temporal lobe damage, including damage to the amygdala, who essentially recognized only two superordinate emotion categories, happy and unhappy, and who misclassified fear into the happy category (Adolphs, Tranel, and Damasio, 2003). Future studies will need to be very careful in controlling for these factors.

A natural follow-up to the findings just presented is the specificity of the impairment for faces. We examined this issue by showing subjects social scenes under two conditions: in one condition the scenes contained emotional facial expressions, in the second the faces were erased in the scenes. Not surprisingly, normal and brain-damaged controls found it easier to recognize the emotion from scenes when they contained emotional expressions than when the expressions had been erased. By contrast, subjects with amygdala damage showed no such advantage. In fact, they were much worse at recognizing emotions from scenes when the scenes



FIGURE 73.5 Recognition of emotion from social scenes is disproportionately severe when the scenes contain facial expressions. (a) Subjects with either unilateral or bilateral amygdala damage were more impaired in recognizing negatively valenced emotions from complex visual scenes only when those scenes contained facial expressions. (b) When faces in the scenes were erased, the subjects' performances became normal. (c) Accuracy in recognizing basic emotions from these stimuli: whereas normal controls (NC) and brain-damaged controls (BDC) always performed much better on the second set of stimuli, with the faces present, subjects with either

unilateral left (L), right (R), or bilateral (bi) amygdala damage showed the inverse pattern of performance specifically for negatively valenced emotions. What was even more surprising, some subjects with bilateral amygdala damage were severely impaired in recognizing scenes when the scenes contained facial expressions, but actually performed better than controls when faces had been erased, possibly suggesting that they learn to partly compensate for their impaired recognition of emotion from faces by developing greater sensitivity to social cues other than faces.

contained faces than when they did not (Adolphs and Tranel, 2003; figure 73.5)! Furthermore, there was even an indication that subjects with bilateral amygdala damage were better than normals in recognizing emotions from scenes when faces had been erased. Taken together, these findings emphasize the importance of the face in signaling emotional information, and the importance of the amygdala in processing precisely that information. Subjects with amygdala damage are sensitive to emotion signaled by the face but are unable to use it normally in order to recognize the emotion; when the face is removed, however, they are able to use information normally from context, body posture, or other cues in order to judge the emotion.

normally judged; second, they were able to rank-order very trustworthy- or approachable-looking people normally but failed to rank-order individuals who were normally judged to look untrustworthy or unapproachable (figure 73.6). This impairment extends the impaired recognition of basic emotions we have described to more complex social judgments. Possibly the two sets of impairments are related: recognition of facial expressions may be impaired disproportionately for those emotions that signal threat or danger in the environment in general, and social judgment may be impaired in regard to threat or danger in the social environment in particular. The impaired ability to judge untrustworthiness is also consistent with the real-life behavior of these subjects, which often features an overly trusting and friendly personality.

**SOCIAL JUDGMENT FROM FACES** What is the significance of the emotion recognition impairment described in the previous section for real-life behavior? It is worth noting that we do not typically use information from faces solely to determine another person's emotional state, but rather to make social judgments regarding the other person's intentions and dispositions and to guide our own behavior toward them. We examined this issue by asking subjects to judge the approachability and trustworthiness of unfamiliar faces. These faces showed people in natural poses, not different strong emotional expressions (the expressions were neutral or smiling). We found a specific impairment in subjects with bilateral amygdala damage: whereas they judged approachable- and trustworthy-looking people normally, they failed to judge unapproachability and untrustworthiness (Adolphs, Tranel, and Damasio, 1998). The impairment consisted of two distinct components: first, subjects with bilateral amygdala damage exhibited an overall positive bias in judging everyone to look more trustworthy and approachable than

This finding from lesion studies has been corroborated by functional imaging studies. A recent study showed that activation within the amygdala correlated with the degree of judged untrustworthiness of the face that was shown to subjects (Winston et al., 2002). Moreover, this correlation held, even when other factors such as expression, sex, ethnicity, and eye gaze were controlled for. There is thus something about the physiognomy of the face on the basis of which we normally judge trustworthiness, and the amygdala is one structure mediating such judgments.

Just as difficult questions arose in regard to the amygdala's specificity for processing fear, there are analogous (broader) questions concerning its role in processing domain-specific social information. We followed up on the experiments described in the preceding section by investigating the preferences that subjects exhibit for nonsocial stimuli, such as pictures of landscapes. To our surprise, we found that subjects with bilateral amygdala damage showed the same

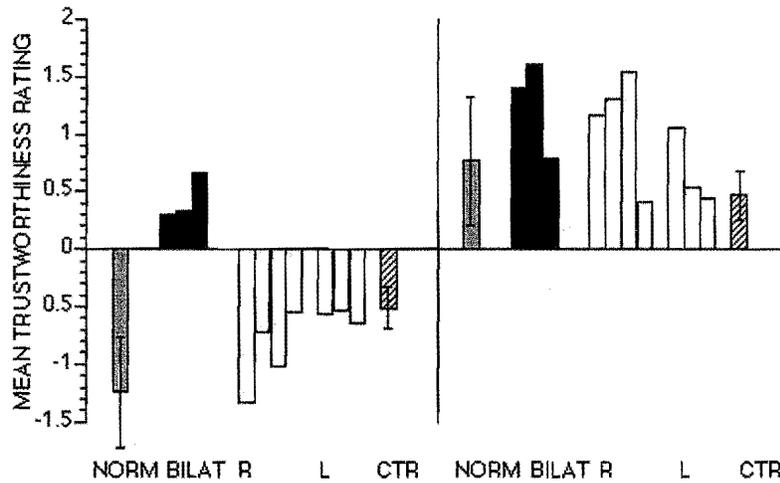


FIGURE 73.6 The amygdala in social judgments of trustworthiness. Bilateral damage to the amygdala (BILAT) selectively impairs the ability to judge untrustworthiness from faces, whereas unilateral damage (R, L), or brain damage elsewhere (BDC) does not.

The two graphs plot mean ratings of untrustworthiness assigned by subjects to 50 faces that are normally rated the most untrustworthy looking (left, normative ratings, NORM) and to 50 faces normally rated the most trustworthy looking (right).

inability to judge aversive nonsocial stimuli: they judged pictures of landscapes, nonsense drawings, colored spheres, and colored Mondrians to be abnormally positive when asked how much they liked them (Adolphs and Tranel, 1999b). It thus appears as though bilateral damage to the amygdala impairs an ability to judge aversive, dangerous, or in some way undesirable stimuli in a manner that is not completely domain-specific. Similar observations have been made in nonhuman primates following experimentally introduced amygdala lesions (Emery et al., 2001).

**RECOGNIZING EMOTION FROM AUDITORY STIMULI** By comparison to the amygdala's role in recognizing emotions from faces, its role in recognition of emotion from auditory stimuli is very unclear. This is surprising. Given the multimodal nature of sensory inputs to the amygdala, one would certainly expect impairments in emotion processing to be parallel across sensory modalities. A small number of functional imaging studies have reported activation of the amygdala to prosodic or other emotional auditory stimuli (Phillips et al., 1998), although some have reported deactivation of the amygdala instead (Morris, Scott, and Dolan, 1999). Some lesion studies have found impaired ability to recognize fear from auditory stimuli following bilateral amygdala damage (Scott et al., 1997), whereas others have not (Anderson and Phelps, 1998; Adolphs and Tranel, 1999a).

We investigated the role of the amygdala in recognizing emotion from prosody and found no significant impairment following bilateral amygdala damage (Adolphs and Tranel, 1999a). Curiously, however, we did find some evidence of variable impairment following temporal lobectomy (Adolphs, Tranel, and Damasio, 2001). A particularly unexpected finding was of a disproportionate impairment in recognizing emotions from faces or from prosody following left

or right amygdala damage, respectively (Adolphs, Tranel, and Damasio, 2002). Although this finding suggests different roles for the left and the right amygdala in processing emotional and social information from certain sensory modalities, it is important to keep in mind that the lesions of the patients in this study (patients with epilepsy who had undergone a temporal lobectomy) included not only unilateral amygdala lesions but also lesions in surrounding cortex and other structures in the anteromedial temporal lobe.

The evidence for the amygdala's role in recognizing emotion from nonprosodic auditory stimuli (e.g., screams, growls, sirens) is more encouraging. Some lesion studies, including unpublished findings with our patient S.M.046, have pointed to such a role (Scott et al., 1997).

**RECOGNIZING EMOTION FROM LEXICAL INFORMATION** Although some functional imaging studies have found amygdala activation to lexical emotional stimuli (Isenberg et al., 1999; Phelps et al., 2001; Hamann and Mao, 2002), lesion studies have generally suggested that the amygdala is not essential for recognizing or judging emotional and social information from explicit, lexical stimuli such as stories. Our studies with S.M.046 are a good case in point: S.M.046 can label emotions from scenarios presented in stories, and she can retrieve considerable declarative knowledge about all emotions, including fear.

There is, however, an interesting wrinkle to this story. S.M.046 does not know that some unpleasant emotions are arousing! In order to probe the categories of emotions whose recognition is impaired, we asked subjects to rate emotional stimuli not in terms of their intensity on basic emotions, as done in the studies cited earlier, but in terms of their valence (pleasantness or unpleasantness) and arousal. Normal subjects judge emotions such as fear and anger to be

both unpleasant and highly arousing. S.M.046, by contrast, judged them to be unpleasant but of low arousal (Adolphs, Russell, and Tranel, 1999). This impairment in recognizing arousal from unpleasant emotions held across labels for the emotions, stories depicting emotions, and facial expressions of emotions, thus reflecting impaired conceptual knowledge in general, irrespective of the nature of the stimulus. For instance, when told a story about someone driving a car down a steep mountain road who had lost the brakes, she correctly recognized that the situation would be very unpleasant, but also gave the highly abnormal judgment that it would make one feel sleepy and relaxed. The impairment was especially striking, since S.M.046 was able to judge arousal normally from positive emotions.

We found a similar impairment in two other subjects who, like S.M.046, had bilateral amygdala damage that was sustained relatively early in life. However, three subjects with complete bilateral amygdala damage due to encephalitis sustained in adulthood showed no such impairment (Adolphs et al., 1997; figure 73.7). How can we reconcile these findings? Our explanation is that normal acquisition of conceptual knowledge of certain emotions depends on the integrity of the amygdala during development. Bilateral amygdala damage would preclude normal emotional arousal responses to stimuli signaling fear or anger: the absence of such responses, as well as of cognitive modulation, explains the online impairment in recognizing fear from facial expressions in such patients. But they would still know, as a declarative fact, what fear is, and how arousing it should be, provided they have experienced such arousal in the past. Developmental damage to the amygdala would prevent such knowledge from arising normally, with the observed impaired knowledge that fear and anger are arousing emotions. This developmental consequence is probably analogous to the consequences of developmental frontal lobe damage: like patients with amygdala damage, they are impaired in their ability to trigger normal emotional responses to stimuli during development, and as in patients with developmental damage to the amygdala but not as in patients with adult-onset damage to either amygdala or prefrontal cortex, this translates into an impaired concept of some aspects of emotional or social knowledge.

**ELECTROPHYSIOLOGICAL RESPONSES IN THE HUMAN AMYGDALA** Single-unit recordings from the monkey amygdala have found neurons whose responses are modulated by the emotional significance of stimuli (Rolls, 1999). Of note, this modulation can be independent of the perceptual properties of the stimulus. For instance, the very same stimulus can evoke differential amygdala activity, depending on its prior association with reward or punishment (Nishijo, Ono, and Nishino, 1988). We have recorded field potentials and single-

unit activity from the amygdala of neurosurgical patients who were undergoing epilepsy monitoring. As in the animal studies, we found neurons whose responses were selectively modulated by the emotion category of stimuli. In our case, these were complex visual stimuli, and we checked to be sure that responses could not be attributed to factors such as differences in luminance or color composition of the categories. The responses we found showed an increase in activity that was selective for aversive stimuli—pictures of mutilation, threat, and war (Oya et al., 2002; figure 73.8). An interesting additional finding was the suggestion of a differential electrophysiological signature (power at different frequency bands), depending on whether the images showed bodily injury to people or disgusting items (e.g., dirty toilets, cockroaches). These latter findings raise the intriguing possibility that different neurons within the amygdala, or possibly even the same neurons participating in a different network, can encode different aspects of emotional information. We have obtained similar findings also when patients were presented with olfactory stimuli: as for the visual stimuli, the neurons responded selectively by increasing their firing rates to unpleasant olfactory stimuli.

### *Summary*

We can now tie some of these diverse strands together. The human amygdala appears to be important both for the acquisition and for the online processing of emotional stimuli. Its role is disproportionate for a particular category of emotional information, possibly that pertaining to evaluating potential threat in the environment. Its processing encompasses both the elicitation of emotional responses in the body and changes in other cognitive processes, such as attention and memory. When these effects occur online, as an emotional stimulus is processed, they also contribute to the acquisition of certain components of concepts of emotions, namely, those components of knowledge dependent on prior emotional responses. This is why damage to the amygdala early in life, as we saw in the case of S.M.046, compromises not only emotional responses and recognition of emotional stimuli, but also abstract knowledge of particular aspects of emotion concepts, specifically that unpleasant emotions can be arousing, an attribute that is particularly pertinent for the emotions fear and anger.

I have highlighted the amygdala as a structure that mediates between perceptual representations of stimuli and the modulation of cognition, but the amygdala should be thought of as only one component of a neural system. Other components with a related function include ventral and medial regions of the prefrontal cortex and the basal ganglia. In many studies these regions are coactivated, and

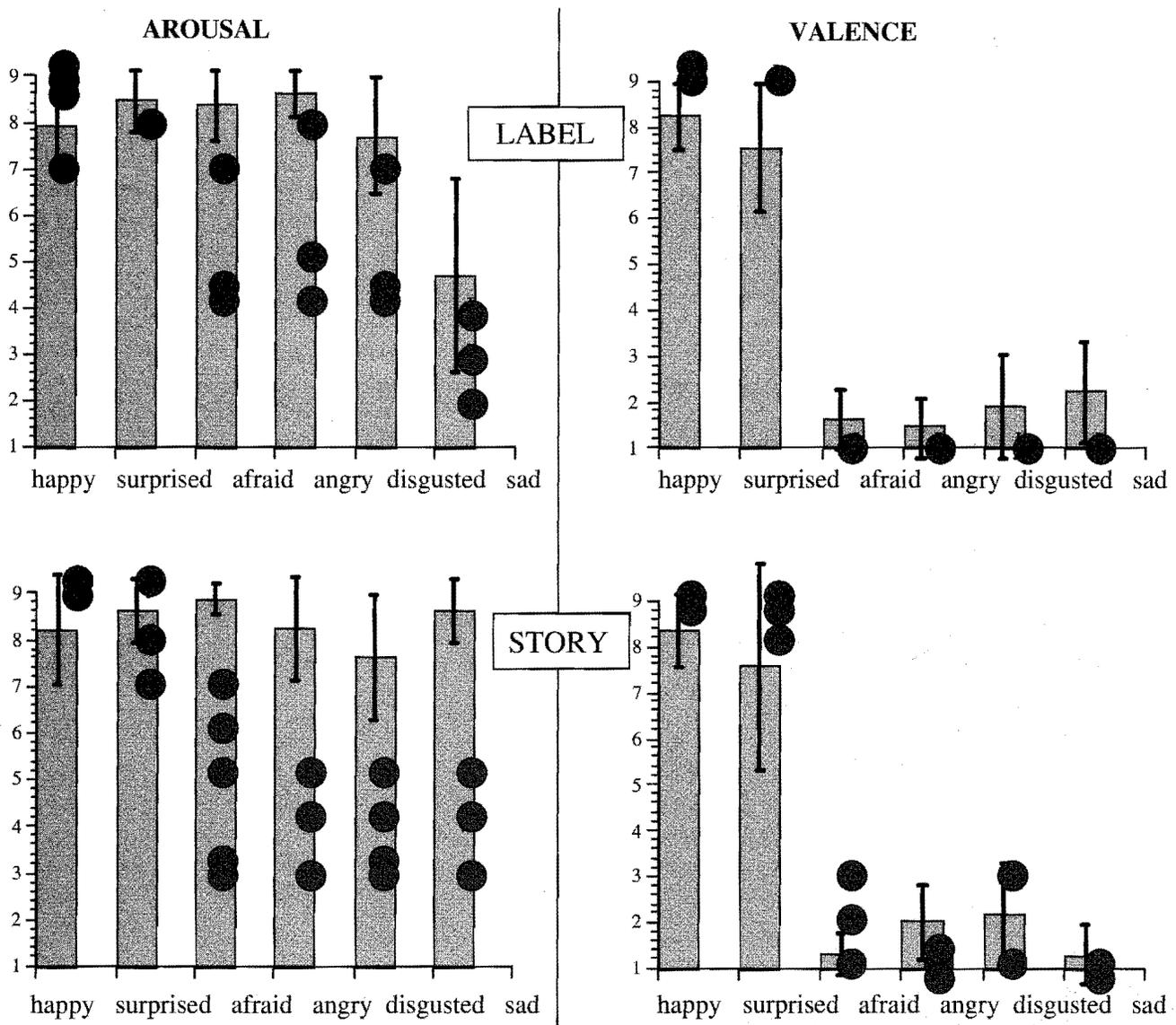


FIGURE 73.7 Developmental damage to the amygdala impairs knowledge of the arousal of unpleasant emotions. Patient S.M.046 was impaired in her knowledge that negatively valenced emotions, especially fear and anger, are also highly arousing. The impairment was evident both for facial expressions of emotions (not shown) and

for lexical stimuli such as the words for the emotions and stories depicting emotions. Bars indicate means  $\pm$  SD of responses by normal controls; circles indicate responses from S.M.046. (See color plate 62.)

in many ways their functions overlap. It remains an important question, therefore, to describe the ways in which they differ. One hypothesis is that the amygdala and the ventral striatum subserve relatively rapid, automatic, and coarse emotional processing driven largely by features of the stimulus, and that sectors of the prefrontal cortex modulate such processing by providing information about the context in which the stimulus occurred and by introducing volitional effects on information processing. This scheme is probably too simple, because it is likely that amygdala and ventral striatum also participate in these latter functions—indeed, there are data demonstrating that their activations can be modulated volitionally, perhaps via top-down influences

from prefrontal cortex. Another reason the scheme is likely to be simplistic is that it does not account for the different roles that different amygdala nuclei will play.

### Future questions

The findings reviewed in this chapter leave us with some important open questions (Adolphs, 2003b). Several of these questions return to issues we identified at the beginning of the chapter. To what extent is social information processing domain-specific, and to what extent does it draw on more general motivational and emotional processing? Where in the causal relations between processes do feelings come in?

## Frequency

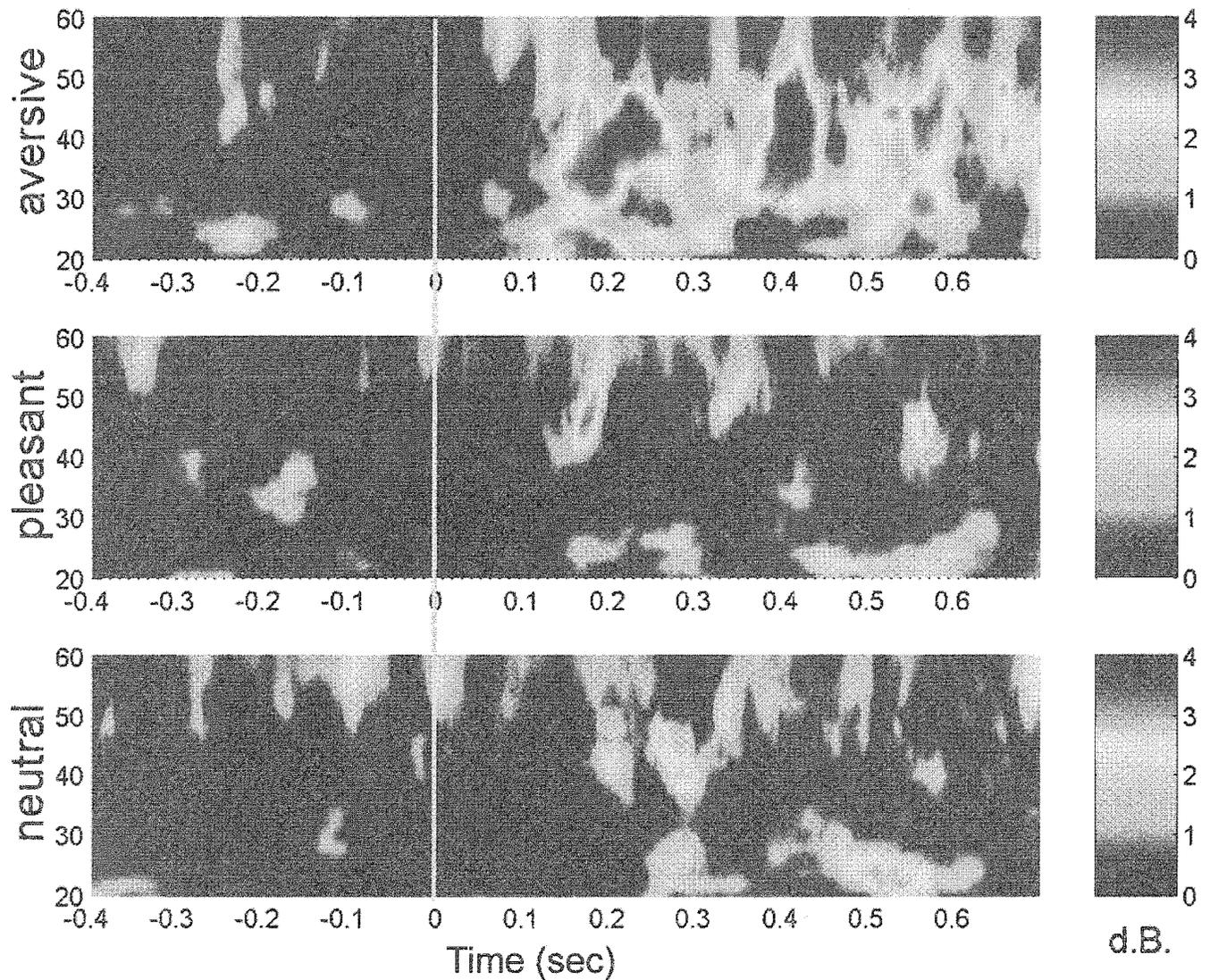


FIGURE 73.8 Time-frequency plots of field potentials recorded from the amygdala in response to visual stimuli. Time is shown on the  $x$ -axis (seconds) and the frequency of the recorded response (20–60 Hz) is shown on the  $y$ -axis. Stimulus onset is indicated by

the white vertical bar at 0s. Grayscale encodes amplitude of the response in dB. Stimuli were sorted into three emotion categories as shown; there were significantly larger responses to aversive stimuli than to pleasant or neutral stimuli. (See color plate 63.)

What role does more extensive cognitive and volitional processing play in emotion and social information processing?

The evidence reviewed clearly points to some domain specificity in the processing of socially relevant information: there are brain mechanisms specialized to detect faces and process threat-related stimuli. But this observation still leaves open two possibilities: such specializations may reflect the operation of systems that are truly specialized to process social information, or they may reflect the fact that social stimuli make particular processing demands, which are, however, subserved by domain-general systems. The question of domain specificity thus concerns the factors that are driving this specificity: are they properties of the stimuli,

tasks, or behaviors or properties of the neural architecture that subserves the processing of such stimuli, tasks, or behaviors?

Although the amygdala does not appear directly essential for feeling emotions, it likely plays an indirect role by triggering components of emotional responses that can in turn be felt. Pilot data from our laboratory indicate that S.M.046 does not feel emotions normally when she views film clips or listens to music, but she can provide relatively normal ratings of feelings when given abstract information or when instructed to feel a certain way. These observations, together with the finding that patients with lesions of the amygdala endorse normal ratings on scales of dispositional affect, make it likely that the amygdala serves to link perceptual

representations of external stimuli to the modulation of cognition and behavior, and therefore can indirectly have an influence on the feelings such stimuli elicit.

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